Neandertal faces were not long; modern human faces are short

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Neandertal faces have been described as being derived with respect to their overall length or degree of anterior projection. A comparison of cranial and mandibular indicators of lower facial projection across archaic and modern *Homo* indicates that Neandertal facial lengths on average are similar to those of preceding archaic *Homo* and principally contrast with those of recent humans. Neandertal facial length is not derived. The shortness of recent human facial skeletons is the evolutionarily derived condition.

Since the discovery of a large male Neandertal skull with an essentially intact facial skeleton at the Bouffia Boneval near La Chapelle-aux-Saints in 1908 (1), descriptions of the Neandertals and comparisons of their facial dimensions have frequently emphasized the large size of their facial skeletons (e.g., refs. 2–9), with them being described recently, for example, as having an “extraordinary forward projection of the face along the midline” (10). Since the La Chapelle-aux-Saints discovery, the sample of sufficiently complete Neandertal crania and mandibles that provides data on facial length has increased significantly. Moreover, similar samples of their archaic *Homo* predecessors back to early *Homo erectus* and of their Late Pleistocene early modern human contemporaries and successors have markedly expanded. From this material, it has been recognized since the 1970s (11–16) that it is principally the combination of a projecting midface and a more posteriorly positioned lateral facial skeleton, along with a series of secondary morphological consequences of that “midfacial prognathism,” that differentiates the Neandertal face from those of other Pleistocene and recent members of the genus *Homo*. However, as the quote above illustrates, it remains unclear whether it is variation in the forward projection of the midface or contrasts in the position of the lateral face and detailed aspects of their facial skeleton that explain the overall configuration of the Neandertal face.

Most of the earlier quantitative comparisons of Neandertal facial projection (e.g., refs. 12 and 13) principally compared Neandertal facial projection to that of recent (late Holocene) human populations, though papers concerning other aspects of their facial skeletons (e.g., refs. 14 and 16–19) have provided data suggesting that their overall facial lengths were similar to those of at least their Middle Pleistocene non-Neandertal predecessors. However, because the assessment of whether the Neandertals have a phylogenetically derived degree of overall prognathism provides a baseline for assessing the polarities and paleobiology of various characteristics of their facial anatomies, it is appropriate to reassess, with the currently available samples, whether the Neandertals did indeed have long faces.

Materials and Methods

Facial length is defined here generally as the direct distance from the middle of the cranial base to the labial incisor alveoli. As such, it is concerned with the degree of lower facial, or dentoalveolar, projection relative to the core of the basal neurocranium. This distance is correlated to some degree in the cranium with upper facial length (measured as basion–nasion length or nasion radius) (20), but upper facial length is more directly influenced

by endocranial volume, and hence is a less appropriate measure of facial projection.

In paleontologically practical terms, given the dearth of crania with a complete foramen magnum and upper facial skeleton (for a basion–prosthion length) and the greater number of preserved mandibles, facial length has been assessed by using two measurements. The first value is the prosthion radius (20), or the mid-sagittal projection of the linear distances between each porion (or auditory meatus) and prosthion (the maxillary mid-sagittal labial incisor alveolar margin). The second measurement is the mid-sagittal projection of the linear distances between the middle of each mandibular condyle and infradentale (the mandibular mid-sagittal labial incisor alveolar margin), or mandibular superior length (17). These two measurements are correlated in a mixed sample of 179 recent humans, 12 Late Pleistocene early modern humans, and 5 late archaic humans ($r^2 = 0.718$, $P < 0.001$; recent humans only: $r^2 = 0.680$, $P < 0.001$), despite some scatter caused by interindividual variation in the distance between porion and the temporomandibular joint and in the patterns of anterior dental occlusion. Given frequent taphonomic damage and resorption to labial incisor alveoli, as well as fossilization and reassembly distortion of fossil crania, these measurements are normally within 1–2 mm of their original values, or $<2\%$ of the original measurements.

To be included in the analysis, mandibles needed to preserve at least an indication of the mid-sagittal plane and the distance from infradentale to the condylar base on one side, requiring at most some estimation of condyle height for a direct distance between the mid-condyle and infradentale. For mandibles preserving both sides, the bi-condylar breadth and the average of the direct distance between each condyle and infradentale were used to compute the superior length. For mandibles lacking sufficient bone on one side, the mid-sagittal plane was approximated by using the dental arcade and/or symphyseal morphology; because the mandibular length will vary as the sine of the angular error in assessing the mid-sagittal plane, small errors of mid-sagittal plane estimation have little effect on the resultant length.

