Neanderthal taxonomy reconsidered: Implications of 3D primate models of intra- and interspecific differences

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The taxonomic status of Neanderthals lies at the center of the modern human origins debate. Proponents of the single-origin model often view this group as a distinct species with little or no contribution to the evolution of modern humans. Adherents to the regional continuity model consider Neanderthals a subspecies or population of *Homo sapiens*, which contributed significantly to the evolution of early modern Europeans. Paleontologists generally agree that fossil species should be equivalent to extant ones in the amount of their morphological variation. Recognition of fossil species therefore hinges on analogy to living species. A previous study by one of the authors and recent work by other researchers [Schillachi, M. A. & Froelich, J. W. (2001) *Am. J. Phys. Anthropol.* **115,** 157–166] have supported specific status for Neanderthals based on analogy to chimpanzees and Sulawesi macaques, respectively. However, these taxa may not be the most appropriate models for Pleistocene humans. Here we test the hypothesis that Neanderthals represent a subspecies of *H. sapiens* by comparing the degree of their morphological differentiation from modern humans to that found within and between 12 species of extant primates. The model taxa comprised >1,000 specimens, including phylogenetic (modern humans and African apes) and ecological (eight papionin taxa) models for Pleistocene humans. Morphological distances between model taxon pairs were compared to the distances between Neanderthals and modern humans obtained by using a randomization technique. Results strongly support a specific distinction for Neanderthals.

Ever since Neanderthals were first discovered in the 19th century, their specific status and contribution to modern human evolution have been debated. The current controversy centers around two contrasting models for modern human evolution (1, 2): the single-origin theory, which frequently views modern humans as a new species arising relatively recently in Africa and replacing indigenous archaic populations around the world; and the regional-continuity model, in which archaic populations contributed to the evolution of modern peoples in each geographic area. Directly tied to these two models is the status of Neanderthals as a distinct species or as a subspecies of *Homo sapiens* at least partially ancestral to modern Europeans. The morphological differences between Neanderthals and modern humans are well documented; however, their magnitude can be meaningfully assessed only within the broader context of primate species variability. Here we used 12 extant catarrhine species as models of 3D craniofacial shape variation. Our sample comprised 1,089 specimens, including modern humans, African apes, and eight species of Old World monkeys. The morphological distinctiveness of Neanderthals from modern humans, as represented by our data, was then compared to the differences between pairs of model taxa.

Although there is consensus that species in paleontology should be equivalent to living ones in the variation that they accommodate (3, 4), there is no absolute degree of difference that defines species boundaries across taxa (5), making the choice of models critical. Recent studies have supported a specific status for Neanderthals based on analogy to chimpanzee (6) and hybridizing Sulawesi macaque (7) craniofacial morphology. These models may not be the most relevant: chimpanzees differ in their geographic distribution and ecology from Pleistocene humans, whereas the Sulawesi macaques are not representative of the full geographic and ecological range of *Macaca*. Modern humans are the most appropriate phylogenetic model for Neanderthals but can provide only intraspecific measures of variation. As the closest living relatives to modern humans, the African apes are often used as models for hominin species (4, 8). Yet these two genera comprise only three species, all of which are ecologically distinct from Pleistocene humans. Papionin monkeys, although more distantly related, are often considered (9–11) similar to hominins in their ecology and population structure, and their evolution was likely shaped by the same Pleistocene environmental fluctuations believed to have influenced hominin evolution (12). This study included both the phylogenetically similar African apes and the ecologically analogous cercopithecines as models for the Neanderthal–modern human comparison.

