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Paranasal sinuses: A problematic proxy for climate adaptation in Neanderthals

Marlijn L. Noback [a], Elfriede Samo [a], Casper H.A. van Leeuwen [b], Niels Lynnerup [c], Katerina Harvati [a, d, *]

[a] *Paleoanthropology, Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Rümelinstrasse 23, 72070 Tübingen, Germany*
[b] *Centre for Ecological and Evolutionary Synthesis, University of Oslo, Department of Biosciences, Post Office Box 1066, 0316 Oslo, Norway*
[c] *University of Copenhagen, Department of Forensic Medicine, Antropologisk Laboratorium, Frederik V's Vej 11, 2100 Copenhagen, Denmark*
[d] *DFG Centre for Advanced Studies 'Words, Bones, Genes, Tools: Tracking Linguistic, Cultural and Biological Trajectories of the Human Past', Eberhard Karls Universität Tübingen, Rümelinstrasse 23, 72070 Tübingen, Germany*

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1. Introduction

As inhabitants of glacial Europe, Neanderthals, with their typical cranial shape, have received much attention with respect to cold adaptation (e.g., Coon, 1962; Schwartz and Tattersall, 1996; Churchill, 1998; Steegmann et al., 2002; Holton and Franciscus, 2008; Hubbe et al., 2009; see also; Harvati, 2015). Recently, Rae et al. (2011a) published a study of Neanderthal sinus volume in relation to climate adaptation. They compared Neanderthal maxillary and frontal sinus volumes with those of a European sample of *Homo sapiens*. Based on similarities between the two groups, they concluded that the Neanderthal face is not cold adapted.

This study was criticized by Holton et al. (2011) for two main reasons: (1) its lack of a geographically widespread comparative sample and (2) the use of irrelevant anatomy (sinus volumes) in the analysis of climate adaptations. In their comment, Holton et al. (2011) showed that, relative to Africans, the maxillary sinuses of Europeans and Neanderthals are hyperpneumatized. They argue that the observed population variation in relative sinus volume is not directly related to cold adaptation, but that this is secondary to climatically relevant differences in nasal cavity shape. Their study included neither frontal sinus data nor data from populations living under extreme cold climates. Rae et al. (2011b) challenged Holton et al.'s (2011) findings on the basis of the origin of their samples (African- and European-derived Americans) and stressed that the new data from Holton et al. (2011) actually supported their own study—namely showing Europeans to be similar to Neanderthals. Importantly, however, they did not address Holton et al.'s (2011) second point of critique, i.e., that sinuses should not be used as indicators for climate adaptation of Neanderthals at all.

This debate illustrates the ongoing discussion about proposed cold adaptations in *Homo neanderthalensis* (e.g., Weaver, 2009 and references therein) and sinus function (e.g., see Table 2 in Marquez, 2008 for an overview, but also Zollikofer et al., 2008; Butaric et al., 2010; Holton et al., 2013). Here, we contribute to the discussion by providing hitherto missing comparative data. In contrast to both Rae et al. (2011a) and Holton et al. (2011), we present data from a native warm climate population from Nubia and an extreme cold climate population from Greenland. We thus cover a broader climatic range and use indigenous samples. Furthermore, unlike Holton et al. (2011), we present both maxillary and frontal sinus volumes. We discuss how these sinus volumes compare to the findings of the original Rae et al. (2011a) publication. If paranasal sinus volumes are related to climate, we expect consistent trends in both frontal and maxillary sinus volumes over the climatic range from warm Nubia to Europe to cold Greenland. Based on our results, we discuss the problematic use of sinuses as indicators of Neanderthal facial cold adaptation.

2. Materials and methods

Our sample consists of crania from 32 Greenlanders (14 females, 15 males, 3 unknown, from the Neo-Eskimo Thule Culture) and 35 Nubians (16 females, 19 males from the Wadi-Halfa region) selected from the osteological collection of the Bioanthropology Department of the University of Copenhagen. Only adult crania with no alveolar resorption (as this might affect maxillary sinus shape) were selected. The Nubian sample encompasses crania from the Meroitic ($n = 17$,

* Corresponding author.
E-mail address: katerina.harvati@ifu.uni-tuebingen.de (K. Harvati).