The available and sufficiently intact Pleistocene archaic and early modern human crania and mandibles are divided into five samples. The first is an early *H. erectus* sample [>1.5 million years before present (ma BP)]; it is insufficient in terms of preservation, sample size and available data for quantitative analysis, but the available information is considered as the evolutionary baseline for later *Homo* facial lengths. The second is a non-Neandertal Middle Pleistocene archaic *Homo* sample, which includes African and Asian specimens between ≈ 800 and 150 thousand years (ka) BP and European specimens before ≈ 400 ka BP. Late Middle Pleistocene fossils from north Africa and southwestern Asia, such as Irhoud 1 and Tabun 2, are included in this sample. The Neandertal sample includes European later Middle Pleistocene to mid-last glacial remains (≈ 200 to 30 ka BP) plus Late Pleistocene western Asian archaic *Homo* specimens (≈ 100 to 40 ka BP). A Middle Paleolithic early modern human sample from the southwestern Asian sites of

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Table 1. Summary statistics for the comparative samples

	Prosthion radius	Mandible superior length
Middle Pleistocene non-Neandertals*	127.8 ± 7.5 (5)	114.4 ± 7.0 (15)
Neandertals†	121.8 ± 5.1 (9)	109.3 ± 6.4 (19)
Middle Paleolithic Early Modern Humans‡	105.5, 113.0, 116.0	109.0, 116.5
Earlier Upper Paleolithic Early Modern Humans§	108.9 ± 4.7 (17)	101.1 ± 7.8 (17)
Recent Humans (n)		
Melanesia (20)	111.0 ± 4.6	104.4 ± 4.3
Australia (21)	109.2 ± 5.2	101.8 ± 5.3
Micronesia (18)	107.3 ± 6.2	99.7 ± 5.0
Sub-Saharan Africa (20)	106.5 ± 4.0	98.2 ± 3.9
Southeast Asia (20)	103.4 ± 4.8	96.2 ± 5.9
Europe (35)	100.8 ± 6.0	92.8 ± 6.2
South Asia (20)	99.9 ± 5.5	92.3 ± 6.4
North Africa (20)	98.4 ± 4.8	93.0 ± 5.0
Total (179)	104.2 ± 6.7	96.9 ± 6.8

Data are given as mean ± standard deviation (in mm), plus *n* in parentheses. Individual values are given for small samples. Recent humans are arranged in descending order of mean prosthion radius.

*Specimens from Arago, Atapuerca-SH, Baringo-Kapthurin, Bodo, Broken Hill, Irhoud, Mauer, Sangiran, Tabun C, Tighenif, and Zhoukoudian.

†Specimens from Amud, Aubesier, Banyoles, La Chapelle-aux-Saints, La Ferrassie, Forbes' Quarry, Guattari, Kebara, Krapina, Montmaurin, Petralona, La Quina, Regourdou, Saccopastore, St. Césaire, Shanidar, Tabun B, Vindija, and Zafarraya.

‡Specimens from Qafzeh and Skhul.

§Specimens from Caviglione, Cro-Magnon, Dolní Věstonice, Kubbaniya, Minatogawa, Mladeč, Nazlet Khater, Oase, Ohalo, Paglicci, Pataud, Pavlov, Předmostí, Sungir, Vogelherd, and Zhoukoudian.

Qafzeh and Skhul is separated out, and it is followed by an earlier Upper Paleolithic European, Asian, and north African sample (≈40 to 18 ka BP).

To assess variability among recent humans, data for eight samples of recent Old World crania and mandibles are provided (Table 1); they include samples of Melanesians, Australians, Micronesians, Sub-Saharan Africans, southeast Asians (Thai), Europeans (central Europeans and Euroamericans), south Asians (Indians), and north Africans (Egyptians). The resultant values for these samples are close to those documented for other samples of recent humans (17, 20). Sample sizes and paleontological sample site compositions are provided in Table 1.