Materials and Methods

All extant hominines were represented, comprising the two commonly recognized species of *Pan* and the three subspecies of *Pan troglodytes*, along with two subspecies of *Gorilla gorilla*. Papionins were represented by all six subspecies of *Papio hamadryas* (13), both species of *Mandrillus*, and five species of *Macaca* from three species groups (14, 15). All subspecies of *P. hamadryas* were included, because they show a large amount of within-species variation and are often thought to be analogous in this to Pleistocene hominins. Mandrills and drills were chosen because they are sister species. Our choice of macaques reflected their hierarchical variability: closely related hybridizing Sulawesi species *Macaca hecki* and *Macaca tonkeana*; within-species group, possibly hybridizing *Macaca fascicularis* and *Macaca mulatta*; and the more geographically and phylogenetically distinct *Macaca sylvanus*. The modern human comparative sample consisted of seven broadly defined geographic populations, representing much of the modern human distribution, as well as a North African Iberomaurusian sample. Most comprised subsamples of Howells' populations (16, 17), in some cases combined to represent samples at the continental level (6). The fossil sample included five Upper Paleolithic European and five Neanderthal specimens (Table 1).

3D coordinates of 15 standard craniofacial landmarks (Fig. 1) were collected with the MICROSCRIBE 3DX 3D digitizer

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Table 1. List of specimens by taxon and known and/or inferred sex

Group	Females	Males	Total
Neanderthals			
Guattari 1		1	
La Chapelle-aux-Saints		1	
La Ferrassie 1		1	
Amud 1		1	
Shanidar 1*		1	
Total		5	5
Upper Paleolithic Europeans			
Mladeč 1	1		
CroMagnon 1		1	
Predmostí 3*		1	
Predmostí 4*	1		
Abri Pataud 1	1		
Total	3	2	5
Modern humans			
Andamanese[†]	17	13	30
Africans (Khoisan, Dogon[†])	29	25	54
Australasian (New South Wales-South Australia, Tolai[†])	23	31	54
Greenland Inugsuk[†]	14	15	29
Western Eurasians (Austrian Berg[†], Israel, Dalmatia, Greece, Italy)	24	26	50
North African Iberomaurusian (Final Paloelithic, Afalou[†], Taforalt[†])	3	5	8
Total	110	115	225
African Apes			
Gorilla gorilla beringei	6	9	15
G. g. gorilla	30	39	69
Pan paniscus	28	21	49
P. troglodytes schweinfurthii	12	18	30
P. t. troglodytes	50	27	77
P. t. verus	12	10	22
Total	138	124	262
Old World Monkeys			
Macaca fascicularis	21	30	51
M. hecki	7	10	17
M. mulatta	12	11	23
M. sylvanus	10	10	20
M. tonkeana	11	9	20
Mandrillus leucophaeus	15	22	37
M. sphinx	12	19	31
Papio hamadryas anubis	43	96	139
P. h. cynocephalus	8	19	27
P. h. hamadryas	3	24	27
P. h. kindae	7	8	15
P. h. papio	1	10	11
P. h. ursinus	74	101	175
Total	224	369	593

*Specimens for which casts were used.
[†]Subsamples of Howells' populations.

(Immersion, San Jose, CA). Landmarks were selected to summarize overall cranial shape rather than anatomical detail. On the one hand, features known to distinguish Neanderthals from modern humans were avoided so as to not inflate the distance between them and because such differences may be irrelevant in comparisons among model taxa. On the other hand, landmarks around the canine region were avoided, because they are highly dimorphic in some model taxa but not in humans. Finally, the choice of landmarks was limited by the preservation of the fossils.

Data were collected by six observers, including the authors. Mean precision (measured as SD) was 0.03 cm for all 45 coordinates. Minimal reconstruction was allowed during data collection for specimens with minor damage through estimation of the position of the structure of interest by using the morphol-ogy of the preserved surrounding areas. Missing bilateral land-marks were estimated during data processing by reflection. Specimens with missing data were least-squares superimposed with their reflections, and the coordinates for each missing landmark were substituted from its fitted homologue. For fossil specimens, an additional level of reconstruction was permitted due to their fragmentary nature. Basion and opisthion were reconstructed for Guattari 1 and Amud 1 by using the mean position of these landmarks from the total Neanderthal sample. The zygomatic suture points for Predmostí 4 were reconstructed based on the configuration of Mladeč 1. These procedures allowed a greater number of fossils and landmarks to be included in the analysis.