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0–350 AD), as well as the X-group ($n = 18$, 350–550 AD). The two Nubian groups were not significantly different from each other in sinus volume or cranial size (Student's t-tests, frontal sinus: $t = 0.48$, df = 30, $p = 0.63$; maxillary sinus: $t = 1.07$, df = 18, $p = 0.30$; cranial centroid size: $t = -0.61$, df = 33, $p = 0.54$) and were thus grouped together to increase the Nubian sample size.

The crania were scanned in the Retsmedicinsk Institut Copenhagen with a Siemens Sensation 4 scanner (0.75 mm slice thickness, 0.3 mm increment). The resulting computed tomography (CT) scans were uploaded in AVIZO (6.1, Visualization Group) and sinus volumes were segmented out using the outlining tools in segmentation mode (Samo, 2013). The right maxillary sinus was measured unless it was filled with matrix, in which case the left sinus was used (total Nubia $n = 20$, total Greenland $n = 17$). In order to segment the frontal sinus, the lower boundary was manually set at the level of the frontal process. Both left and right frontal sinuses were segmented separately to acquire data on partial (hypoplasia) or complete absence (aplasia) of the frontal sinus (total Nubia $n = 35$, total Greenland $n = 32$). Upper facial width was measured as the distance between left and right frontomalare temporale. To compare our results with those of Rae et al. (2011a), we included in our graphs the trend line from their Lithuanian sinus volume data, representing 'Europeans,' as well as their Neanderthal sinus measurements: two unilateral maxillary sinus volume measurements (Forbes' Quarry 1, Guattari 1) and four bilateral frontal sinus volume measurements (Forbes' Quarry 1, Guattari 1, Krapina 3, Tabun).

Differences between Nubian and Greenland populations in rates of frontal sinus aplasia were tested using chi-squared analyses. Differences in frontal and maxillary sinus volumes between the populations were tested using Student's t-tests (in case data were normally distributed with homogeneous variances), or Welch's two sample t-tests in cases of unequal variances. We tested for differences in both absolute and relative sinus volumes; the latter was obtained by dividing the volumes by upper facial width (to enable direct comparison to previously published work). Linear regressions were performed for each population to test whether the natural log of sinus volumes depended on the natural log of upper facial width. The regressions were plotted following the layout and axes of Rae et al. (2011a). All analyses were performed in R (R-Development Core Team, 2015).

3. Results and preliminary discussion

3.1. Maxillary sinus volumes

There were no significant differences in absolute or relative maxillary sinus volumes between the Nubian and Greenland populations (Table 1). For Nubians, individuals with larger upper facial width had significantly larger maxillary sinuses, but no such effect was found in Greenlanders (Fig. 1). Both the Nubian and Greenlandic sample show relatively smaller maxillary sinus volumes compared to the European data from Rae et al (2011a; our Fig. 1), but this was not explicitly tested further here. Earlier studies showed European sinuses to be larger than those of Africans (Fernandes, 2004; Holton et al., 2011). The similarity between Nubian and Greenlandic maxillary sinus volumes in our study illustrates the unclear relationship between climate and maxillary sinus volume, and calls into question climate as a main driver of maxillary sinus volume. Our findings agree with the results of Butaric et al. (2010), who found no clear climatic trend in maxillary sinus volumes across a large geographic sample.

Forbes' Quarry 1 has a maxillary sinus volume that falls between the trendlines of the European and Nubian samples. Nevertheless, some Greenlandic maxillary sinus volumes also fall within this range. The Guattari 1 maxillary sinus volume is relatively large, but

Table 1
Maxillary and frontal sinus volumes in cm^3 and facial width in mm for Nubian and Greenland populations.[a]

	Nubians Mean ± sd	Greenlanders Mean ± sd	t	df	p-Value
Frontal sinus volume	2.74 ± 1.63	0.66 ± 0.55	6.50	48.9	<0.001
Relative frontal sinus volume (corrected for upper facial width)			6.97	48.0	<0.001
Maxillary sinus volume	13.98 ± 4.54	15.35 ± 5.83	−0.80	35	0.43
Relative maxillary sinus volume (corrected for upper facial width)			−0.50	33	0.62
Upper facial width	99.38 ± 5.02	100.80 ± 3.16	−1.23	47.3	0.22

[a] Differences between populations are indicated by Student's two sample t-tests, or Welch's two sample t-tests in cases of unequal variances. Crania with frontal sinus aplasia were excluded from the frontal sinus analyses.

according to Rae et al. (2011a) still falls within the European trend line. The fact that the Greenland sample does not show a significant correlation between upper facial width and maxillary sinus volume indicates that it is potentially problematic to assume that Neanderthals should follow a similar scaling pattern to that of modern humans—as within modern humans, these scaling patterns can also differ among populations or be altogether absent.

