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Response to Comment on "A Middle Pleistocene *Homo* from Nesher Ramla, Israel"

Hila May[1,2]*†, Rachel Sarig[2,3]*†, Ariel Pokhojaev[1,2,3], Cinzia Fornai[4,5,6], María Martinón-Torres[7,8], José María Bermúdez de Castro[7,8], Gerhard W. Weber[5,9,10], Yossi Zaidner[11], Israel Hershkovitz[1,2]*†

[1]Department of Anatomy and Anthropology, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv, Israel. [2]Shmunis Family Anthropology Institute, Dan David Center for Human Evolution and Biohistory Research, Tel Aviv University, Tel Aviv, Israel. [3]Department of Oral Biology, Maurice and Gabriela Goldschleger School of Dental Medicine, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv, Israel. [4]Vienna School of Interdisciplinary Dentistry, Klosterneuburg, Austria. [5]Department of Evolutionary Anthropology, University of Vienna, Vienna, Austria. [6]Institute of Evolutionary Medicine, University of Zurich, Zurich, Switzerland. [7]Centro Nacional de Investigacion sobre la Evolucion Humana, Burgos, Spain. [8]Department of Anthropology, University College London, London, UK. [9]Core Facility for Micro-Computed Tomography, University of Vienna, Vienna, Austria. [10]Human Evolution and Archaeological Sciences, University of Vienna, Vienna, Austria. [11]Institute of Archaeology, Hebrew University of Jerusalem, Jerusalem, Israel.

*Corresponding author. Email: mayhila@tauex.tau.ac.il (H.M.); sarigrac@tauex.tau.ac.il (R.S.); anatom2@tauex.tau.ac.il (I.H.)

†These authors contributed equally to this work.

Marom and Rak claim, on the basis of a few mandibular features, that the Nesher Ramla (NR) *Homo* is a Neanderthal. Their comments lack substance and contribute little to the debate surrounding the evolution of Middle Pleistocene *Homo*. Limitations and preconceptions in their study prevented them from achieving resolution beyond a dichotomous interpretation of the NR as either a Neanderthal or a modern human.

In Hershkovitz *et al.* (*1*), the NR *Homo* was recognized as part of a Middle Pleistocene (MP) paleodeme together with other Levantine fossils exhibiting affine morphology (*1*). Although this *Homo* group presents some Neanderthal-like mandibular and dental characteristics, it differs substantially from Neanderthals in several important features, manifested mainly in the archaic morphology of the parietal (reflected in its flatness and thickness, unique endocranial surface topography, shape, size, and vessel imprints) and the mandible shapes, as extensively described and analyzed in the supplementary materials of our paper (*1*). In contrast to the claim implied by Marom and Rak (*2*), we did not interpret the NR fossils as a new species. The term paleodeme (*3*) is quite conservative, and "is both appropriate and necessary in studies of the hominin fossil record at various levels" (p. 204), thus reflecting our cautious rather than "radical" approach. Whether the NR *Homo* should be considered an example of *H. neanderthalensis* depends entirely on how this *Homo* group is defined. Similar to Marom and Rak, we amply acknowledged the morphological similarities of the NR mandible to Neanderthal mandibles. However, unlike them, we maintain that the archaic traits observed in the NR parietal and mandible account for important evolutionary differences from classic Neanderthals, which cannot be disregarded. In fact, we suggested that the NR *Homo* might have been a predecessor along the Neanderthal lineage (Fig. 1).

