



The Neanderthal face is not cold adapted

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ABSTRACT

Many morphological features of the Pleistocene fossil hominin *Homo neanderthalensis*, including the reputed large size of its paranasal sinuses, have been interpreted as adaptations to extreme cold, as some Neanderthals lived in Europe during glacial periods. This interpretation of sinus evolution rests on two assumptions: that increased craniofacial pneumatization is an adaptation to lower ambient temperatures, and that Neanderthals have relatively large sinuses. Analysis of humans, other primates, and rodents, however, suggests that the first assumption is suspect; at least the maxillary sinus undergoes a significant *reduction* in volume in extreme cold, in both wild and laboratory conditions. The second assumption, that Neanderthal sinuses are large, extensive, or even 'hyperpneumatized,' has held sway since the first specimen was described and has been interpreted as the causal explanation for some of the distinctive aspects of Neanderthal facial form, but has never been evaluated with respect to scaling. To test the latter assumption, previously published measurements from two-dimensional (2D) X-rays and new three-dimensional (3D) data from computed tomography (CT) of Neanderthals and temperate-climate European *Homo sapiens* are regressed against cranial size to determine the relative size of their sinuses. The 2D data reveal a degree of craniofacial pneumatization in Neanderthals that is both commensurate with the size of the cranium and comparable in scale with that seen in temperate climate *H. sapiens*. The 3D analysis of CT data from a smaller sample supports this conclusion. These results suggest that the distinctive Neanderthal face cannot be interpreted as a direct result of increased pneumatization, nor is it likely to be an adaptation to resist cold stress; an alternative explanation is thus required.

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Introduction

Homo neanderthalensis is a species of Pleistocene hominin from western and central Eurasia. Originally discovered and described in the nineteenth century, it is now one of the best represented and well-differentiated groups in the hominin fossil record (Stringer, 1982). Its remarkable facial and nasal skeleton exhibits a suite of traits, considered autapomorphic, which has attracted many different functional explanations (Heim, 1976; Rak, 1986; Demes, 1987; Schwartz and Tattersall, 1996).

The fact that European Neanderthals lived during periods characterised by glacial conditions has been an enduring theme in discussions of Neanderthal characteristics (Howell, 1952). Many aspects of Neanderthal morphology continue to be attributed to cold adaptation (e.g., Steegmann et al., 2002), including the size of

their paranasal sinuses (e.g., Churchill, 1998). In mammals, paranasal sinuses are bony cavities of the craniofacial skeleton lined with a type of respiratory epithelium; they are formed during growth as extensions of the nasal capsule, and communicate with the nasal cavity proper in the adult via openings referred to as ostia (Negus, 1958). Extant Homininae (or African apes: *Pan*, *Gorilla*, and *Homo*) possess the maximum number of separate sinuses found in Primates: paired frontal and maxillary sinuses, the multi-locular ethmoidal sinus, and the single sphenoidal sinus (Wegner, 1936; Cave and Haines, 1940). Extinct members of the *Homo* clade also possess the full array of paranasal sinuses, although usually only the frontal and maxillary are preserved and/or reported.

It has been argued that Neanderthals had large paranasal air spaces since the first scientific description of the original cranium from the Neander Valley (Busk, 1861). This has often been interpreted as an adaptation to the 'ice age' climate (Sergi, 1944). Coon (1962:534) codified this, stating that "the expansion of the maxillary sinuses [in Neanderthals]...may have had a survival value under conditions of extreme cold." This has remained the dominant

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Table 1
Summary statistics of sinus area (mm²), volume (cc), and upper facial width (mm)^a

	Relative temp.	Left maxillary sinus area ^b	Left + right frontal sinus area ^b	Maxillary sinus vol.	Left + right frontal sinus vol.	Biorbital width
La Ferrassie 1	Cold		3038.08			112
La Quina 5	Cold		2036.8			100
Shanidar 1	Cool		740			115
Spy 1	Cold		2299.08			113
La Chapelle 1	Cold	1818.3	1393.56			114
Guattari 1	Cool	3105.96	1642.56	40.87	7.77	111
Forbes' Quarry 1	?Cool	1947.5	813.44	22.93	7.34	108
Krapina 3?					9.55	111
Tabun	?Cool				4.64	107
Lithuanian <i>Homo sapiens</i> (n = 26)	Cool	1167.4–2478.5	222.9–2551.4	9.13–35.46	0.39–23.21	87.7–104.5

? represents uncertainty in the palaeotemperature estimates.

^a Maxillary sinus data for the left side only; frontal sinus values represent a combined measurement from both left and right sinuses. Biorbital width measured at frontomale.

