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Evolution

Significance of some previously unrecognized apomorphies in the nasal region of *Homo neanderthalensis*

(Neanderthals/human evolution/nasal morphology)

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ABSTRACT **For many years, the Neanderthals have been recognized as a distinctive extinct hominid group that occupied Europe and western Asia between about 200,000 and 30,000 years ago. It is still debated, however, whether these hominids belong in their own species, *Homo neanderthalensis*, or represent an extinct variant of *Homo sapiens*. Our ongoing studies indicate that the Neanderthals differ from modern humans in their skeletal anatomy in more ways than have been recognized up to now. The purpose of this contribution is to describe specializations of the Neanderthal internal nasal region that make them unique not only among hominids but possibly among terrestrial mammals in general as well. These features lend additional weight to the suggestion that Neanderthals are specifically distinct from *Homo sapiens*.**

Over the past century and a half, paleoanthropologists have come to recognize the Neanderthals as a highly distinctive extinct hominid group that inhabited a wide swath of Europe and western Asia (east from the Atlantic to Uzbekistan, and south from Wales to Gibraltar and the Levant) in the period from about 200,000 to 30,000 years ago (1). Nonetheless, possibly because of their large brain volumes, paleoanthropologists have in recent years been reluctant to recognize the Neanderthals as a distinct species of the genus *Homo* (e.g., ref. 2). Our recent studies of Neanderthal crania have, however, indicated that these hominids are autapomorphic (uniquely derived) in several respects that have previously gone unremarked, and our purpose here is to draw attention to some characteristics of the Neanderthal nasal region that not only distinguish these extinct human relatives from *Homo sapiens*, but also make them unique among hominids—and primates—in general.

These previously undescribed features are particularly well illustrated in the Gibraltar 1 (Forbes' Quarry) skull, the first adult Neanderthal to be discovered (ref. 3; Fig. 1). Most striking is the presence of 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. This medial projection fades superiorly into a low ridge that continues to frame the nasal cavity within its external margin. On its posterior side, the horizontal inferior margin of the rim may be rounded, and the vertical portion is bounded by an open lacrimal groove (Fig. 2*a*). Varying only in relative size, the vertical medial projection is present (if usually damaged) in all the adult Neanderthal specimens we have examined in which this region is preserved (i. e., Gibraltar 1, Spy 1, La Ferrassie 1, La Chapelle-aux-Saints, and St-Césaire) and is also clearly visible in published photographs of other Neanderthals (e.g., Shanidar 1; see Figure 76 in ref. 4).

Although the conchal crest of extant mammals (5, 6), including *Homo sapiens* (ref. 6; Fig. 2*b*), 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. It also differs morphologically from the raised and bulky Neanderthal medial eminence in being low and relatively poorly defined. The human conchal crest is the anterior line of contact with the nasal wall of the paper-thin inferior nasal concha, which arises from its own center of ossification (7). The inferior concha also contacts the thin sheet of bone that covers the lacrimal groove in modern humans. Given the unique conformation of both of these areas in Neanderthals, it is evident that the inferior nasal concha of these extinct hominids must have differed fundamentally in structure from that of modern humans (and of primates in general; ref 6)—if, indeed, one was present at all, which is not demonstrable with the current evidence. Among the other fossil hominids in our sample (Table 1), only the Steinheim cranium, taxonomically equivocal but often viewed as a Neanderthal precursor (8), shows any sign of a medial projection. In this fossil, the structure is, however, less bulky and less intrusive into the cavity than in the Neanderthals. Like *Homo sapiens*, other non-Neanderthal middle Pleistocene hominids we have examined (e.g., Kabwe; ref. 9) retain the conchal crest, which we take to be the primitive configuration. This also appears to be the case for the 300,000-year-old Sima de los Huesos (Atapuerca) cranium 4, which was recently figured by Arsuaga *et al.* (ref 10; Fig. 1) and suggested by them to belong to a potentially proto-Neanderthal group. Further, our review of the literature has revealed no mention of the specialized "Neanderthal-like" medial projection either in the Steinheim cranium or anywhere else among hominids.