These results do not support any correlation between climate and maxillary sinus volume in either modern humans or Neanderthals. Maxillary sinus volume is instead possibly determined by a combination of factors, such as an indirect link to climate through accommodating changes in nasal cavity breadth (Rae et al., 2003;

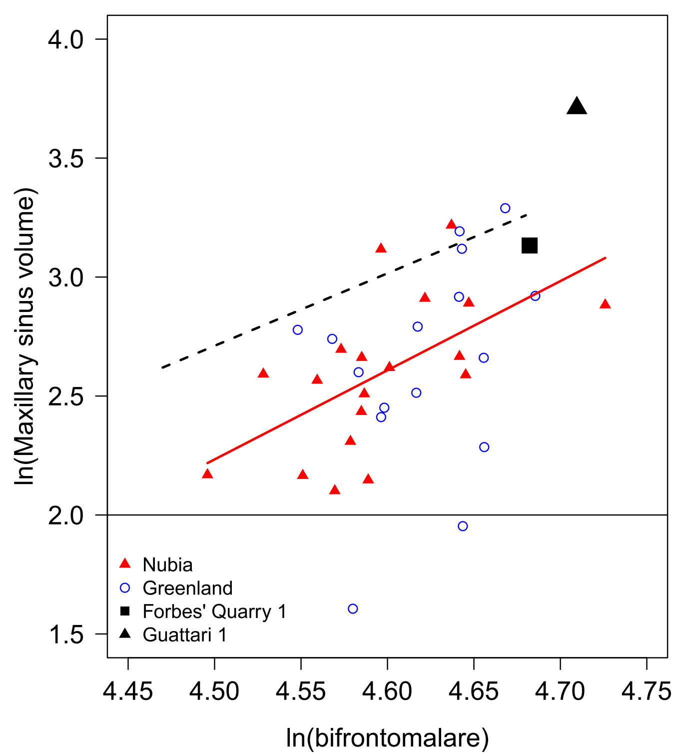

Figure 1. Log–log regressions of maxillary sinus volumes (in cm^3) for populations with different climatic origins in relation to upper facial width. Maxillary sinus regression was significant for Nubians ($F_{1,17} = 9.00$, $p = 0.01$, $R^2 = 0.35$, $y = 3.7 * x - 14.6$; red line), but not for Greenlanders ($F_{1,14} = 1.80$, $p = 0.20$). European samples as derived from Rae et al. (2011a) are indicated by the dashed black line. For comparison, the horizontal black line indicates the boundary of the original graph in Rae et al. (2011a, their Fig. 3, right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Holton et al., 2013), biomechanical factors related to bite force resistance and reduction of cranial weight (Preuschoft et al., 2002), and opportunistic pneumatization of available space between orbits and dental arch (Zollikofer and Weissmann, 2008). Interestingly, Rae et al. (2003, 2011a,b) themselves also noted the possibility that maxillary sinus volumes change only indirectly with climate, as a result of adaptations in surrounding structures. Our results suggest that maxillary sinus volume does not track climate, and therefore its use as a possible indicator of cold adaptation is inappropriate.

3.2. Frontal sinus volumes

In our study, frontal sinus volumes were significantly smaller in extreme cold-climate Greenlanders compared to warm-climate Nubians, both in terms of absolute values and when corrected for upper facial width (Table 1). In neither sample was frontal sinus volume related to upper facial width (Fig. 2). Frontal sinus aplasia was significantly higher in Greenland (38.2%) than in Nubian (8.6%) populations ($\chi^2 = 13.9$, df = 1, $p < 0.001$). However, frontal sinus hypoplasia was not significantly different (32.4% in Greenland versus 14.2% in Nubia, $\chi^2 = 2.2$, df = 1, $p = 0.14$). These results illustrate that frontal sinus volumes also do not follow a consistent climatic trend. As shown in Figure 2, instead of being intermediate between the warm climate Nubians and extreme cold climate Greenlanders, the European samples actually show the largest frontal sinus volumes. All four Neanderthal frontal sinus volumes included fall close to the Nubian samples, and according to Rae et al. (2011a), are also within the European sample's regression.