^b Derived from linear measurements taken from Tillier (1977).

explanation of Neanderthal craniofacial pneumatization to the present day (e.g., Holton and Franciscus, 2008), although there is no consensus with respect to the mechanism by which such a function is thought to have been achieved (Hylander, 1977).

The interpretation that large sinuses in Neanderthals represent an adaptation to cold rests on two premises: that expanded craniofacial pneumatization is an adaptation to low ambient temperatures, and that Neanderthals are characterised by enlarged paranasal sinuses. The first of these assertions has been the focus of recent work on mammalian pneumatization and climate. The results, however, reveal a relationship precisely the opposite of that proposed; Recent Arctic *Homo sapiens* have smaller maxillary (Shea, 1977) and frontal (Koertvelyessy, 1972; Hanson and Owsley, 1980) sinuses in more northerly localities, and the same biogeographic pattern is seen in the maxillary sinuses of Japanese macaques (Rae et al., 2003). Moreover, when reared in artificially cold conditions, rats show a reduction in maxillary sinus volume, suggesting that this is a developmental response (Rae et al., 2006). These studies strongly suggest that if Neanderthals possess large sinuses, it cannot be attributed to low ambient temperatures. In fact, we would expect the opposite; that cold adaptation would be associated with sinus volumes that were substantially smaller than those of temperate/tropical comparators.

The second premise, that the sinuses of Neanderthals are actually large, has been repeated for over a hundred years. Although temporal bone pneumatization is typically believed to have reduced during the evolution of the genus *Homo* (Sherwood et al., 2002), Neanderthals have been reported to possess sinuses that are large, expanded, or “hyperpneumatized” (Tillier, 1977; Salvadei et al., 1991; Tattersall and Schwartz, 2006). In fact, the alleged expansiveness of Neanderthal sinuses has been cited as the explanation for both their large supraorbital torus (Blake, 1864) and their lack of a canine fossa (Heim, 1974, 1978). These attributions, however, have not been evaluated systematically using volumetric measures, nor have most Neanderthals had their sinus size evaluated relative to cranial size (but see Zollikofer et al., 2008); as a result, it has been impossible to judge whether the sinuses of Neanderthals are larger than would be expected for a hominin of their size.

Therefore, the purpose of the present study is to determine the relative size of Neanderthal sinuses and, in doing so, resolve whether the paranasal pneumatization present in Neanderthals supports an interpretation of adaptation to extreme cold. To address this question, scaling analyses were performed on two data sets: previously collected plane X-ray data on Neanderthals and CT examination of a smaller sample of *H. neanderthalensis* crania (Forbes' Quarry 1, Guattari 1, Krapina 3, Tabun), both of which are compared to a *H. sapiens* sample. If Neanderthals are ‘hyperpneumatized,’ we would expect them to display sinus volumes

comparatively larger than that seen in similarly-sized hominins. Similarly, if Neanderthal pneumatization reflects cold adaptation in the same manner as that seen in other mammals, their sinuses should be relatively smaller.

To provide a conservative test of the size of the sinuses in the fossils, material from two central European archaeological *H. sapiens* populations was chosen as a baseline comparator. This was done to a) minimise geographic variation, b) avoid any effects of modern domestic heating, and c) provide a large sample of crania intact enough to permit measurement of both maxillary and frontal sinuses. Our aim was not to attempt to characterise the overall relationship of hominin sinuses to climate, nor to repeat existing work showing reduced paranasal pneumatization in Arctic humans (e.g., Koertvelyessy, 1972; Shea, 1977; Hanson and Owsley, 1980); we accept that these studies demonstrate that sinuses in hominins exposed to very low temperatures are smaller than those found in more temperate environments, as is true of other mammals (Rae et al., 2003, 2006). Rather, we endeavour to determine whether relative sinus size in Neanderthals differs substantially from that of other members of the tribe Hominini living on the same continental land mass in non-glacial environmental conditions. We consider this to be the most appropriate null hypothesis.

Materials and methods

The Neanderthals examined for the present study are limited to those for which relatively complete crania (with at least one sinus present) are preserved and for which either a) sinus dimensions or b) computed tomography (CT) scan sets are freely available (Table 1). The sample includes specimens from a range of palaeoclimates, from cold (e.g., La Ferrassie) to less extreme, ‘cool’ temperatures (e.g., Guattari 1), which should allow for differentiation between the fossils, if (for example) only those found in the lowest temperatures display sinus volume adaptation. The *H. sapiens* samples chosen for comparison to the fossils are from the Lithuanian archaeological sites of Plinkagalys, dated to the 5th to 6th century, and Alytus, dated to the 14th to the 17th century (Palubeckaitė and Jankauskas, 2001). Only complete, young adult crania (determined by the presence of a complete permanent dentition with little tooth wear) were included.

