

Does *Homo neanderthalensis* Play a Role in Modern Human Ancestry? The Mandibular Evidence

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ABSTRACT Data obtained from quantifying the upper part of the mandibular ramus (the coronoid process, the condylar process, and the notch between them) lead us to conclude that Neandertals (both European and Middle Eastern) differ more from *Homo sapiens* (early specimens such as Tabun II, Skhul, and Qafzeh, as well as contemporary populations from as far apart as Alaska and Australia) than the latter differs from *Homo erectus*. The specialized Neandertal mandibular ramus morphology

emerges as yet another element constituting the derived complex of morphologies of the mandible and face that are unique to Neandertals. These morphologies provide further support for the contention that Neandertals do not play a role in modern human biological ancestry, either through “regional continuity” or through any other form of anagenetic progression. *Am J Phys Anthropol* 119: 199–204, 2002. © 2002 Wiley-Liss, Inc.

The celebrated absence of a chin at the front of the Neandertal mandible is a well-known primitive character that historically overshadowed the species’ derived mandibular characters. Only the bulging supraorbital ridges attracted more attention. These two primitive traits are a keystone of the anagenetic view of modern human origins, according to which Neandertals are a direct predecessor of modern *Homo sapiens* and occupy a lower rung in the evolutionary ladder. Indeed, many researchers have tended to assign the Neandertals’ other autapomorphic (unique) features, both mandibular and facial, the status of primitive characters or to dismiss them altogether (Franciscus and Trinkaus, 1995; Smith, 1983; Smith and Paquette, 1989; Suzuki, 1970; Trinkaus, 1983, 1984, 1987). Both of these solutions, we suspect, were the outcome of a reluctance to acknowledge the phylogenetic implications of the autapomorphic features, since their presence would upset the alleged evolutionary sequence, or, in other words, the traditional ancestral role of Neandertals. A perfect example is the morphology of the upper portion of the mandibular ramus.

In modern and early *H. sapiens*, as indeed in other hominid and nonhuman primate species, the ascending mandibular ramus terminates in two processes that are of almost equal elevation and are separated by a deep notch. The deepest point of the notch is located at approximately the midpoint between the two processes (Fig. 1). In Neandertals, the configuration is quite different. The anterior, or coronoid, process appears larger and more elevated than the posterior, or condylar, process. A shallow

notch lies between the processes, with its deepest point situated adjacent to the posterior one.

The morphology of the upper part of the mandibular ramus was the object of attention as early as 1928, when Werth (1928) described the shallow notch of the Mauer mandible as a primitive anatomy. Hence, he placed it at one end (the primitive one, according to him) of his morphocline. The modern human morphology lay at the other end of this sequence, and the Neandertal morphology, not surprisingly, was placed in between as an intermediate stage. This sequence apparently disturbed the renowned paleoanthropologist F. Weidenreich, who, in his monograph on the anatomy of the *H. erectus* mandible, stated, “Werth’s series appear to illustrate nothing else but a great illusion” (Weidenreich, 1936, p. 93). The discontent of Weidenreich (1936) was predictable, given that the early, primitive *H. erectus*, which, in his well-known, anagenetically oriented view, was certainly more primitive than the Neandertals, displayed an identical ramus to that of modern *H. sapiens*. Hence, in what seems to be an attempt to demonstrate that ramus morphology was not diagnostic at all, Weidenreich (1936) provided a sequence of his own to refute the implications of

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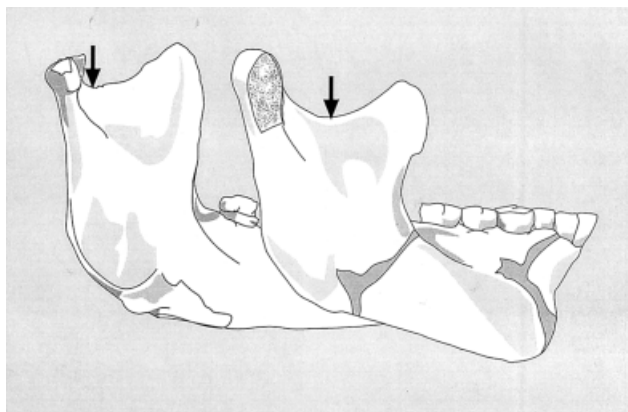