The "internal nasal margin," with its remarkable medial projection, does not, however, appear to be the only peculiarity of the Neanderthal nasal region. In the Gibraltar 1 specimen (Fig. 1), the enlarged posterior portion of the nasal cavity shows evidence of another unusual structure: a distinct swelling of the lateral nasal wall. From surface breaks, as well as from comparisons with the Spy 1 specimen (Fig. 2*a*), it appears that this swelling houses a medially expanded maxillary sinus. This area is not preserved in any other specimens we have examined, but this observation suggests that the Neanderthals were specialized in the posterior as well as the anterior nasal region relative to other terrestrial mammals (5, 6), including *Homo sapiens* (ref. 11; Fig. 2*b*). 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 (5) with two, three, or even

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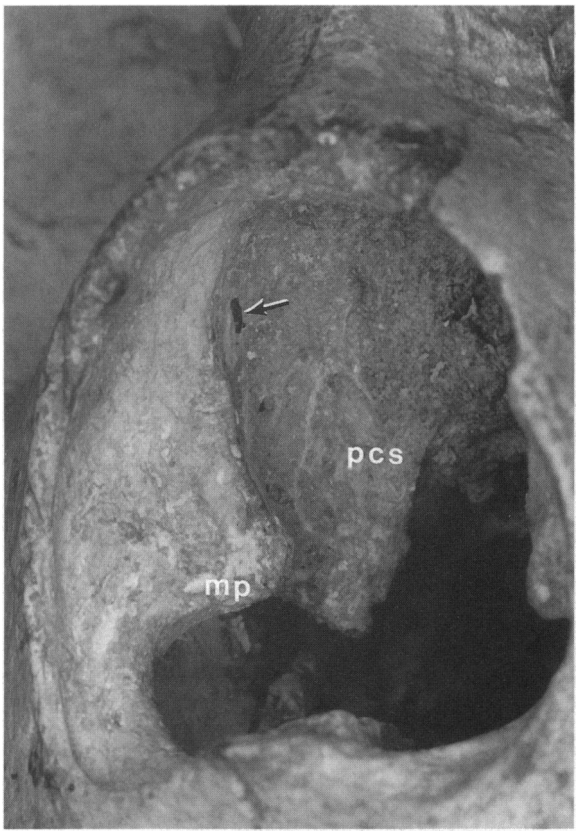

FIG. 1. Frontal view of the nasal cavity of the Gibraltar 1 cranium, illustrating the internal margin bearing a large internal projection (mp), behind which is the large swelling (pcs) within the posterior component of the nasal cavity, partly obscured in this view by matrix. The arrow indicates the hole in the wall of the swelling that reveals the enlarged maxillary sinus.

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 in Neanderthals, it appears likely that the turbinates of these extinct hominids, and possibly also the ethmoid, were configured in an unusual manner. Whether the medial swelling in the Gibraltar Neanderthal is functionally a specialized nasal structure, as the medial projection appears to be, or whether it is merely a passive result of maxillary sinus expansion remains to be determined.

Two of the three immature Neanderthals we studied (Engis and Roc de Marsal; Fig. 2*c*) are sufficiently well preserved to demonstrate that the medial projection has already begun to develop by the age of 3–4 years. However, at this age the wall of the nasal cavity has not expanded medially, nor has the maxillary sinus encroached anteriorly as far as in the adult (i.e., into the maxillary frontal processes), although as among adults the lacrimal groove is exposed. By comparison, in newborn *Homo sapiens*, the lacrimal groove is already partially roofed over, but the conchal crest, which arises as a series of irregularities during the second postnatal year, is not yet discernible. The maxillary sinus itself is not readily apparent in our species until the third or fourth year of life (12). Development of the features of the nasal fossa thus proceeded very differently in Neanderthals than in *Homo sapiens*, and the most striking characteristic of this region—the medial projection—became established very early in postnatal life.

It thus appears that at least three notable apomorphies (derived characters) distinguish the structure of the Neanderthal internal nasal cavity not only from that of other hominids but also from primates in general (6). Indeed, it is quite