Coordinate data were processed by using geometric morpho-metric techniques (18, 19). These methods preserve spatial
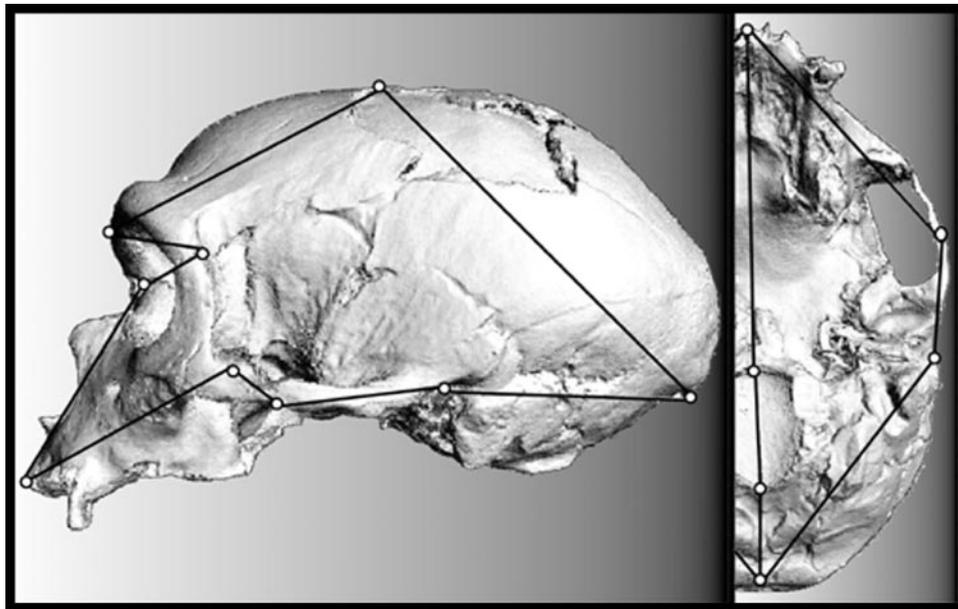
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Fig. 1. Landmarks (white dots) used in this study, as seen in lateral (*Left*) and ventral views (*Right*). Although only one side is shown, both were included for bilateral landmarks. (*Left*) Lateral view, counterclockwise from far right: inion, bregma, glabella, frontomalare temporale, nasion, prosthion, superior aspect of the temporozygomatic suture, inferior aspect of the temporozygomatic suture, and porion. (*Right*) Ventral view, counterclockwise from bottom: inion, opisthion, basion, prosthion, inferior aspect of the temporozygomatic suture, and porion. Lines do not represent data but are shown for the purposes of visualization.

relationships among landmarks and are therefore more powerful than traditional morphometrics in distinguishing among shape differences (20). Landmark configurations were superimposed by generalized Procrustes analysis by using the software TPS-SMALL (21). This procedure translates specimen configurations to a common origin, scales them to unit centroid size, and rotates them to best fit by using a least-squares criterion. The parametric squared Mahalanobis distance (D^2) was estimated from the superimposed data. This estimate of D^2 summarizes the morphological variation among populations (22). To simulate stochastic effects caused by the small Neanderthal sample of five specimens, a randomization test using equal sample sizes was used. D^2s were calculated based on a reduced sample of five specimens per population, chosen randomly. This procedure was repeated 10,000 times. The probability distributions obtained were used in one-tailed tests ($\alpha = 5\%$) of the hypothesis that the Neanderthal–modern human distance is not greater than the distances between pairs of related model taxa. The average of the mean D^2s between Neanderthals and each of the seven modern human populations (hereafter, NMD2) was used as an estimate of the morphological difference between the two hominins. The

smallest mean D^2 between Neanderthals and any of the modern human populations (CNMD2) was used as a second, more conservative estimate of this difference. If distances among model taxa were smaller than NMD2 or CNMD2 (i.e., the null-hypothesis is rejected), then a species rank for Neanderthals would be supported.