Fig. 1. Comparison of two rami: a Neandertal from the Amud cave (Amud I, left) and an early *Homo sapiens* specimen from Tabun (Tabun II, right). The arrows indicate the deepest point of each notch. Note in the Amud specimen how much larger the coronoid process is than the condylar process, and how shallow the mandibular notch is. Also note the proximity of the notch's deepest point to the condylar process.

Werth (1928). In the sequence of Weidenreich (1936), one end of the morphocline featured *H. erectus*, with its deep notch and two long, equally sized processes (a configuration like that of modern *H. sapiens*), while the other end featured a single, apparently atypical modern Eskimo mandible. Weidenreich (1936) placed Neandertals between these two ends. (The Eskimo specimen that Weidenreich (1936) chose as a representative of modern *H. sapiens* was undoubtedly an anomaly; we will demonstrate later that its mandibular notch contour does not resemble the contour of any of the notches we examined on 22 modern Eskimo specimens.) By claiming that the morphology of the upper part of the ramus was not taxonomically diagnostic, Weidenreich (1936) avoided dealing with the phylogenetic implications of this morphology.

Perhaps because of the widespread influence of Weidenreich, few scholars seem to have paid attention to ramus morphology, and those who have, tend to describe it in nonquantitative, nonstatistical terms (e.g., Rak, 1998).

On the basis of our visual observations, we hypothesize that 1) the ascending ramus of Neandertals differs in morphology from that of other hominids, and 2) the degree to which non-Neandertal hominids differ from each other in this respect is less than the degree to which they differ from Neandertals. To test this hypothesis, we developed a method to quantify the curve of the mandibular notch. The results indicate that Neandertal ramus morphology is indeed unique and, in contradiction to the contention of Weidenreich (1936), constitutes a diagnostic feature. A resemblance is revealed between *H. erectus*, early *H. sapiens*, and modern *H. sapiens* that leads us to conclude that the Neandertal anatomy is the derived one.

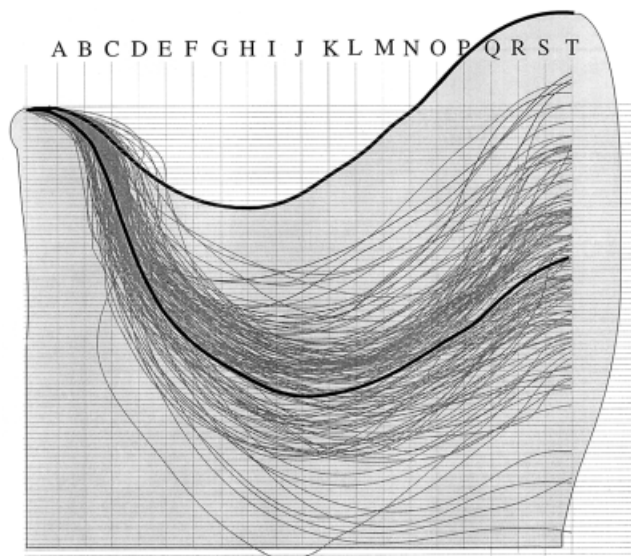


Fig. 2. Outline of mandibular notch in the Regourdou I Neandertal, represented by thick line at top of shaded area, compared with mean outline of 250 modern human specimens represented by lower thick line. Thin gray lines show distribution of modern *Homo sapiens* sample. Regourdou I is portrayed because it is the most extreme example of ramus configuration among the Neandertals. All other hominid contours in the sample fall within the area of the Regourdou I contour, represented by shading.