Two-dimensional (2D) data were derived from linear measurements of Neanderthal maxillary and frontal sinuses taken from Tillier's (1977) Ph.D. thesis; Tillier took these measurements from plane radiographs (standard X-rays). Equivalent measurements were taken from CT scans of the *H. sapiens* crania and the Forbes' Quarry Neanderthal (FQ1) using ImageJ 1.40 g (rsb.info.nih.gov/ij/), and were checked for equivalence by blind evaluation of FQ1, for which both Tillier's measurements and a CT scan set were

available. Maxillary sinus area was derived by multiplying the maximum anteroposterior length by the maximum superoinferior depth of the left maxillary sinus. Frontal sinus area was derived by multiplying maximum superoinferior depth of the left sinus by the sum of the mediolateral widths of the left and right frontal sinuses. These 2D areas were used in preference to volumes, which would require an additional measurement, to maximise the number of fossils that could be evaluated, as not all measurements were available for each specimen.

The three-dimensional (3D) data of Neanderthals were derived from previously collected CT scan sets acquired from NESPOS (www.nespos.org). *H. sapiens* CT data were obtained from 26 previously reported archaeological crania (Koppe et al., 2006, 2007) using a Siemens Sensation 16 (Siemens AG; Munich, Germany) collected at 1 mm intervals (120 kV, 75 mA, pixel spacing 0.32) and exported as 512×512 images in either raw or DICOM format.

For the 3D analysis, virtual three-dimensional reconstructions (Fig. 1) were created using Avizo 5.0 (Mercury Computer Systems, Chelmsford, MA, USA). Sinus volumes were then extracted from the virtual crania using the 'magic wand' fill tool implemented in the Avizo segmentation subroutine. The volumes of both left and right frontal sinuses were determined for all crania; frontal sinus volume is the sum of these two measures. Due to the infilling of matrix in the nasal cavity and subsequent damage in the fossils, only the left maxillary sinus of FQ1 and the right maxillary sinus of Guattari 1 were evaluated, and compared to the left maxillary sinus volumes for the comparative sample.

To determine the relative size of the structures, sinus size (either 2D area or 3D volume) was scaled against a measure of craniofacial size. Due to damage, many of the standard univariate measurements used as size proxies (e.g., basicranial length) were unavailable for the fossil material. Similarly, the adoption of a multidimensional scalar such as the grand mean, although preferable (Jungers et al., 1995; Rae and Koppe, 2000), would have reduced the sample size of available fossil specimens by an unacceptable amount. Instead, to err on the side of inclusivity, a univariate measure of upper facial width (bifrontomolare temporalis), preserved in nearly all specimens, was used as a size proxy. All of the regressions are plotted in log–log space using natural logs (ln).

Results

The results are summarised in Table 1. The raw figures show that some Neanderthals have absolute frontal and maxillary sinus sizes that are indeed outside the range of Recent *H. sapiens* (Vlček, 1967). This interpretation is not sufficient, however, as a significant component of sinus size in hominoids is explained by cranial size; the scaling relationship is either isometric (Rae and Koppe, 2000) or allometric (Blaney, 1986), depending on the sinus studied.

Figure 2 shows the regression of 2D maxillary and frontal sinus area onto facial width. For both 2D and 3D analyses, the human-only sample shows significant correlations between the size surrogate and the sinus measurement in all cases (maxillary sinus – 2D, $n = 25$, $r = 0.426$, $p = 0.034$; 3D, $n = 26$, $r = 0.427$, $p = 0.030$; frontal sinus – 2D, $n = 23$, $r = 0.477$, $p = 0.021$; 3D, $n = 25$, $r = 0.446$, $p = 0.026$). These results differ from those obtained from more widespread human samples (e.g., Butaric et al., 2010), probably due to differences in the relative size of sinuses between human populations from various geographic regions. Although the fossil sample is too small to derive a meaningful comparison of regression equation parameters on its own, it is clear that the distribution of Neanderthals is not easily distinguished from that of recent *H. sapiens*. In all cases, the values for the fossils fall within the 95% confidence limits of the human comparative sample. This suggests that the fossil sinuses are neither enlarged nor noticeably smaller relative to those of their extant congeners.

Figure 3 shows the bivariate plots for 3D volumetric data. The values for both sinuses in Neanderthals are close to the *H. sapiens* least squares regression estimate and comfortably within the 95% confidence limits of the comparative sample; their placement indicates that *H. neanderthalensis* is not characterised by relatively large paranasal sinuses. Neither are they substantially smaller than those of the Recent temperate-region *H. sapiens*, suggesting that the species does not show the characteristic reduction in sinus volume associated with extreme cold adaptation (Koertvelyessy, 1972; Shea, 1977; Hanson and Owsley, 1980). The distributions suggest that there is not a substantial effect of palaeotemperature; there is no consistent pattern between Neanderthals from 'cold' time periods and from 'cool' intervals.

