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Is The Late Neandertal Mandibular Sample from Vindija Cave (Croatia) Biased?

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A B S T R A C T

The late Neandertal sample from Vindija (Croatia) has been described as transitional between the earlier Central European Neandertals from Krapina (Croatia) and modern humans. However, the morphological differences indicating this transition may rather be the result of different sex and/or age compositions between the samples. This study tests the hypothesis that the metric differences between the Krapina and Vindija mandibular samples are due to sample bias. Mandibles are the focus of this paper because past studies have posited this region as particularly indicative of the Vindija sample's transitional nature. The results indicate that the metric differences between the Krapina and Vindija mandibular samples are not due to sample bias. This conclusion is consistent with an earlier analysis of sample bias for the Vindija supraorbital sample.

***Key words**: Vindija, Neandertal, Modern Human Origins, Human Evolution, Bootstrap, Resampling*

Introduction

The site of Vindija Cave is located in northwest Croatia and has yielded numerous fossil remains from the Paleolithic. The hominid fossils from Vindija Cave have played a crucial role in arguments concerning the fate of Neandertals and the origins of modern Europeans[1,2]. The majority of the Vindija discoveries span from 25–45 kya, which correlates with the disappearance of Neandertals and the Middle-Upper Paleolithic transition in Europe. Of particular interest are the Neandertal remains from level G_1, which date to ≈32–33 kya[3], making them some of the youngest Neandertals known.

Many of the anatomical features seen in the Vindija Cave Neandertals have been described as transitional between earlier Neandertals and early modern Europeans[1,4–9]. The intermediate nature of the Vindija hominids, when compared to the Krapina hominids and modern humans, has been argued as evidence for Neandertal – modern human conspecificity[2,5,10]. Some criticisms of the transitional nature of the Vindija hominids have stated that the intermediate appearance is due to sample bias, specifically an over-representation of females and/or young at the Vindija site[11,12]. Ahern et al.[8] have shown that sample bias cannot explain the transitional appearance of the Vindija supraorbital sample, yet other important elements have not been examined.

This paper metrically compares the Vindija mandibles with those from the earlier Neandertal Krapina sample and a sample of modern humans. Like the supraorbital region, the mandibular samples from Krapina and Vindija are represented by multiple individuals and the Vindija mandibles are reported to be more modern-like than those from Krapina[1,7]. Variables that place the Vindija mandibles as intermediate between the earlier Neandertals and modern humans are further analyzed for sample bias. The null hypothesis tested is that there is no difference between the populations represented by the Vindija and Krapina mandibular samples that cannot be attributed to sample bias.

Materials

Three samples of mandibles were used for the purpose of this paper: 1) the late Neandertals from Vindija Cave, Croatia, 2) the early Neandertals from Krapina Rockshelter, Croatia, and 3) a combined sample of recent modern humans. The first sample for this project came

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from Vindija Cave, Croatia, which is located approximately 55 km NNE of Zagreb. The site is located in an area of Croatia known as the Hrvatsko Zagorje. Only mandibular specimens from Vindija level G_3 were included in this study. This level dates to approximately 41,000 to 42,000+ years ago based upon radiocarbon[13] and U-Th[14] dates and sedimentary and faunal correlation with sites from the Moravian Karst[5]. Although the G_3 fossils are not the most recent Neandertals from Central Europe, they represent some of the last Neandertals present before the appearance of the Upper Paleolithic in the region. Preservation of the five Vindija mandibles ranges from a symphyseal fragment (Vi 306) to a mandible that preserved all of the ramus and corpus of one side with a portion of the anterior corpus of the other side (Vi 226).

Since this paper deals with the position of the Vindija specimens in relation to the earlier Neandertals from Krapina and anatomically modern humans, appropriate samples representing these groups were taken. The early Neandertal sample is composed of the six adult mandibles (Table 1) from the Croatian site of Krapina. The Krapina specimens were excavated between 1899 and 1905 by Dragutin Gorjanović-Kramberger[15,16] and have been described in detail by Smith[17] and Radovčić et al.[18]. Preservation of the specimens ranged from a nearly complete mandible (Kr 59) to a fragment preserving the corpus from the mesial wall of the right canine to most of the left M_2 socket (Kr 56). The modern human comparative sample comprised mandibles from Native Americans (n = 21), Northwest Plains frontier Euroamericans (n = 16), and Bronze Age Bosnians (n = 12).