METHODS

The method we employed began with the tracing of the mandibular notch contour of each specimen. The tracing is a simple procedure. Since the mandibular ramus is essentially a flat, two-dimensional structure, we needed only to press the lateral surface against a sheet of paper and, holding a thin pencil in a vertical position, follow the contour of the bone. (Identical contours were obtained from photographs of the ramus with the camera positioned perpendicular to the bone's surface, and also from photocopies produced by pressing the ramus on the glass plate of the machine.)

Each contour was then plotted on a specifically constructed system of coordinates, shown in Figure 2, with the posterior margin of the ramus always oriented vertically. Next, the mandibular notch contour was expanded proportionally until the tips of the two processes were separated horizontally by a distance that remained constant for all specimens. The tip of each condylar process was placed at the upper left end of the graph at a fixed point (a "zero" point), and the tip of the coronoid process, at the right end, at the level of the vertical line T. Thus, the effect of size was eliminated. Note that our choice of the condylar process as the fixed point was arbitrary (regarding this choice, see Discussion, below).

The notch contour was subsequently translated into 20 numerical variables, each representing a point of intersection with one of the 20 vertical lines. The horizontal axis marks the numerical value of the point of intersection. We used the 20 consecutive mandibular coordinates, taken at fixed intervals, as

variables in a discriminant function analysis (Afifi and Clark, 1995; Bernstein, 1988). The calculations were performed with Statistica for Macintosh (version 4.0, StatSoft, Inc., Tulsa, OK).

To evaluate the precision of the method, we repeated the entire procedure on 20 randomly selected mandibles from the modern *H. sapiens* sample and compared the two sets of readings. The second set differed insignificantly from the first, as demonstrated by the 1.7% discrepancy between the sums of the values of each set's 20 variables.

MATERIALS

We examined a total of 268 individuals, of whom 9 are conventionally regarded as Neandertals, 9 are various non-Neandertal fossil hominids, and 250 are modern humans. Except for the fossil KNM-WT 15000, all specimens represent mature individuals, i.e., individuals in whom M3 is fully erupted.

The fossils were chosen on the basis of the availability to the authors of either an original specimen or a high-quality cast. The Neandertal specimens that we examined are Amud I, Krapina 59, Krapina 63, Krapina 66, La Ferrassie 1, Regourdou I, Shanidar II, Tabun I, and Zafarraya. The sample of non-Neandertal fossil specimens consists of Haua Fteah 1, Haua Fteah 2, KNM-WT 15000, Qafzeh 9, Skhul V, Tabun II, Upper Cave Zhoukoudian, Zhoukoudian GI, and Zhoukoudian HI.

When selecting the modern specimens, we attempted to include representatives of populations as geographically dispersed as accessibility allowed. The modern human group of 250 includes 164 specimens from the Levant, 27 of which are Natufian mandibles and all of which are housed in the human anthropological collection at the Sackler Faculty of Medicine, Tel Aviv University. From the same collection, we examined 36 mandibles from India, 5 from China, and one each from central Africa and Europe. From the collection at the British Museum of Natural History, we obtained data on 20 mandibles of Australian Aborigine origin and one mandible from a native population in South America. Twenty-two mandibles of unspecified Canadian Eskimo origin were traced at the Museum of Anthropology in Vancouver (British Columbia, Canada).

RESULTS

All variables used in the analysis were distributed normally except for the first (the starting point for all the contours). We created a final classification matrix for the evaluation of the initial classification of mandibles, and posterior probabilities were used for identifying misassigned cases.

The analysis of variance indicates that group centroids (N, M, and F in Fig. 3) are significantly different ($F_{[36,296]} = 2.31$, $P < 0.0001$). Post hoc tests between group means show a significant difference between modern humans and Neandertals ($F_{[18,248]} = 3.86$, $P < 0.0001$) and between fossil

hominids and Neandertals ($F_{[18,248]} = 1.77$, $P < 0.029$), but not between modern humans and the non-Neandertal fossil hominids ($F_{[18,248]} = 0.54$, $P < 0.937$).