Whereas Marom and Rak did not report any flaws in our multi-methodological morphometric analyses, we found drawbacks in their analyses and interpretation of the results:

1. **Neanderthal mandibular traits:** None of the six mandibular traits Marom and Rak claimed to be unique to Neanderthals are actually exclusive to this *Homo* group. A well-developed medial pterygoid tubercle, for example, is present in the Early Pleistocene ATD6-96 specimen, in some of the Atapuerca–Sima de los Huesos (SH) mandibles, and in other non-Neanderthal specimens (*4*–*6*). Taurodontism is also observed in the SH molars, as well as in the M3 of ATD6-96 (*6*) and even in *H. erectus* (*7*).
2. **Significance of mandibular traits:** Marom and Rak (*2*) claimed that "Because the mandibular anatomy is responsible for the unique function of the mandible, these traits are inherently associated with each other…" In other words, they suggested that these six traits must covary to make the Neanderthal mandible function properly. However, this statement can be easily refuted by observing that, for example, *H. antecessor* did not possess all of these traits, yet their masticatory system was functional. Had Marom and Rak desired to provide a biomechanical explanation of the Neanderthal mandible distinctiveness,

they should have carried out a 3D shape analysis of the mandibles (i.e., geometric morphometric analysis) rather than linear measurements, as 3D shape better represents the loads applied to the mandible (*8*).

3. **Number of traits used:** Unlike Marom and Rak, who used six traits of the mandible to support their argument, we analyzed 47 traits with known discriminant power (*9*, *10*) to compare NR to other fossils (*1*).

4. **The retromolar space:** In our paper, we reported that the "NR-2 possesses a retromolar space. This feature is a dominant characteristic of the Neanderthal mandible." Yet we specified that the morphology of the retromolar space differs from that of classic Neanderthals: "The area behind the third molar is short and slightly inclined (the primitive condition), whereas in Neanderthals it is large and horizontal" [supplement of (*1*), p. 14]. This further observation of the retromolar space presentation (Fig. 2) was not considered by Marom and Rak.

5. **The morphology of the lower second molar:** Marom and Rak discussed the presence of taurodontism, but they ignored other morphological traits that would have led them to recognize the similarities between NR and Qesem Cave and Atapuerca SH teeth. The rationale behind the authors' choice to address selected characteristics while ignoring the comparison to the pre-Neanderthal populations remains unclear to us.

6. **The parietal:** Our interpretation of the NR *Homo* as a distinct paleodeme relied on detailed analyses of the parietals (10 text pages + 9 figures + 2 tables in the supplement alone) that unequivocally possessed an archaic morphology. There is no mention of the parietals in the comments made by Marom and Rak.

7. **Comparative sample:** Marom and Rak compared the NR mandible to a sample that, following their own taxonomic attribution of the specimens, consisted only of Neanderthals and *H. sapiens*. This approach necessarily forced their classification of the NR remains into a binary choice between *H. sapiens* or *H. neanderthalensis*. Worse than that, by grouping seven Atapuerca specimens into their Neanderthal sample (expressing their a priori assumption that SH are *H. neanderthalensis*), they created a circular reasoning that gives no choice but to classify NR as a Neanderthal.

8. **Use of estimated measurements and reconstructed anatomical structures:** Because the NR mandible is incomplete (Fig. 2A), Marom and Rak had to make several assumptions regarding the morphology, size, and position of some missing anatomical structures to obtain their measurements. As most of their "Neanderthal" mandibles lack anatomical regions of interest, we assume that similar assumptions were made for other specimens as well. We believe that the use of such tentative measurements requires caution. In particular, the authors described the NR condyle and the crest leading to it as Neanderthal-like. However, as shown in Fig. 2B, the condyle and its neck are missing in the NR mandible. Moreover, even if their free depiction of the NR condyle was correct, the morphology they described is not exclusive to Neanderthals; it can also be found in MP fossils. Their assessment of the retromolar size (Fig. 2C) is another example of their speculative approach, as the third molar is broken and its size was not correctly evaluated (Fig. 2C). Furthermore, the reconstruction of the occlusal plane is impossible given that the only incisor present is broken (or heavily eroded) but was nonetheless reported by Marom and Rak (Fig. 2A).