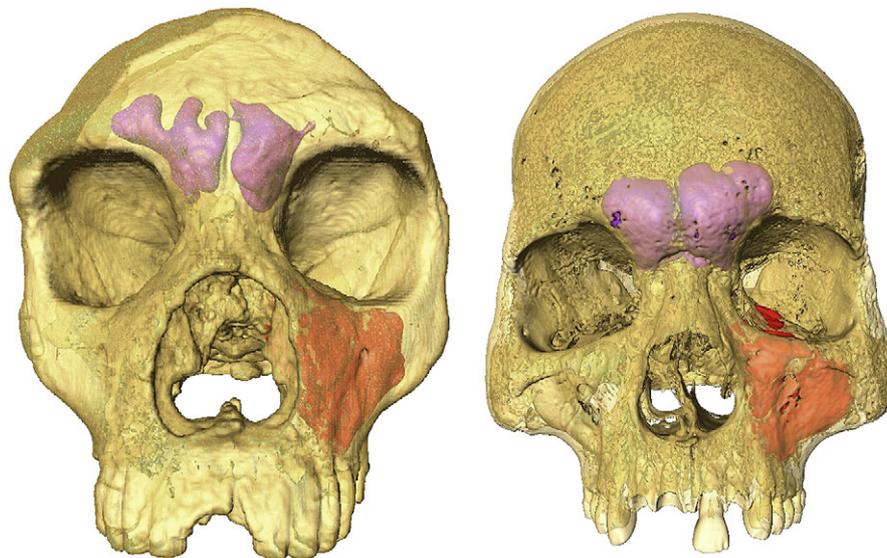


Fig. 1. The Forbes' Quarry Neanderthal FQ1 (left) and a Recent *Homo sapiens* cranium (right). The crania have been rendered partly transparent to highlight the frontal (purple) and maxillary (red) sinuses. The amount of pneumatized space is broadly similar in the two individuals. Not to scale (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

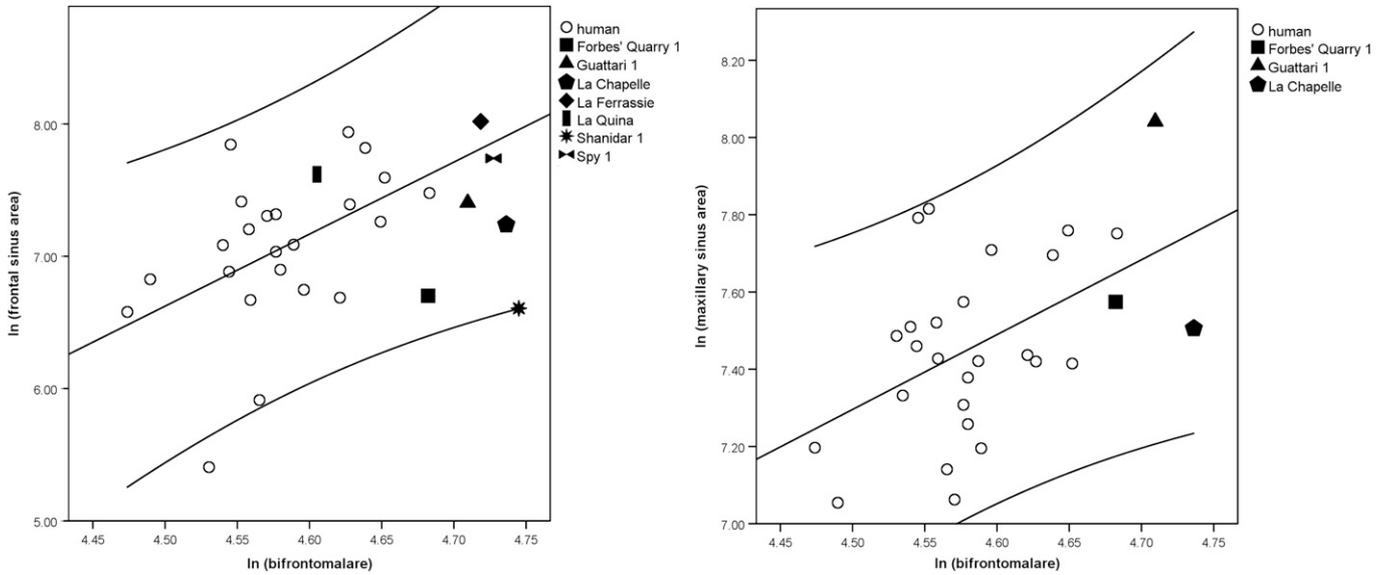


Fig. 2. Log–log regressions (ln) of two-dimensional frontal and maxillary sinus size on facial width for extant and fossil hominins. In both cases, the Neanderthals (indicated by the filled symbols) are well within the Recent human distribution. Least squares regression line and 95% confidence limits for individuals for Recent human data only.