To accommodate the large differences between the sizes of the three groups, we selected an equal a priori classification probability (0.333). The final classification matrix shows that all nine mandibles initially assigned as Neandertals are, in fact, classified as such (N, Fig. 3). All the other fossil hominid mandibles are also classified as originally assigned (F, Fig. 3). However, among the modern humans, only 35.6% are classified according to their initial assignment. Sixteen (6.4%) mandibles that were initially assigned as modern humans are classified as Neandertals, and 142 (56.8%), as non-Neandertal fossil hominids.

The first canonical variable accounts for 89.2% of the variance, and the second, for the remaining 10.8%. The variables K–N and C–G constitute the highest loads in the first and second factor, respectively.

When *H. erectus* is considered separately, as a fourth group of hominids, the picture remains essentially the same. The position of *H. erectus* in the graph is unchanged: its centroid still lies closer to *H. sapiens* than to Neandertals. (The other non-Neandertal fossils fall even closer to the modern *H. sapiens* centroid.) The mean probability that *H. erectus* will be assigned with modern humans (0.031 ± 0.038) is eight times greater than the probability that it will be assigned with Neandertals (0.004 ± 0.003).

DISCUSSION

The results suggest that, as hypothesized, the mandibular ramus is a truly diagnostic character for Neandertals. Easily classified, this element alone can serve to distinguish Neandertals from other hominids, a great advantage when only fragmentary material has survived, as is so often the case. The ramus of Tabun I, for example, is readily differentiated from that of the isolated, enigmatic Tabun II mandible. As seen in Figure 3, Tabun I is situated well within the Neandertal cluster, whereas Tabun II plainly falls within the generalized group. The generalized morphology of the ramus (the notch and the relationship between the notch's crest and the width of the condyle), along with the presence of a chin, led Rak (1998) to conclude that this specimen is an early *H. sapiens* like other specimens with a similar morphology (those from Skhul and Qafzeh). Similarly, the isolated ramal fragments from Haua Fteah can clearly be identified as non-Neandertal specimens, as they too fall within the generalized group.

From our analysis, the morphology of the Neandertal ramus emerges as a derived trait and as such can be added to the suite of derived characters in the Neandertal face and braincase that clearly indicate the species' unique taxonomic status. Howells (1975)