9. **Would Marom and Rak's reconstructions change our results?** To test this possibility, we carried out an analysis based on 3D landmark configurations of all mandibles, where we estimated the position of the condyle and coronoid of the NR mandible using four alternative reconstructions: the mean positions in African MP, European MP, SH, and Neanderthals. The principal components analysis clearly showed that regardless of the reconstruction used, the NR mandible always plotted within the SH range of distribution, rather than within the Neanderthal or other *Homo* clusters (Fig. 2D).

10. **Chronology:** To understate the importance of the NR *Homo* chronology, Marom and Rak wrote: "Only recently was the Tabun skeleton assigned to the younger layer B, a date change that fit the prevailing consensus that the Neanderthal's presence in the Middle East began much later, at 40 to 50 ka." This comment lacks basis because nowhere in our paper did we state that Tabun 1 is 40,000 to 50,000 years old; on the contrary, we stressed that it is much older [see supplement of (*1*)].

An exact taxonomic attribution of the NR fossils, if ever possible, was beyond the scope of our *Science* contribution (*1*), which instead examined these Levantine findings in a broader perspective and discussed their role in the MP human peopling of Europe and Asia (Fig. 1). Interestingly, even the SH *Homo*, which is clearly related to Neanderthals and was proven to be genetically close to them, has not been classified as Neanderthal (*11*).

Marom and Rak's comments support our major premise that NR is morphologically and thus phylogenetically related to the Neanderthals. As shown, however, we found flaws in the attribution of their comparative specimens as well as in the form and content of their methods. Marom and Rak's assessment of the NR fossils is limited by the exclusion of the parietals, which is pivotal for recognizing NR as a distinct paleodeme. Moreover, they interpreted their results in a conservative way without taking into account the wealth of data available and especially the complexity of human history. The comprehensive supplements attached to the main text (57 pages of evidence) should have been more carefully considered before formulating a critique of this kind. We analyzed the NR fossils comparatively, using descriptive and quantitative analyses of all aspects of the preserved structures to acquire the most thorough and accurate morphological and morphometric evaluation of the NR remains. Despite that, we are aware that the interpretation of the fossil evidence and the reconstruction of human evolution are challenging tasks. Therefore, we remain open-minded and welcome informed scientific debates on the NR paleodeme.