Discussion

The idea of the cold-adapted Neanderthal has been deeply entrenched in anthropological thinking; it appears in introductory anthropology textbooks from the previous and present centuries (Stein and Rowe, 1982; Boyd and Silk, 2003). This position, while arguably defensible in terms of postcranial measures (Trinkaus, 1983; Holliday, 1997), is less justifiable with respect to the facial evidence. Neanderthals possess a prognathic face and wide nose, both of which are the opposite of the condition most often seen in arctic mammals, including humans (Wolpoff, 1968; Prestrud, 1991).

Increasingly, workers have been forced to look for ways of explaining away the ‘paradox’ of an allegedly cold-adapted form showing traits generally associated with warm conditions. For example, Holton and Franciscus (2008) investigated claims that wide nasal apertures in Neanderthals may have been due to wide intercanine distances. Their results, although demonstrating a positive,

significant correlation between those variables, suggested that prognathism may have been a more influential factor on nasal width, as the correlation coefficient between the latter two is higher. It is important to note, however, that correlation does not equal causation; as these results were based on analysis of raw (i.e., unscaled) measurements, it is likely that all of the variables described covary significantly with size, making correlations between them inevitable but not necessarily informative. It is also unclear what the functional relationship between prognathism and nasal width could be. Finally, Allen’s rule would lead us to suspect that cold-adapted forms would decrease their prognathism; thus, linking nasal width to prognathism simply transfers the paradox to another trait. If we accept the results reported here, however, it is no longer necessary to ‘explain away’ the non-cold-adapted craniofacial morphology of Neanderthals.

These results are supported by alternative opinions of Neanderthal adaptation that have emerged in the last few years. For example, the idea that postcranial proportions of Neanderthals are

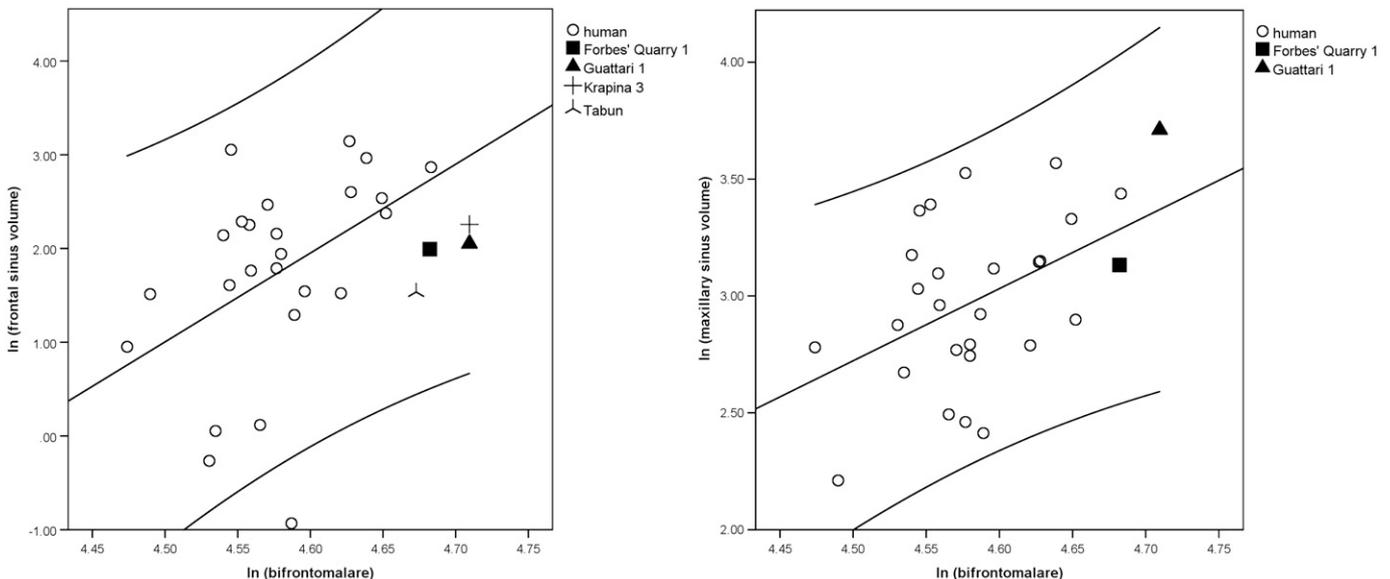


Fig. 3. Log–log regressions (ln) of three-dimensional frontal and maxillary sinus volume on facial width for extant and fossil hominins. In both cases, the Neanderthals (indicated by the filled symbols) are well within the Recent human distribution. Least squares regression line and 95% confidence limits for individuals for Recent human data only.

due to cold stress has been challenged by the recent suggestion that short distal limb elements may be due to forest adaptation (Stewart, 2005), as seen in African ungulates (Plummer and Bishop, 1994). This sort of interpretation also may help to explain the presence of Neanderthal traits at more southerly sites not significantly affected by glacial cold.