The majority of the measurements was taken personally on the original specimens or are from primary descriptions of the remains. These were supplemented by measurements from resin casts, corrected against published measurements for shrinkage. In addition, because the prosthion radius is not available for some specimens but basion-prosthion length is, the latter was converted to the prosthion radius for three Neandertals and eight early modern humans by using a least squares regression based on a pooled Pleistocene and recent human sample ($r^2 = 0.878$, $n = 43$, $SE_{est} = 0.8 \pm 0.2$ mm). Similarly, the description of the Atapuerca-Sima de los Huesos mandibles (21) provides only the condyle to gnathion direct distances, which were converted to mandible superior lengths by using a least squares regression based on Middle Pleistocene mandibles with a similar degree of symphyseal retreat ($r^2 = 0.712$, $n = 10$, $SE_{est} = 1.9 \pm 0.4$ mm). Specimens, for whom the maxilla has been positioned by using the articulated mandible but have an insufficient osseous connection between the maxilla and the neurocranium (Amud 1, Dolní Věstonice 15 and Tabun 1), are not included in the prosthion radius comparisons. The resultant sample represents

all of the currently available archaic *Homo* specimens and most of the early modern human remains that preserve sufficient portions of the mandible and/or cranium for reasonable determinations of these measurements.

Comparisons were initially done across the total range of samples, followed by pairwise *t* tests assuming heteroscedasticity; the *t* tests are one-tailed given the expectation that Neandertal facial lengths exceeded those of the other samples, with an H_0 of equality. Sequentially rejective Bonferroni multiple comparison corrections did not alter the results. Parametric tests were used based on the normality of these data in the recent human samples, but nonparametric assessments on the small paleontological samples provide similar *P* values.

Results

Rather than documenting an increase in facial projection through archaic *Homo* and peaking with the Neandertals, the plots of prosthion radius and mandible superior length across these samples (Figs. 1 and 2) document a modest decrease through the Middle and Late Pleistocene among archaic *Homo*, followed by a more marked decrease, especially among recent humans.

In prosthion radius, there is a significant change across the five samples (ANOVA, $P < 0.001$) and across the Neandertal to early modern human samples (ANOVA, $P < 0.001$). The distribution of points suggests a decrease from Middle Pleistocene archaic *Homo* to the Neandertals, but the difference does not reach significance (*t* test, $P = 0.080$). The Neandertal sample is highly significantly different from the pooled Late Pleistocene early modern human sample (*t* test, $P < 0.001$) and from the recent human one (*t* test, $P < 0.001$). The early modern humans are similar to the recent human samples with the longest faces but contrast with the majority of the recent human samples in facial length (Table 1 and Fig. 1).

The Neandertal cranial sample is dominated by large males, including La Chapelle-aux-Saints 1, La Ferrassie 1, Guattari 1, and Shanidar 1 and 5, and this may accentuate the difference between the Neandertal sample and the subsequent early modern human samples. However, the early modern human samples also have more males than females (66.7% in the Qafzeh-Skhul sample, 58.8% in the earlier Upper Paleolithic sample), making the significance of the gender bias unclear.

The distribution of mandible superior lengths provides a more gradual decrease through the Pleistocene (Fig. 2). The overall trend remains highly significant (ANOVA, $P < 0.001$). The contrast between the Neandertals and the pooled early modern human sample remains pronounced (*t* test, $P = 0.003$). The absolute difference between the means of the Middle Pleistocene and Neandertals samples is similar to the decrease with prosthion radius (5.1 mm versus 6.0 mm), but the larger sample size makes the difference significant (*t* test, $P = 0.018$). Again, the Neandertals and the recent humans remain highly significantly different in this measurement (*t* test, $P < 0.001$). The distribution of individual values shows major overlaps between the Pleistocene samples, but only the earlier Upper Paleolithic mandibles significantly overlap the recent human sample range. Again, the mean early modern human value is similar to the recent human samples with the most projecting lower faces.

The few early *H. erectus* remains providing indications of their degrees of facial projection appear to be similar to the Middle Pleistocene and Neandertal samples. The only east African mature cranium providing a measurement, KNM-ER 3733, has a basion-prosthion length of 120 mm (22), which converts (from a scaled cast) to a prosthion radius of 120 mm; this value is relatively small for later archaic *Homo*, with only Irhoud 1 among the Middle Pleistocene specimens having a shorter face. However, the KNM-ER 992 mandible, though insufficiently preserved for a length measurement, is much longer than the

Fig. 1. Prosthion radius for individual Pleistocene *Homo* specimens (Left) and box plots of recent human samples (Right). Squares, Africans; triangles, Asians; inverted triangles, Europeans. Box plots provide the medians, quartile ranges, and 95% ranges. Recent samples: 1, Melanesia; 2, Australia; 3, Micronesia; 4, Sub-Saharan Africa; 5, southeast Asia; 6, Europe; 7, south Asia; 8, north Africa.

mandibles that fit the KNM-ER 3733 cranium. It is similar in its preserved length (posterior ramus to mesial canine) to specimens such as Tighenif 3 and La Ferrassie 1, whose mandible lengths of 125 and 122 mm, respectively, fall at the tops of their respective samples. The facial length of the immature KNM-WT 15000 skull is also greater than that of KNM-ER 3733 (23), and it would have been substantially longer had the individual lived to maturity. In addition, the Dmanisi early *H. erectus* sample includes both specimens with short faces and at least one very long mandible (24–26).