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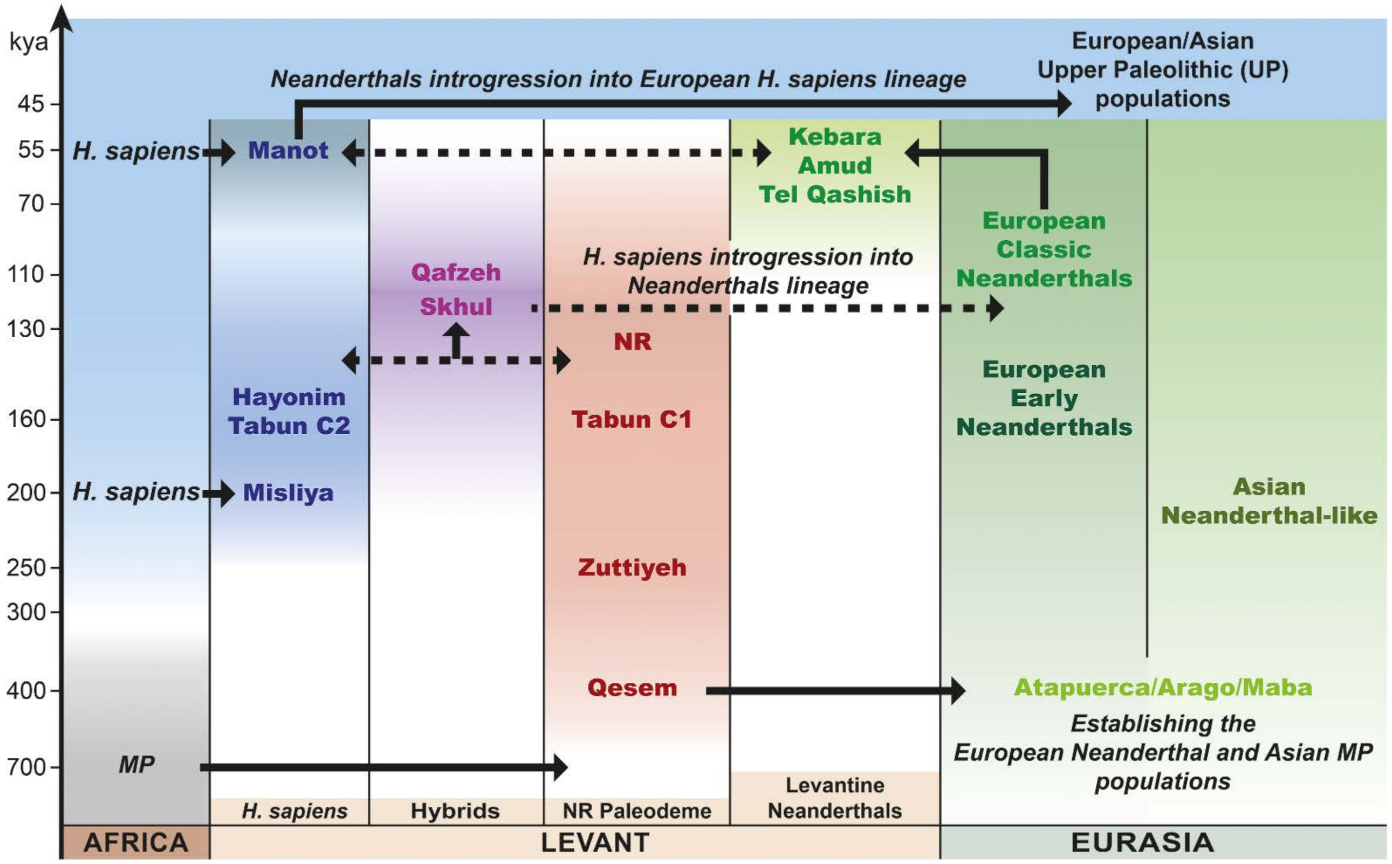

Fig. 1. The various Levantine Late Middle/Late Pleistocene *Homo* groups and their likely intra- and inter-relationships. This chart is based on the current and previous studies (*1*, *12*–*15*). The NR *Homo* group (red box) dominated the region throughout the Late Middle Pleistocene, migrated from the Levant to Eurasia to establish sister populations, and later interbred with *H. sapiens* that reached the Levant ~200,000 years ago. The chart emphasizes the dynamics of Middle/Late Pleistocene populations and the key role that Levantine populations played in human history. Color gradient indicates local evolution of *Homo* groups: red, NR; blue, *H. sapiens*; purple, hybrids between NR *Homo* group and *H. sapiens*; green, Eurasia MP and Neanderthal/Neanderthal-like populations. Solid arrows, migration; dashed arrows, introgression; kya, thousands of years ago.