The demonstration that Neanderthal maxillary and frontal sinuses are not substantially different from those of Recent European *H. sapiens* highlights the necessity of both testing previous assumptions and comparative analysis. From the first publications on the remains from the Neander Valley, the perception of researchers has been that the cranium of Neanderthals was heavily pneumatized—often without any quantification or, more crucially, comparison. This opinion has been perpetuated, by reference to authority, for over a hundred years, erroneously providing grist to the mill of those promoting the interpretation of cold adaptation in the species. Similarly, the seeming disingenuousness of arguing that Neanderthals were large, bulky, stocky, robust individuals while simultaneously comparing raw measurements of sinus size in *H. neanderthalensis* and *H. sapiens* is hard to fathom in hindsight. It does serve, however, to stress the importance of making sure that there is a phenomenon that requires explanation; if Neanderthal sinuses are the same relative size as ours, there is simply no need to invoke adaptation—the two species likely inherited the condition unchanged from their common ancestor.

That Neanderthal paranasal pneumatization is neither expanded (as previously assumed) nor reduced (as analyses of low-temperature species would lead us to predict) removes one of the morphological elements cited in support of the interpretation of the Neanderthal face as specifically adapted to extreme cold. This may not be entirely surprising, however, as the bulk of the available evidence suggests that *H. sapiens* did not originate in temperate climes; if *H. neanderthalensis* is the sister taxon of extant humans, as current consensus suggests (Stringer, 1994), the splitting event is likely to have taken place where the extremes of cold would not have exerted selection pressure on the first Neanderthals (e.g., the Middle East). Although some postcranial characteristics of Neanderthals may indicate adaptation to glacial conditions (Trinkaus, 1983; Holliday, 1997), the Neanderthal face does not appear to be cold adapted, even where they experienced low temperatures. As a result, alternative explanations must be evoked for the unique form of the face of *H. neanderthalensis* (Stringer, 1974).

One potential reason for the distinctive shape of the Neanderthal facial skeleton is biomechanical; there is a body of work suggesting that Neanderthal face shape is an adaptation to paramasticatory stress, such as the use of the anterior dentition as a vice (Rak, 1986; Trinkaus, 1987; Smith, 1991; Spencer and Demes, 1993), similar to the situation seen in extant arctic human populations (Hylander, 1977), although it is worth noting that these extant *H. sapiens* bear little overall resemblance to Neanderthals. In addition, the prognathism of Neanderthals makes their faces less efficient in resisting anterior loading than their orthognathic congeners, making it unlikely that facial elongation is an adaptation to paramasticatory activity (Antón, 1994). Nevertheless, the biomechanical interpretation is consistent with the results reported here, in that we might expect similarity in relative sinus size between species (*H. sapiens*, *H. neanderthalensis*) with different biomechanical regimes; species of *Cebus* with radically different masticatory stresses are also indistinguishable in relative maxillary sinus volume (Rae and Koppe, 2008).

Alternatively, it may be that no directed selective pressure was active at the point of separation between the species. It has been argued that many of the cranial differences between *H. neanderthalensis* and *H. sapiens* show a pattern similar to that expected by genetic drift (Antón, 1994). For example, by comparing the

variance of standard cranial measurements in the two species, and checking the pattern against that of some genetic microsatellite data for humans, Weaver et al. (2007: 143) were able to show that “diversifying natural selection has not left an obvious signature on differences” between these two species. Indeed, their analysis suggests that the differences in metric characteristics between humans and Neanderthals are indistinguishable from the results of random drift. This represents a significant advance; future tests should be aimed at addressing the probabilities of these non-climatic explanations of Neanderthal craniofacial shape relative to this null hypothesis. This may go some way towards the elimination of “complicated hypotheses concerning the selective advantages of structures that do not need to be explained” (Antón, 1994: 692).