Results

Means and range statistics of D^2 between Neanderthals and modern human populations are shown in Table 2. Table 3 presents mean D^2s among model taxa. Intra- and interspecific pairwise comparisons relative to NMD2 are shown in Fig. 2, whereas the mean values are summarized in the cluster diagram of Fig. 3. It must be emphasized that Fig. 3 is a phenogram, rather than a phylogenetic tree; as such, it reflects morphological differences due not only to phylogeny but also to adaptation and other factors. Nonetheless, this diagram recovered all genera as clusters and all species as clusters of included subspecies or populations (even if specific and subspecific relationships do not always conform to prevailing views); African apes clustered with papionins because they are more similar to one another in the

Table 2. Mean and range statistics of D^2 between Neanderthals and modern human populations

Neanderthals to	Mean D^2	95th percentile	5th percentile
H. sapiens (African)	97.0559	131.8926	69.7917
H. sapiens (Andamanese)	128.3440	170.7854	94.8123
H. sapiens (Australasian)	101.4564	136.9099	73.7745
H. sapiens (Iberomaurusian)	132.6143	183.6187	94.5229
H. sapiens (W. Eurasian)	106.7007	143.8439	77.2229
H. sapiens (Inugsuk)	110.0157	149.7921	78.1660
H. sapiens (Upper Paleolithic)	92.0132*	119.2181	70.2604
Mean	109.7429†	148.0087	79.7930

*CNMD2.
†NMD2.

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Table 3. Mean D² between pairs of taxa and *P* values of the comparisons with NMD2 (109.7429) and CNMD2 (92.0132)