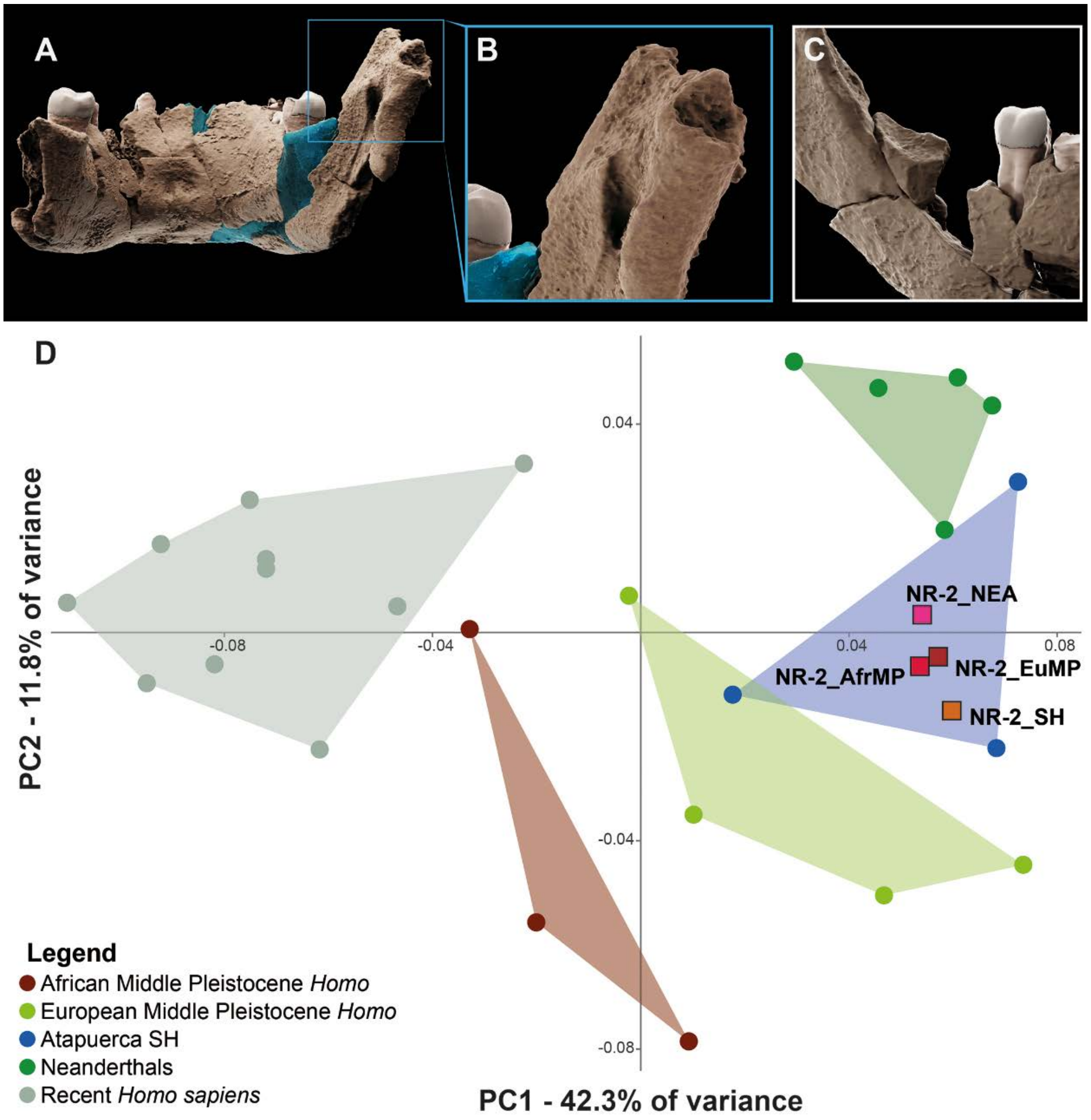

Fig. 2. Different views of the reconstructed NR mandible. (**A**) Posterior view showing eroded incisor. (**B**) Posteromedial view showing that the condyle is missing. (**C**) Anterolateral view of the molar region showing an inclined retromolar space and a missing M_3. (**D**) Principal components analysis plot in space shape for the mandibles. Analysis was carried out on specimens presenting intact condyle and coronoid (excluding NR). The shape of each mandible was represented by 15 landmarks. The position of the condyle and coronoid in the NR mandible was reconstructed using the mean position in each of the following archaic *Homo* groups: African MP (NR-2_AfrMP), European MP (NR-2_EuMP), Atapuerca SH (NR-2_SH), and Neanderthals (NR-2_NEA). The various *Homo* groups are separated along the PC1 and PC2 axes. Regardless of the reconstruction of the position of the coronoid and condyle, all NR reconstructions (squares) are plotted within the shape variation of the SH sample and outside the shape variation of other *Homo* groups. Brown, African MP; light green, European MP; blue, Atapuerca SH; green, Neanderthals; gray, recent *H. sapiens*.

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