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References

- Antón, S.C., 1994. Mechanical and other perspectives on Neanderthal craniofacial morphology. In: Corruccini, R.S., Ciochon, R.L. (Eds.), *Integrative Paths to the Past: Palaeoanthropological Advances in Honor of F. Clark Howell*. Prentice Hall, Englewood Cliffs, pp. 677–695.
- Blake, C., 1864. On the alleged peculiar characters, and assumed antiquity of the human cranium from the Neanderthal. *J. Anthropol. Soc. London* 2, cxxxix–clvii.
- Blaney, S., 1986. An allometric study of the frontal sinus in *Gorilla*, *Pan*, and *Pongo*. *Folia Primatol.* 47, 81–96.
- Boyd, R., Silk, J., 2003. *How Humans Evolved*. W.W. Norton, New York.
- Busk, G., April 1861. Translation with comments of “On the crania of the most ancient races of man” by D. Schaafhausen. *Nat. Hist. Rev.*, 155–175.
- Butaric, L., McCarthy, R., Broadfield, D., 2010. A preliminary 3D computed tomography study of the human maxillary sinus and nasal cavity. *Am. J. Phys. Anthropol.* 143, 426–436.
- Cave, A., Haines, R., 1940. The paranasal sinuses of the anthropoid apes. *J. Anat.* 74, 493–523.
- Churchill, S., 1998. Cold adaptation, heterochrony, and neanderthals. *Evol. Anthropol.* 7, 46–61.
- Coon, C., 1962. *The Origin of Races*. Alfred A. Knopf, New York.
- Demes, B., 1987. Another look at an old face – biomechanics of the Neanderthal facial skeleton reconsidered. *J. Hum. Evol.* 16, 297–303.
- Hanson, C.L., Owsley, D.W., 1980. Frontal sinus size in Eskimo populations. *Am. J. Phys. Anthropol.* 53, 251–255.
- Heim, J.-L., 1974. Les hommes fossiles de la Ferrassie (Dordogne) et le problème de la définition des Néandertaliens classiques. *L’Anthropologie (Paris)* 78, 321–378.
- Heim, J.-L., 1976. Le gisement, les squelettes adultes: crâne et squelette du tronc. *Arch. de l’Institut de paléontologie humaine* 35, 1–331.
- Heim, J.-L., 1978. Contribution du massif facial à la morphogénèse du crâne Néandertalien. In: Piveteau, J. (Ed.), *Les Origines Humaines et les Époques de l’Intelligence*. Masson, Paris, pp. 183–215.
- Holliday, T.W., 1997. Body proportions in Late Pleistocene Europe and modern human origins. *J. Hum. Evol.* 32, 423–447.
- Holton, N.E., Franciscus, R.G., 2008. The paradox of a wide nasal aperture in cold-adapted Neandertals: a causal assessment. *J. Hum. Evol.* 55, 942–951.
- Howell, F., 1952. Pleistocene glacial ecology and the evolution of “Classic Neanderthal” man. *Southwest. J. Anthropol.* 8, 377–410.
- Hylander, W.L., 1977. The adaptive significance of Eskimo craniofacial morphology. In: Dahlberg, A.A., Graber, T.M. (Eds.), *Orofacial Growth and Development*. Mouton Publishers, The Hague, pp. 129–169.
- Jungers, W., Falsetti, A., Wall, C., 1995. Shape, relative size, and size-adjustments in morphometrics. *Yearb. Phys. Anthropol.* 38, 137–161.
- Koertvelyessy, T., 1972. Relationships between the frontal sinus and climatic conditions: a skeletal approach to cold adaptation. *Am. J. Phys. Anthropol.* 37, 161–172.
- Koppe, T., Schöbel, S.L., Bärenklau, M., Bruchhaus, H., Jankauskas, R., Kaduk, W., 2007. Factors affecting the variation in the adult temporomandibular joint of archaeological human populations. *Ann. Anat.* 189, 320–325.