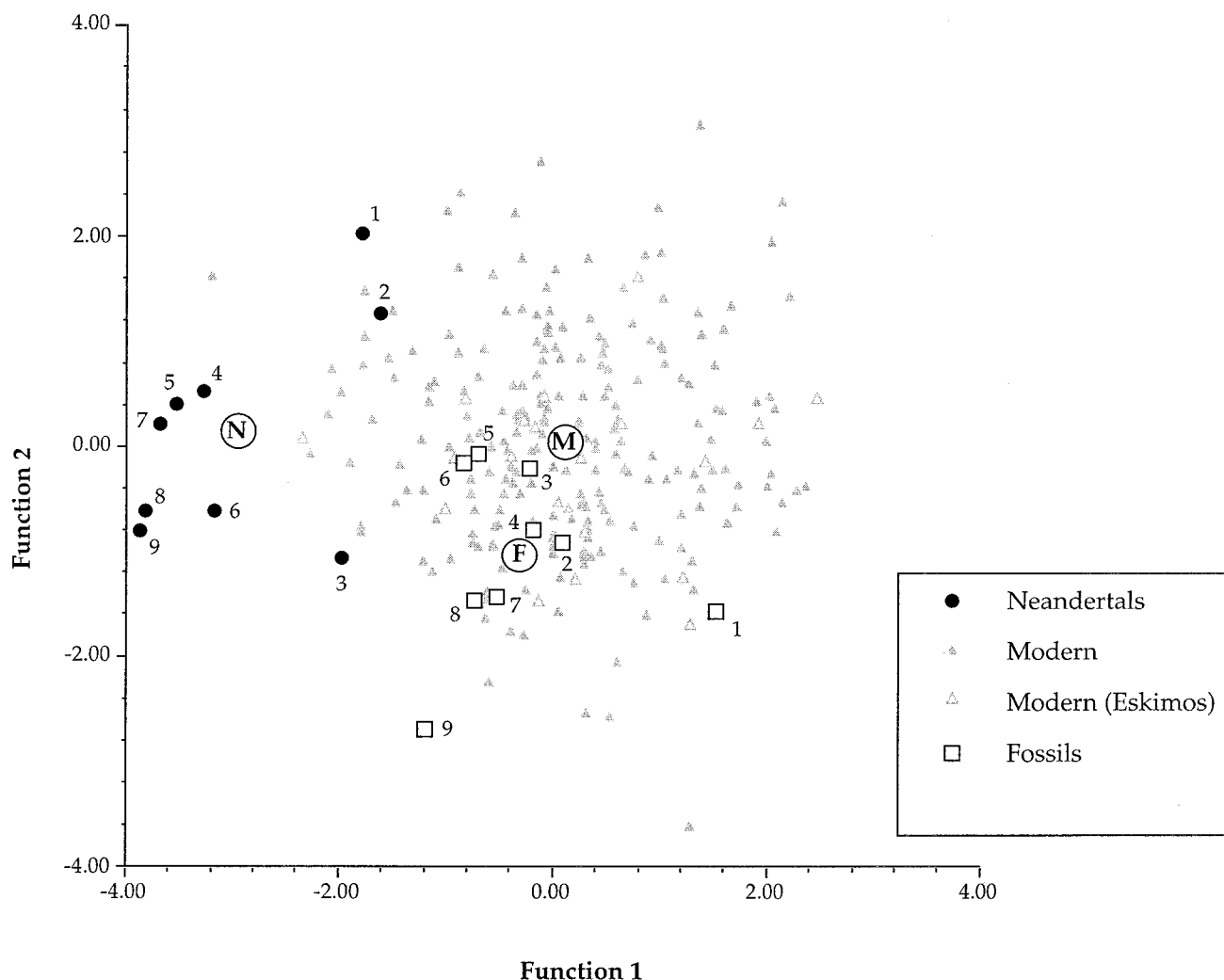


Fig. 3. Scatter diagram of three population samples; group centroids are represented by N (Neandertals), M (modern humans), and F (non-Neandertal fossil hominids). Neandertal specimens (represented by solid circles) are: 1, La Ferrassie 1; 2, Krapina 59; 3, Krapina 63; 4, Zafarraya; 5, Tabun I; 6, Krapina 66; 7, Amud I; 8, Shanidar II; and 9, Regourdou I. Non-Neandertal fossil hominid specimens (represented by open squares) are: 1, Haua Fteah 1; 2, Haua Fteah 2; 3, KNM-WT 15000 B; 4, Skhul V; 5, Tabun II; 6, Qafzeh 9; 7, Zhoukoudian GI; 8, Upper Cave Zhoukoudian; and 9, Zhoukoudian HI. The notch on Zhoukoudian GI and Zhoukoudian HI is slightly damaged, and the present form on both is the original reconstruction of Weidenreich (1936). The only other African specimen of relevance, KNM-ER 992, undoubtedly exhibits the modern (i.e., generalized) configuration; however, because only the coronoid process survives, the specimen was not included here. Note normal distribution of modern Eskimo population around the centroid of the modern human sample. Also note that the two Tabun specimens do not fall in the same cluster. The Mousterian Tabun II mandible falls in the modern *Homo sapiens* cluster, whereas Tabun I falls in the Neandertal cluster.

concluded that Neandertals differ more in their facial features from *H. sapiens* than does *H. sapiens* from *H. erectus*. We can state our results vis-à-vis the mandibular ramus in the same way: Neandertals differ more from *H. sapiens* in ramus morphology than does *H. sapiens* (including its early representatives) from *H. erectus*. This deviation of Neandertal ramus morphology must imply a profound specialization of the masticatory system (Hylander and Rak, in preparation) and joins with other elements of the face and the mandible that support such an interpretation (Rak, 1986, 1993, 1998; Rak et al., 1994).