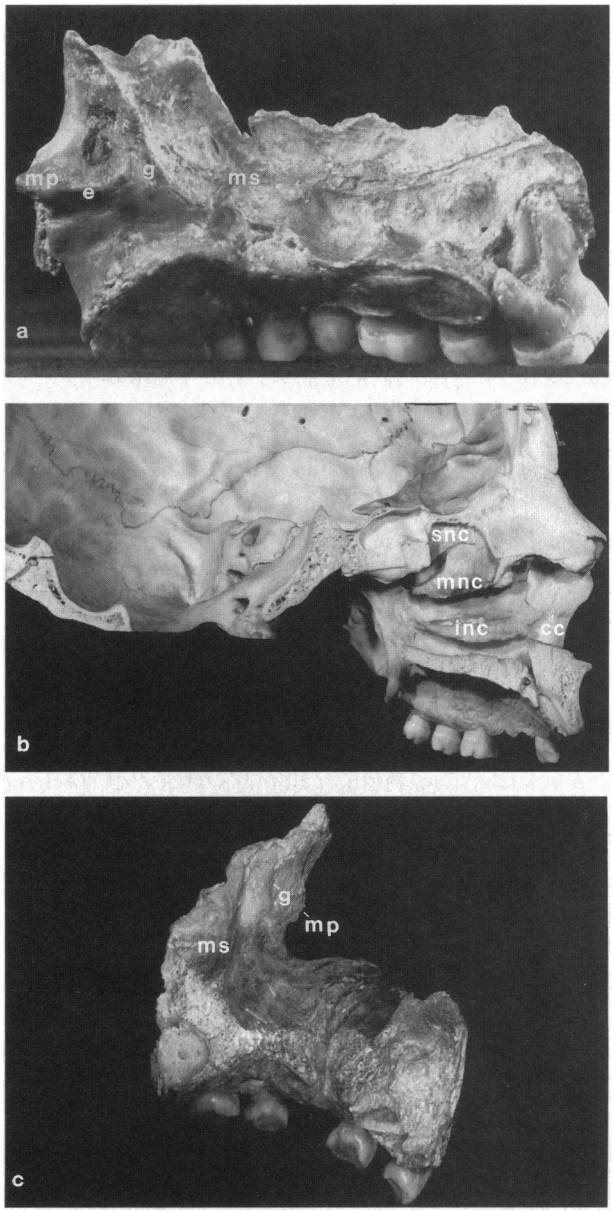

FIG. 2. (*a*) Medial view of right maxilla of Spy 1, illustrating the medial projection of the internal margin of the nasal cavity (mp), the edge along its base (e), the vertical furrow that continues the lacrimal groove (g), and the expansive maxillary sinus (ms). (*b*) Adult *Homo sapiens* (AMNH VL 4578), showing the relations of the superior nasal concha (snc) to the middle nasal concha (inc) and to the conchal crest (cc), with the inferior concha also covering the lacrimal groove. (*c*) Posterior view of the palate and maxilla of the Engis child, illustrating the extent of expansion of the maxillary sinus (ms), the vertical furrow that continues the lacrimal groove (g), and the medial projection of the internal margin of the nasal aperture (mp).

possible that they find no parallel among other terrestrial mammals (5). The apomorphies are the development of an internal nasal margin bearing a well-developed and vertically oriented medial projection, the swelling of the lateral nasal cavity wall into the capacious posterior nasal cavity, and the lack of an ossified roof over the lacrimal groove.

Finally, the extraordinary architecture of the internal nasal area of Neanderthals is of particular interest, given the frequently quoted suggestion that both the unusual appearance of the external nasal region and the large size of the nasal fossa in Neanderthals represent anatomical accommodations to cold environmental conditions and/or low humidities (1, 13–16). Future hypotheses of this kind will also have to include

Table 1. Middle/late Pleistocene hominids examined for this study in which internal nasal regions are adequately preserved

Locality/specimen(s)	Group	Age, years
Cro-Magnon 1	*Homo sapiens*	26,000
Engis 2*	Neanderthal	Unknown
Gibraltar 1 and 2*	Neanderthal	Unknown
Kabwe	*Homo heidelbergensis*	400,000**
La Chapelle-aux-Saints	Neanderthal	60,000–70,000
La Ferrassie 1	Neanderthal	40,000–50,000
Pech de l'Azé*	Neanderthal	100,000**
Roc de Marsal*	Neanderthal	65,000
St-Césaire	Neanderthal	36,000
Skhul V	*Homo sapiens* (?)	90,000
Spy 1	Neanderthal	Unknown
Steinheim	*Homo* sp.	250,000–350,000**

Immature specimens are identified by asterisks. Most ages are approximate, those with double asterisks are particularly so.

functional consideration of the unique internal Neanderthal nasal structure. This makes it particularly unfortunate that the full internal nasal morphology of Neanderthals is not known. For while the unique projections and swellings we have described in these extinct hominids might well have made available additional surface area for mucous/ciliated membranes to humidify and warm incoming air, this increase might not have compensated for surface area lost if the Neanderthals had consequently lacked any of the standard components of the turbinate system. Further, all the Neanderthal specimens examined so far that preserve the morphologies described here are relatively late in the long Neanderthal time span; definitive association of these features with frigid conditions will require determination of exactly when they were acquired. It may be significant, however, that on the evidence of the Steinheim cranium, an incipient medial projection characterizes at least one pre-Neanderthal form.

Taken together, the apomorphies described here suggest a radical reorganization of internal nasal anatomy among the Neanderthals. This observation alone does not necessarily demonstrate that Neanderthals constitute a species separate from *Homo sapiens*, but it is very strongly consistent with this conclusion. The presence of a poorly developed medial projection in the Steinheim specimen (which, though not a Neanderthal, is plausibly of a related species) suggests the possibility of a morphocline involving this feature; and together with other evidence, this in turn implies that in the suite of hominid fossils known from the middle and late Pleistocene of Europe, there is evidence for an entire Neanderthal clade rather than simply for a single Neanderthal species.

Note Added in Proof. Since this article was submitted, we have observed further evidence of the swelling of the lateral nasal wall in the Neanderthal maxilla from Kulna, Czech Republic.

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