- Koppe, T., Weigel, C., Bärenklau, N., Kaduk, W., Bayerlein, T., Gedrange, T., 2006. Maxillary sinus pneumatization of an adult skull with an untreated bilateral cleft palate. *J. Cranio. Maxill. Surg.* 34, 91–95.
- Negus, V., 1958. *The Comparative Anatomy and Physiology of the Nose and Paranasal Sinuses*. E & S Livingstone, Edinburgh.
- Palubeckaitė, Ž., Jankauskas, R., 2001. Dental enamel hypoplasia in Lithuanian paleopopulations. *Acta Med. Lituanica (Suppl. 8)*, 12–17.
- Plummer, T., Bishop, L., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. *J. Hum. Evol.* 27, 47–75.
- Prestrud, P., 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic* 44, 132–138.
- Rae, T.C., Hill, R.A., Hamada, Y., Koppe, T., 2003. Clinal variation of maxillary sinus volume in Japanese macaques (*Macaca fuscata*). *Am. J. Primatol.* 59, 153–158.
- Rae, T.C., Koppe, T., 2000. Isometric scaling of maxillary sinus volume in hominoids. *J. Hum. Evol.* 38, 411–423.
- Rae, T.C., 2008. Independence of biomechanical forces and craniofacial pneumatization in *Cebus*. *Anat. Rec.* 291, 1414–1419.
- Rae, T.C., Strand Viðarsdóttir, U., Jeffery, N., Steegmann Jr., A.T., 2006. Developmental response to cold stress in *Rattus*: implications for the interpretation of climatic adaptation in fossil hominins. *Proc. Roy. Soc. B.* 273, 2605–2610.
- Rak, Y., 1986. The Neanderthal: a new look at an old face. *J. Hum. Evol.* 15, 151–164.
- Salvadei, L., Massani, D., Passarello, P., 1991. Tomographic analysis of the paranasal sinuses of the Neandertal cranium of the Guattari Cave. In: Piperno, M., Scichilone, G. (Eds.), *The Circeo 1 Neandertal Skull: Studies and Documentation*. Istituto Poligrafico e Zecca dello Stato, Rome, pp. 311–320.
- Schwartz, J., Tattersall, I., 1996. Significance of some previously unrecognized apomorphies in the nasal region of *Homo neanderthalensis*. *Proc. Natl. Acad. Sci. U.S.A.* 93, 10852–10854.
- Sergi, S., 1944. Craniometria e craniografia del primo paleantropo di Saccopastore. *Ricerche di Morfologia* 20–21, 733–791.
- Shea, B., 1977. Eskimo craniofacial morphology, cold stress and the maxillary sinus. *Am. J. Phys. Anthropol.* 47, 289–300.
- Sherwood, R., Ward, S., Hill, A., 2002. The taxonomic status of the Chemeron temporal (KNM-BC 1). *J. Hum. Evol.* 42, 153–184.
- Smith, F., 1991. The Neandertals: evolutionary dead ends or ancestors of modern people? *J. Anthropol. Res.* 47, 219–238.
- Spencer, M., Demes, B., 1993. Biomechanical analysis of masticatory system configuration in neandertals and inuits. *Am. J. Phys. Anthropol.* 91, 1–20.
- Stegmann, A., Cerny, F., Holliday, T., 2002. Neandertal cold adaptation: physiological and energetic factors. *Am. J. Hum. Biol.* 14, 566–583.
- Stein, P., Rowe, B., 1982. *Physical Anthropology*. Plenum, New York.
- Stewart, J., 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of oxygen isotope stage 3. *Quatern. Int.* 137, 35–46.
- Stringer, C., 1974. Population relationships of later Pleistocene hominids: a multivariate study of available crania. *J. Archaeol. Sci.* 1, 317–342.
- Stringer, C., 1982. Towards a solution to the Neanderthal problem. *J. Hum. Evol.* 11, 431–438.
- Stringer, C., 1994. Out of Africa: a personal history. In: Nitecki, M., Nitecki, D. (Eds.), *Origins of Anatomically Modern Humans*. Plenum Press, New York, pp. 151–172.
- Tattersall, I., Schwartz, J., 2006. The distinctiveness and systematic context of *Homo neanderthalensis*. In: Harvati, K., Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer, Dordrecht, pp. 9–22.
- Tillier, A., 1977. La pneumatization du massif cranio-facial chez les hommes actuels et fossiles. *Bull. Mem. Soc. Anthropol. Paris* 4, 177–189, 287–316.
- Trinkaus, E., 1983. *The Shanidar Neandertals*. Academic Press, New York.
- Trinkaus, E., 1987. The Neandertal face: evolutionary and functional perspectives on a recent hominid face. *J. Hum. Evol.* 16, 429–443.
- Vlček, E., 1967. Die Sinus frontales bei europäischen Neandertalern. *Anthropol. Anz.* 30, 166–189.
- Weaver, T., Roseman, C., Stringer, C., 2007. Were Neandertal and modern human cranial differences produced by natural selection or genetic drift? *J. Hum. Evol.* 53, 135–145.
- Wegner, R.N., 1936. Sonderbildungen der Kieferhöhle bei den Anthropoiden. *Anat. Anz.* 83, 161–240.
- Wolpoff, M., 1968. Climatic influence on the skeletal nasal aperture. *Am. J. Phys. Anthropol.* 29, 405–424.
- Zollikofer, C.P.E., Ponce de León, M.S., Schmitz, R.W., Stringer, C.B., 2008. New insights into mid-Pleistocene fossil hominin paranasal sinus morphology. *Anat. Rec.* 291, 1506–1516.