As mentioned earlier, the decision to place the tips of the condylar processes on a fixed point (zero) was

arbitrary. By the same token, we could have placed the coronoid tips on a fixed point. In this manner we would have exposed the variation in the height of the condylar process, and Neandertals would have emerged as displaying the lowest condylar processes. Tentative results of a study currently in progress (Hylander and Rak, in preparation) indicate that, indeed, it is the Neandertals' condylar process that is lower in absolute terms (closer to the occlusal plane) than in other hominids, whereas the coronoid process appears to be situated at approximately the same height in Neandertals and in other hominids (e.g., compare the height of the coronoid process in the Regourdou I and Skhul V mandibles). In other words, it appears that the height of the

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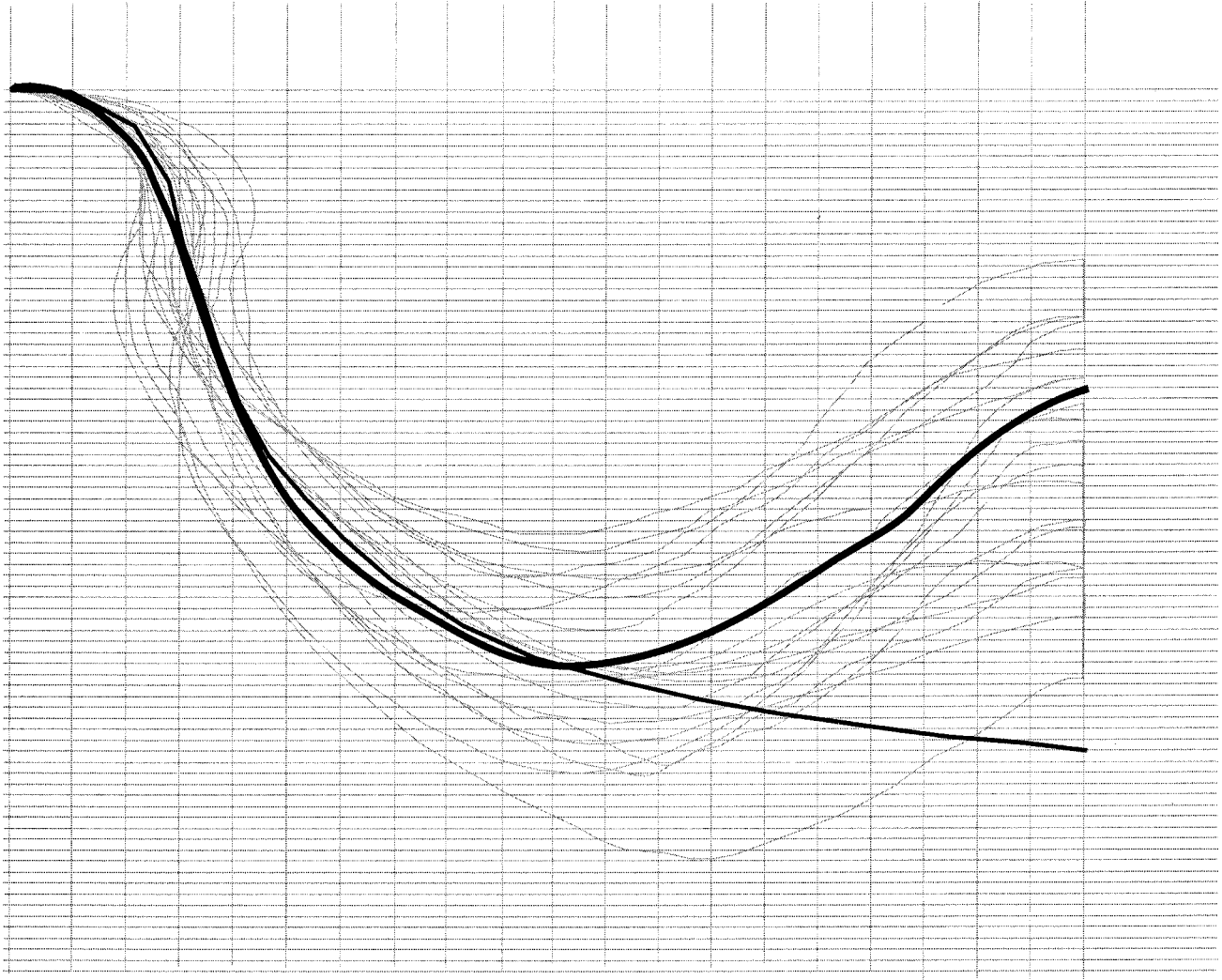