Taxon 1	Taxon 2	Mean D²	P < NMD2	P < CNMD2
Intraspecific comparisons				
H. sapiens (African)	*H. sapiens* (Andamanese)	39.3634	0.0008*	0.0034*
H. sapiens (African)	*H. sapiens* (Australasian)	36.3810	0.0001*	0.0008*
H. sapiens (African)	*H. sapiens* (Iberomaurusian)	52.0286	0.0042*	0.0229*
H. sapiens (African)	*H. sapiens* (Eurasian)	41.9322	0.0004*	0.0018*
H. sapiens (African)	*H. sapiens* (Inugsuk)	41.7882	0.0001*	0.0007*
H. sapiens (African)	*H. sapiens* (Upper Paleolithic)	44.9620	0.0009*	0.0033*
H. sapiens (Andamanese)	*H. sapiens* (Australasian)	44.4934	0.0002*	0.0007*
H. sapiens (Andamanese)	*H. sapiens* (Iberomaurusian)	46.6421	0.0002*	0.0042*
H. sapiens (Andamanese)	*H. sapiens* (Eurasian)	49.6895	0.0018*	0.0024*
H. sapiens (Andamanese)	*H. sapiens* (Inugsuk)	47.9740	0.0003*	0.0071*
H. sapiens (Andamanese)	*H. sapiens* (Upper Paleolithic)	67.1967	0.0057*	0.042*
H. sapiens (Australasian)	*H. sapiens* (Iberomaurusian)	51.4822	0.0015*	0.0126*
H. sapiens (Australasian)	*H. sapiens* (Eurasian)	47.8071	0.0009*	0.0066*
H. sapiens (Australasian)	*H. sapiens* (Inugsuk)	42.9549	0.0000*	0.0013*
H. sapiens (Australasian)	*H. sapiens* (Upper Paleolithic)	37.9880	0.0000*	0.0000*
H. sapiens (Iberomaurusian)	*H. sapiens* (Eurasian)	52.9945	0.0023*	0.0177*
H. sapiens (Iberomaurusian)	*H. sapiens* (Inugsuk)	55.9712	0.0021*	0.0179*
H. sapiens (Iberomaurusian)	*H. sapiens* (Upper Paleolithic)	64.2578	0.0022*	0.0225*
H. sapiens (Eurasian)	*H. sapiens* (Inugsuk)	44.9439	0.0005*	0.0042*
H. sapiens (Eurasian)	*H. sapiens* (Upper Paleolithic)	46.9205	0.0000*	0.0004*
H. sapiens (Inugsuk)	*H. sapiens* (Upper Paleolithic)	43.8637	0.0000*	0.0006*
G. g. gorilla	*G. g. beringei*	82.6833	0.1663	0.3364
P. t. schweinfurthii	*P. t. troglodytes*	39.9971	0.0000*	0.0005*
P. t. schweinfurthii	*P. t. verus*	38.2437	0.0000*	0.0012*
P. t. troglodytes	*P. t. verus*	43.1508	0.0003*	0.0016*
P. h. anubis	*P. h. cynocephalus*	30.8500	0.0000*	0.0000*
P. h. anubis	*P. h. hamadryas*	43.2651	0.0005*	0.0030*
P. h. anubis	*P. h. kindae*	59.7916	0.0069*	0.0351*
P. h. anubis	*P. h. papio*	38.0004	0.0000*	0.0002*
P. h. anubis	*P. h. ursinus*	39.4953	0.0000*	0.0006*
P. h. cynocephalus	*P. h. hamadryas*	49.5201	0.0004*	0.0033*
P. h. cynocephalus	*P. h. kindae*	50.6787	0.0014*	0.0108*
P. h. cynocephalus	*P. h. papio*	45.7100	0.0003*	0.0024*
P. h. cynocephalus	*P. h. ursinus*	29.7199	0.0000*	0.0001*
P. h. hamadryas	*P. h. kindae*	59.6932	0.0037*	0.0261*
P. h. hamadryas	*P. h. papio*	52.7494	0.0004*	0.0069*
P. h. hamadryas	*P. h. ursinus*	59.3571	0.0055*	0.0288*
P. h. kindae	*P. h. papio*	59.5886	0.0017*	0.0170*
P. h. kindae	*P. h. ursinus*	68.8428	0.0376*	0.1195
P. h. papio	*P. h. ursinus*	56.4546	0.0015*	0.0145*
Intrageneric specific comparisons				
P. paniscus	*P. t. schweinfurthii*	49.5878	0.0011*	0.0059*
P. paniscus	*P. t. troglodytes*	67.2973	0.0208*	0.0885
P. paniscus	*P. t. verus*	69.5734	0.0268*	0.1143
M. fascicularis	*M. hecki*	146.8860	0.8875	0.9807
M. fascicularis	*M. mulatta*	83.2139	0.1172	0.3011
M. fascicularis	*M. sylvanus*	46.1650	0.0005*	0.0043*
M. fascicularis	*M. tonkeana*	117.9832	0.5855	0.8492
M. hecki	*M. mulatta*	94.5357	0.2097	0.4985
M. hecki	*M. sylvanus*	155.9038	0.9502	0.9957
M. hecki	*M. tonkeana*	55.2513	0.0027*	0.0156*
M. mulatta	*M. sylvanus*	84.6489	0.1318	0.3303
M. mulatta	*M. tonkeana*	101.2535	0.3139	0.6238
M. sylvanus	*M. tonkeana*	118.2337	0.5882	0.8671
M. leucophaeus	*M. sphinx*	46.0753	0.0006*	0.0038

*, *P* values of 0.05 or less.

proportions of face to braincase, whereas humans are highly derived in this regard.