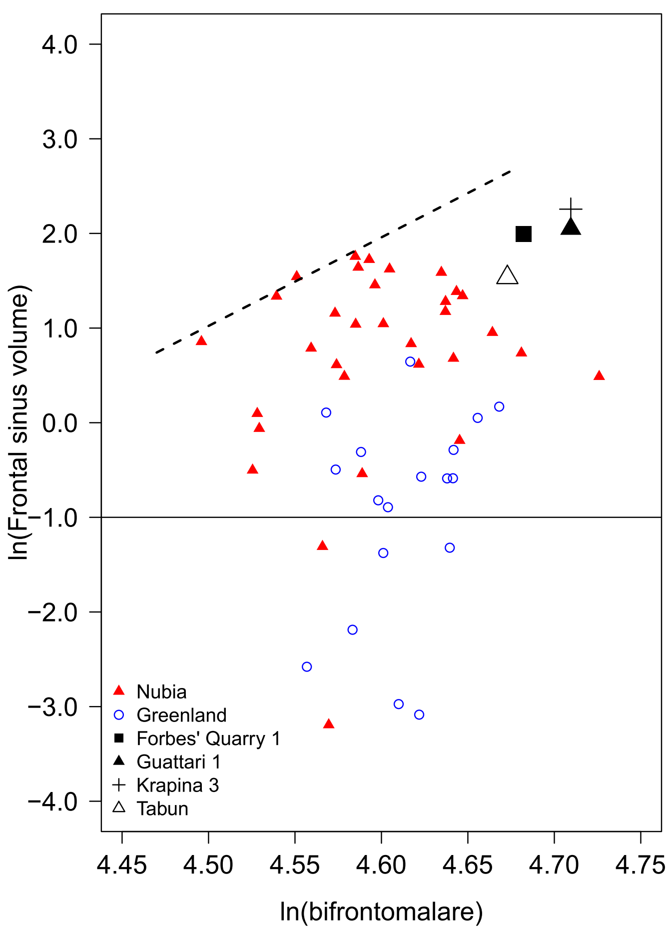

Figure 2. Log–log regression of frontal sinus volumes (in cm^3) for populations with different climatic origins in relation to upper facial width. Frontal sinus regression was significant for neither Nubians ($F_{1,30} = 1.31$, $p = 0.26$), nor Greenlanders ($F_{1,16} = 1.64$, $p = 0.22$). European samples as derived from Rae et al. (2011a) are indicated by the dashed black line. For comparison, the horizontal black line indicates the boundary of the original graph in Rae et al. (2011a, their Fig. 3, left).

Focusing only on our own dataset, it might be concluded that cold adaptation would entail a reduction in frontal sinus volume, leading even as far as sinus aplasia. Such a relationship has been proposed on the basis of studies of the cranial remains of cold- versus warm-raised rats, which show a relative decrease in maxillary sinus volume interpreted as a response to developmental stress (Rae et al., 2006), as well as on an observed clinal variation in maxillary sinus volume among Japanese macaques (Rae et al., 2003). As noted above, no such effect was found in the maxillary sinuses of our samples. With regard to the frontal sinus, aplasia also occurs in our Nubian sample, as well as in other warm climate populations (e.g., Danesh-Sani et al., 2011 and references therein), thus indicating that it cannot be explained by a response to cold climate alone. Furthermore, when we compare our results with the European sample from Rae et al. (2011a), a climatic cline is no longer supported. European sinus volumes do not fall between the Nubian and Greenland sample, as would be expected if a climatic trend in sinus volume were present. Both the inconsistent results of our study and those of Rae et al. (2011a) call into question the use of the frontal sinus as an appropriate indicator for climatic adaptation.

Instead, frontal sinus volumes are probably influenced by population history and random pneumatization processes. Lynnerup et al. (1999) found a trend in frontal sinus volume within a climatically constant geographic region, which showed a decrease from West to East Greenland, closely tracking ancient migrations and population history rather than climate. A study comparing Mid-Late Pleistocene hominin paranasal sinuses with those of modern humans and extant apes suggests the most likely explanation for frontal sinus size and shape is a combination of cranial shape and stochastic processes that underlie sinus morphogenesis (Zollikofer et al., 2008).