Fig. 4. Distribution of mandibular notch contours found in Eskimos in reference to mean contour of other modern human populations (thickest black line). Note normal distribution of Eskimo contours around the modern mean. Also note unusual curve of the black line of medium thickness, which stands for the single specimen that Weidenreich (1936) selected as representative of Eskimos. We took this curve from Weidenreich (1936) and oriented it according to our method.

condylar process is, in fact, what governs the Neandertal ramus morphology. If these observations are borne out, they will have significant repercussions regarding the size of the Neandertals' gape, since, all other factors considered equal, the lower the condyle is, the greater the extent of maximum gape.

Despite a certain resemblance in the body proportions and anterior dental wear pattern of Neandertals and modern Eskimos (presumably the outcome of similar environmental conditions and behaviors), the ramus morphology of the latter does not differ from that of other modern human populations (an issue that takes us back to the claim of Weidenreich (1936), discussed earlier). In other words, the Eskimos we examined still exhibit the generalized ramus anatomy as shown in Figure 3. Our Eskimo population does not lump as a separate group, nor does it display any particular trend. Distributed evenly

around the modern human centroid, the Eskimo group does not at all lean toward the Neandertal centroid. Similarly, Figure 4 demonstrates the normal distribution of the actual contours of the Eskimo mandibular notch around the mean contour of the other modern human populations in the sample. (Also note the unusual curve of the medium black line, which represents the single specimen that Weidenreich [1936] selected to represent the Eskimo population.)

Neither casts nor original specimens of the early Neandertal fossils from the Sima de los Huesos site in Atapuerca, Spain, were available to the authors during the research. However, illustrations in the published material clearly indicate that at least some of the mandibles already bear the notch morphology described here (Rosas, 1995, 2001), although it does not appear in the lists of Neandertal

characters compiled by Rosas (1995, 2001). Visual inspection by one of us (Y.R., with permission kindly granted by Dr. J.L. Arsuaga) of some of the actual fossils in Madrid confirms what we observed in the published illustrations. Not unexpectedly, the facial elements of these fossils manifest the facial topography of the Neandertals. The Atapuerca specimens seem to be the earliest fossils to demonstrate the Neandertal mandibular pattern described here.

The authors are not aware of a similar morphology in any other fossils outside the areas commonly considered the Neandertal domain, i.e., Europe and western Asia.

Although juveniles were not included in this study, Neandertal ramal morphology is clearly present in infant and juvenile specimens, as can be seen in a comparison of Roc de Marsal, Teshik-Tash, and Krapina 53 with modern *H. sapiens* individuals of comparable age. The presence of this ramal morphology (as one element of the already notable specializations of the masticatory system, the face included) in juvenile Neandertals, even those of suckling age, seems to suggest that this anatomy is not merely an epigenetic trait.

CONCLUSIONS

A taxonomy that is based on the ramus, which, along with the face, constitutes part of a highly specialized masticatory system, has far-reaching phylogenetic implications, as it suggests that *Homo neanderthalensis* forms a side branch that evolved separately from the modern human branch. The possibility that a reversal in the ramus morphology occurred is highly unlikely (like any reversal), particularly given that this morphology is an inherent element of the derived masticatory complex. Thus, without any need for a tedious formal cladistic analysis, we are led to the conclusion that Neandertals do not play a role in our biological ancestry, through either "regional continuity" or any other form of anagenetic progression, a conclusion that is in full conformity with other autapomorphic Neandertal morphologies (Howells, 1989; Rak, 1993; Rak et al., 1994), as well as with recently published molecular data (Krings et al., 1997, 2000; Ovchinnikov et al., 2000).

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