Thirty-nine of the 40 intraspecific comparisons were significantly smaller than NMD2 (109.74), the only exception being that between the two gorilla subspecies. Six of 14 interspecific comparisons within genera were also significantly smaller than NMD2, including all three distances between *Pan paniscus* and the *P. troglodytes* subspecies, the distance between the hybridizing *M. hecki* and *M. tonkeana* as well as the non-hybridizing *Macaca fascicularis* and *M. sylvanus*, and that between the two
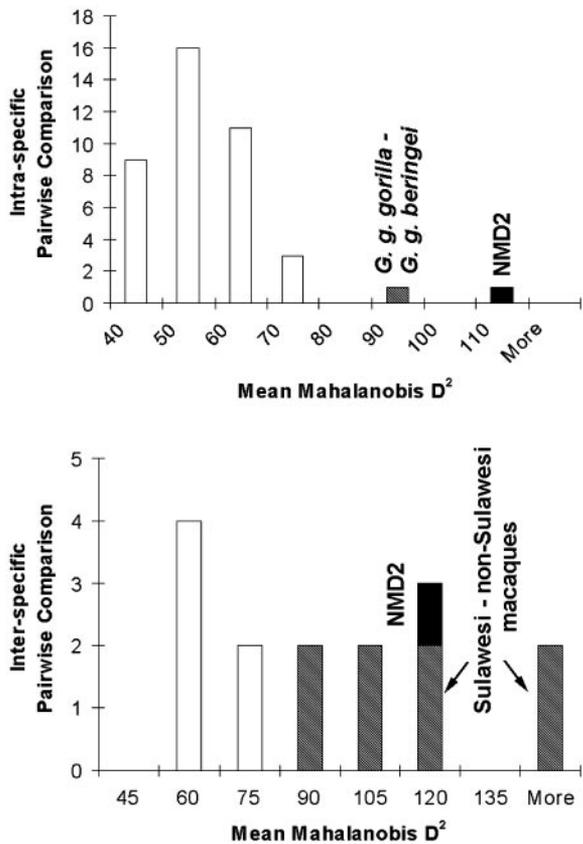
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Fig. 2. Mean D²s for intraspecific (*Upper*) and interspecific (*Lower*) pairwise comparisons between model groups. Open bins are significantly smaller than NMD2, shown in black. Hatched bins are not significantly smaller than NMD2.

species of *Mandrillus*. The eight remaining interspecific distances were those between the other macaque species. Of the intergeneric comparisons, five of the *Mandrillus sphinx–P. hamadryas* and two of the *M. leucophaeus–P. hamadryas* distances were significantly smaller.

As a more conservative measure, CNMD2 was used: Neanderthals–Upper Paleolithic Europeans (92.01). CNMD2 was very large relative to distances among modern human populations. It does not imply any similarity between Neanderthals and Upper Paleolithic Europeans to the exclusion of other modern human groups, as shown in Fig. 3. This distance was not statistically significantly different from the other distances between Neanderthals and modern humans and was very close to the second smallest distance (Neanderthals–Africans). Thirty-eight of the 40 infraspecific distances were significantly smaller than CNMD2. In addition to the gorilla subspecies comparison, only the distance between *P. h. kindae* and *P. h. ursinus*, the smallest and largest baboon subspecies, respectively, was not significantly smaller than CNMD2. Four of the within-genus interspecific comparisons were still significantly smaller than CNMD2 (*M. tonkeana–M. hecki*, *M. fascicularis–M. sylvanus*, *M. sphinx–M. leucophaeus*, and *P. paniscus–P. t. schweinfurthii*). Of the intergeneric comparisons, the distances between *M. sphinx* and four of the *P. hamadryas* subspecies were still significantly smaller.