4. Discussion

In this study, we presented additional data on both frontal and maxillary sinus volumes of native warm and cold climate population samples. We found no clear pattern in sinus volumes in relation to climate, confirming the results of earlier studies (Koertvelyessy, 1972; Butaric et al., 2010; Butaric, 2015; Ito et al., 2015). Based on our two additional population samples, we strengthen the notion that maxillary and frontal sinus volumes are more likely related to other factors, including population history, changes in surrounding facial structures, and stochastic processes (e.g., Lynnerup et al., 1999; Zollikofer et al., 2008; Holton et al., 2013; Butaric, 2015). Therefore, the use of sinus volume data as indicators for climatic adaptations in fossil humans seems not to be appropriate. In other words, the fact that Neanderthal sinus volumes are similar to those of modern Europeans has no bearing on the assessment of a possible cold adaptation in Neanderthal facial morphology.

A possible future direction in sinus research would be the investigation of sinus shape variation and sinus location relative to other facial structures (see Holton et al., 2013; Noback, 2014). For example, the proximity of the maxillary sinus to the respiratory and masticatory components of the face suggests a potentially important role for the maxillary sinus in accommodating changes in cranial shape (e.g., Rae and Koppe, 2004). Responses of the nasal cavity (e.g., Shea, 1977; Franciscus and Long, 1991; Holton and Franciscus, 2008; Yokley, 2009; Noback et al., 2011) and the midface (e.g., Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Evteev et al., 2014) to climatic pressures have recently received particular attention, and therefore may indirectly affect sinus volumes (Holton et al., 2013; Butaric, 2015).

We conclude that using sinus volume to study climate adaptation in either *H. sapiens* or *H. neanderthalensis* is problematic. As long as the function and evolution of sinus volume and shape are not well understood in our own species (e.g., Marquez, 2008), conclusions based on sinus morphology of Neanderthals should be interpreted with great caution.