Discussion

These data should be sufficient to indicate that the Neandertals did not have unusually long faces. Indeed, their overall facial projection, when all of the more or less but sufficiently complete specimens are included, is (i) average for a Pleistocene *Homo* sample, (ii) similar to or modestly reduced from that of their non-Neandertal archaic *Homo* predecessors, (iii) moderately

greater than those of early modern humans, and (iv) principally contrasting with recent, late Holocene humans. Consequently, there is nothing uniquely derived in Neandertal facial length, whatever may be derived in individual aspects of their facial skeletons. It is the less projecting faces of modern humans that are derived in the context of Pleistocene *Homo* evolution.

There are indeed some Neandertals with very large faces, such as La Chapelle-aux-Saints 1, La Ferrassie 1, and Shanidar 5, and the relative completeness and extensive publication of the first two for most of a century has fostered an image of enormous Neandertal faces. However, their facial lengths are matched or exceeded by Middle Pleistocene specimens, such as Arago 13, Bodo 1, Broken Hill 1, and Tighenif 3, and Early Pleistocene specimens, such as KNM-ER 992 and Dmanisi 2600. Moreover, there are also some rather short faced Neandertal specimens, such as Aubesier 11, Forbes' Quarry 1, Regourdou 1, Tabun 1, and Vindija 226. It is, of course, the sample's distribution, and not a few impressive specimens, which needs to be evaluated.

Fig. 2. Mandible superior length for individual Pleistocene *Homo* specimens (Left) and box plots of recent human samples (Right). Symbols and samples as in Fig. 1.

It should be noted that Neandertals have also been described as having relatively long upper facial lengths, measured between basion (or porion) and nasion (16, 27), relative to earlier *Homo* and especially recent humans. Currently available data (16, 27, 28) appear to confirm this inference. However, nasion–basion length, as well as the nasion radius, reflects endocranial length plus the degree of anterior projection of the mid-sagittal supraorbital torus and nasal root. Only the supraorbital and nasal components of this measurement can be rightly considered as a portion of facial projection. In this context, the apparently greater upper facial projection of the Neandertals undoubtedly reflects their higher endocranial capacities when compared with Early and Middle Pleistocene archaic *Homo* (28–30) and their more pronounced nasal and supraorbital regions relative to early and recent modern humans (31, 32).

These considerations of lower facial projection have treated absolute facial length as an independent variable, even though it (as with most other size-related aspects of human biology) is undoubtedly correlated to some degree with overall body size. There appears to be positive allometry between facial length and overall cranial size among humans, at least within populations (33), a pattern also evident within and among closely related species of Anthropoid Primates (34–36). In any case, indications of body mass for Pleistocene *Homo* (29, 37) indicate little average change in body mass through time, with the Neandertals being possibly moderately heavier on average, and a significant decrease taking place principally in the Holocene. It is possible that the Holocene facial shortening in part reflects the decrease in body mass. However, the possibly higher body masses of the Neandertals, if anything, should increase their scaled facial

lengths relative to earlier samples, whereas their faces are similar or slightly smaller.

These data, and especially the degree of overlap in facial length between the samples despite contrasting facial configurations, raise additional issues regarding the underlying evolutionary biology of the Pleistocene human face. Facial length, as quantified here, is a composite of a series of morphofunctional and developmental complexes, including the pharynx, the internal nasal cavity and the alveolar process in the cranium and involving the condyle, the ramus, the corpus and the alveolar process for the mandible. Because these cranial and mandibular aspects are functionally, spatially and developmentally interrelated to produce viable organisms throughout the life cycle, it remains to be determined to what extent each of these contributed to the changing anteroposterior dimensions of the mature Pleistocene and recent human face.

Conclusion

When viewed in their proper evolutionary context, Neandertals did not have long and projecting faces. They largely maintained the distribution in facial length characteristic of at least the first 1.6 million years of the genus *Homo*. It is with the evolution of modern humans, especially in the Holocene, that there is a derived facial length, and it is an overall shortening.

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