Conclusion

These findings demonstrate that the choice of model taxa greatly affects species recognition in paleontology. An approach that examines alternative models is clearly warranted yet may yield contradictory results. Analysis of Neanderthal craniofacial shape demonstrated an unusually high level of morphological differentiation from modern humans, including the Upper Paleolithic European specimens, compared to subspecific differences in the 12 catarrhine models used here. Both the most appropriate phylogenetic (modern humans, *Pan*) and ecological (papionins) models supported distinction at the species level. Nevertheless, this support was not unequivocal. The mean morphological differentiation between subspecies of *G. gorilla* was not significantly smaller than the Neanderthal–modern human distances, as would have been expected if all subspecies distances were less than any interspecific distance. However, some overlap of such distances may be expected given normal patterns of variation. Moreover, Groves (23) considers these *Gorilla* taxa as separate species, in which case they would represent the lower end of the specific range of difference. Furthermore, one comparison in the
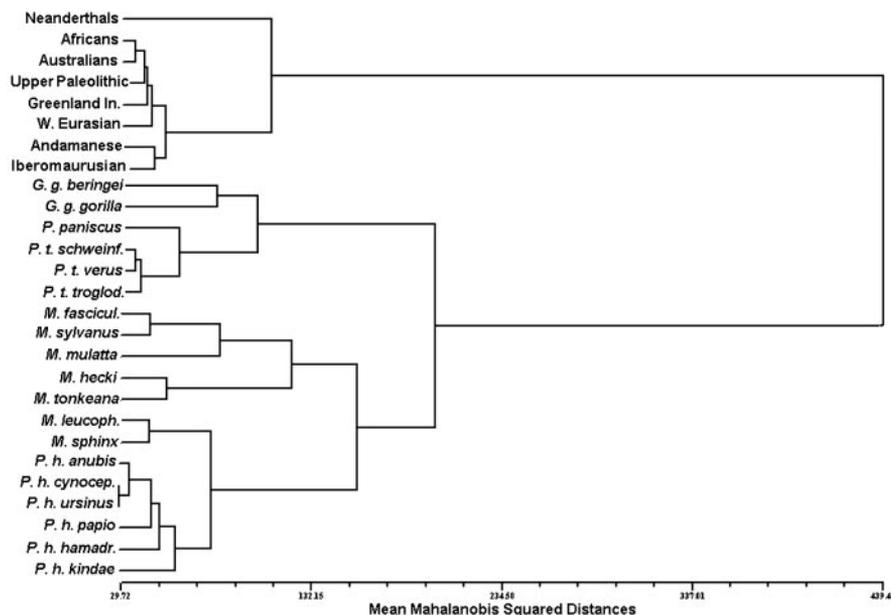

Fig. 3. Cluster diagram (unweighted pair-group method, arithmetic average) of studied populations based on the mean D² among samples.

baboon model (*P. h. kindae–P. h. ursinus*) did not support specific distinction of Neanderthals when the more conservative measure (CNMD2) was used. Although these results cannot completely rule out a subspecific designation for Neanderthals, specific status is strongly suggested by the total comparative evidence presented here. Taking these caveats into consideration, the morphological differentiation found between Neanderthals and modern humans relative to most of these 12 catarrhine species agrees with evidence from nonmetric traits (24, 25), other metric analyses (17, 26–29), ontogenetic (30), genetic (31–34), and archaeological (35) data pointing to the recognition of Neanderthals as a separate species.

The specific status of Neanderthals is important beyond taxonomic considerations due to its implications for modern human origins. Under the regional continuity model, Neanderthals are considered to be a subspecies of *H. sapiens* that contributed to the ancestry of at least the early modern Europeans. On the other hand, the recognition of Neanderthals as a species distinct from, but sympatric with, early modern humans strongly implies that they were not ancestral to any extant human populations, even if limited interbreeding occurred. The extreme morphological difference between Neanderthals and modern humans relative to subspecific differences among other catarrhines is not consistent with their subspecific designation, as postulated by the regional continuity model. Moreover, Neanderthal ancestry for the sympatric and roughly synchronic early

modern Europeans is also refuted: the morphological distance found between these two fossil groups was equivalent to those between Neanderthals and other modern human populations. We interpret the evidence presented here as supporting the view that Neanderthals represent an extinct human species and therefore refute the regional continuity model for Europe.

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