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References

Butaric, L.N., 2015. Differential scaling patterns in maxillary sinus volume and nasal cavity breadth among modern humans. Anat. Rec. 298, 1710–1721.
Butaric, L.N., McCarthy, R.C., Broadfield, D.C., 2010. A preliminary 3D computed tomography study of the human maxillary sinus and nasal cavity. Am. J. Phys. Anthropol. 143, 426–436.
Churchill, S.E., 1998. Cold adaptation, heterochrony, and Neandertals. Evol. Anthropol. 7, 46–61.
Coon, C.S., 1962. The origin of races. Alfed A. Knopf, Inc., New York.
Danesh-Sani, S.A., Bavandi, R., Esmaili, M., 2011. Frontal sinus agenesis using computed tomography. J. Craniofac. Surg. 22, E48–E51.
Evteev, A., Cardini, A.L., Morozova, I., O'Higgins, P., 2014. Extreme climate, rather than population history, explains mid-facial morphology of northern Asians. Am. J. Phys. Anthropol. 153, 449–462.
Fernandes, C.L., 2004. Volumetric analysis of maxillary sinuses of Zulu and European crania by helical, multislice computed tomography. J. Laryngol. Otol. 118, 877–881.
Franciscus, R.G., Long, J.C., 1991. Variation in human nasal height and breath. Am. J. Phys. Anthropol. 85, 419–427.
Harvati, K., 2015. Neanderthals and their contemporaries. In: Tattersal, I., Henke, W. (Eds.), Handbook of paleoanthropology. Springer, New York, pp. 2243–2279.
Harvati, K., Weaver, T., 2006. Human cranial anatomy and the differential preservation of population history and climate signatures. Anat. Rec. 288A, 1225–1233.
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.
Holton, N.E., Yokley, T.R., Franciscus, R.G., 2011. Climatic adaptation and Neandertal facial evolution: A comment on Rae et al. (2011). J. Hum. Evol. 61, 624–627.
Holton, N., Yokley, T., Butaric, L., 2013. The morphological interaction between the nasal cavity and maxillary sinuses in living humans. Anat. Rec.-Adv. Integ. Anat. Evol. Biol. 296, 414–426.
Hubbe, M., Hanihara, T., Harvati, K., 2009. Climate signatures in the morphological differentiation of worldwide human populations. Anat. Rec. 292, 1720–1733.
Ito, T., Nishimura, T.D., Hamada, Y., Takai, M., 2015. Contribution of the maxillary sinus to the modularity and variability of nasal cavity shape in Japanese macaques. Primates 56, 11–19.
Koertvelyessy, T., 1972. Relationships between the frontal sinus and climatic conditions: a skeletal approach to cold adaptation. Am. J. Phys. Antropol. 37, 161–172.
Lynnerup, N., Homøe, P., Skovgaard, L.T., 1999. The frontal sinus in ancient and modern Greenlandic Inuit. Int. J. Anthropol. 14, 47–54.
Marquez, S., 2008. The paranasal sinuses: The last frontier in craniofacial biology. Anat. Rec.-Adv. Integ. Anat. Evol. Biol. 291, 1350–1361.
Noback, M.L., 2014. Diet- and climate-related variation of the human cranium. Ph.D. Dissertation, Eberhard Karls Universität Tübingen.
Noback, M.L., Harvati, K., Spoor, F., 2011. Climate related variation of the human nasal cavity. Am. J. Phys. Anthropol. 145, 599–614.
Preuschoft, H., Witte, H., Witzel, U., 2002. Pneumatized spaces, sinuses and spongy bones in the skulls of primates. Anthropologischer Anzeiger; Bericht uber die biologisch-anthropologische Literatur 60, 67–79.
R-Development-Core-Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL. http://www.R-project.org.
Rae, T.C., Koppe, T., 2004. Holes in the head: Evolutionary interpretations of the paranasal sinuses in catarrhines. Evol. Anthropol.: Issues, News, and Reviews 13, 211–223.
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., Vidarsdottir, U.S., Jefferey, N., Steegmann Jr., A.T., 2006. Developmental response to cold stress in cranial morphology of *Rattus*: implications for the interpretation of climatic adaptaion in fossil hominins. Proc. R. Soc. B 273, 2605–2610.
Rae, T.C., Koppe, T., Stringer, C.B., 2011a. The Neanderthal face is not cold adapted. J. Hum. Evol. 60, 234–239.
Rae, T.C., Koppe, T., Stringer, C.B., 2011b. Hyperpneumatized Neanderthals? Reply to Holton et al. (2011). J. Hum. Evol. 61, 628–629.
Roseman, C.C., 2004. Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. Proc. Nat. Aca. Sci. USA 101, 12824–12829.
Samo, E., 2013. Far apart? The paranasal sinuses of Inuit and Nubians. An inquiry into the anatomy of the frontal and maxillary sinuses of historic Greenlandic Inuit and Meroitic and X-Group Nubians. M.Sc. Thesis, Eberhard Karls Universität Tübingen.
Schwartz, J.H., Tattersall, I., 1996. Significance of some previously unrecognized apomorphies in the nasal region of Homo neanderthalensis. Proc. Natl. Acad. Sci. USA 93, 10852–10854.
Shea, B.T., 1977. Eskimo craniofacial morphology, cold stress and the maxillary sinus. Am. J. Phys. Anthropol. 47 (2), 289–300.
Steegmann Jr., A.T., Cerny, F.J., Holliday, T.W., 2002. Neandertal cold adaptation: Physiological and energetic factors. Am. J. Hum. Biol. 14, 566–583.
Weaver, T.D., 2009. The meaning of Neandertal skeletal morphology. Proc. Natl. Acad. Sci. USA 106, 16028–16033.
Yokley, T.R., 2009. Ecogeographic Variation in Human Nasal Passages. Am. J. Phys. Anthropol. 138, 11–22.
Zollikofer, C.P.E., Weissmann, J.D., 2008. A morphogenetic model of cranial pneumatization based on the invasive tissue hypothesis. Anat. Rec.: Adv. Integ. Anat. Evol. Biol. 291, 1446–1454.
Zollikofer, C.P.E., De Leon, M.S.P., Schmitz, R.W., Stringer, C.B., 2008. New insights into mid-late Pleistocene fossil hominin paranasal sinus morphology. Anat. Rec.-Adv. Integ. Anat. Evol. Biol. 291, 1506–1516.

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