Methods

The twenty-two variables used in this study are listed in Table 2. Measurements of the ramus were not included since only one of the symphysis-preserving Vindija specimens (Vi 226) preserves this area. All linear measurements were taken using standard vernier calipers. The symphyseal angle was measured from digital *norma lateralis* images using ImageJ v1.28. Although both sides of a bilateral variable were recorded, preference was given to the left dimension.

Three types of thickness measurements were made. These are maximum corpus thickness, basal corpus thickness, and alveolar corpus thickness. Both the maximum and basal thickness variables were made holding the caliper parallel to the occlusal plane. On the other hand, alveolar thickness measurements were made with the caliper positioned perpendicular to the inclination of the alveolus. Only at the levels of the mental tubercle and the medial symphysis did this positioning deviate from the occlusal plane. At these points on many specimens, the alveolus sloped in a manner that deviated from a perpendicular to the occlusal plane. Maximum corpus thickness measurements were taken at the level of the dental junctures. For example, maximum corpus thickness at M_1 (variable #1, Table 2) was actually taken at the level of the P_4/M_1 septum.

Measurements of mandibular corpus height and length were also made. Corpus height was measured as the maximum height of the corpus at a given point, with the caliper held perpendicular to the occlusal plane. For example, corpus height at the medial symphysis (#11 CpHtS, Table 2) is taken from the alveolar margin between the I_1 sockets to the basal margin below pogonion. All of the length variables measure the projection of symphyseal points in relation to given posterior points. Pogonion (#17 PogProj, Table 2) and infradental (#18 InfProj, Table 2) projections use a plane perpendicular to the occlusal plane at the level of the right and left P_4/M_1 septi. For complete specimens, this was accomplished by running a string between the septi and by holding the caliper in the occlusal plane. Half specimens were held in the occlusal plane over graph paper while pogonion or infradental and the posterior points were marked on the paper. The dimension was measured from the markings.

The fourth broad category of measurements are those of the symphyseal region. This group can be further subdivided into three groups. These are: 1) trigonal dimensions (#21 MTrHt and #22 MTrBr, Table 2), 2) the symphyseal angle (#23 SanOcc, Table 2), and 3) digastric fossa dimensions (#27 DiFLn and #28 DiFBr, Table 2). All of these variables are described in Table 2. Measure-

TABLE 1
SAMPLES

Sample	Specimens	Institution
Early Neandertals	n = 6	Hrvatski prirodoslovni muzej (Zagreb)
Krapina[1]	n = 6	
Late Neandertals	n = 5	Zavod za geologiju i paleontologiju kvartara (Zagreb)
Vindija[2]	n = 5	
Recent Modern Humans	n = 49	Logan Museum of Anthropology (Beloit, U.S.A.)
Native American	n = 21	
N.W. Plains Euroamerican	n = 16	University of Wyoming (Laramie, U.S.A.)
Bosnian Bronze Age	n = 12	Hrvatski prirodoslovni muzej (Zagreb)

[1] Kr 54, 55, 56, 57, 58, 59
[2] Vi 206, 226, 231, 250, 306

TABLE 2
METRIC VARIABLES OF THE MANDIBLES

Measurement Number	Description	Abbreviation
1	Maximum corpus thickness at M_1	CpThM1
2	Maximum corpus thickness at C	CpThC
3	Maximum corpus thickness at I_2	CpThI2
4	Maximum corpus thickness at symphysis	CpThS
5	Alveolar thickness at med. symphysis	AlthMS
6	Alveolar thickness at mental tubercle	AlthMT
7	Basal thickness at symphysis	BsThS
8	Basal thickness at mental tubercle	BsThMT
9	Basal thickness at M_3	BsThM3
10	Alveolar thickness at M_3	AlThM3
11	Corpus height at medial symphysis	CpHtS
12	Corpus height at mental tubercle	CpHtMT
13	Corpus height at M_1/M_2	CpHtM1–2
14	Corpus height at I_2/C	CpHtI2-C
15	Corpus height at I_1/I_2	CpHtI1–2
16	Distance from mylohyoid line to alveolar border at the level of P_4/M_1	MhAlvP4M1
17	Pogonion projection: distance from a coronal plane intersecting left and right P_4/M_1 septum to pogonion	PogProj
18	Infradental projection: distance from coronal plane described for measurement 17 to infradental	InfProj
19	Distance from mental foramen to pogonion	MfPog
20	Superior margin of mental foramen to alveolar margin	MfAlvHt
21	Mental trigon height: distance from apex of trigon to basal margin at medial symphysis	MTrHt
22	Mental trigon breadth: distance between left and right mental tubercles	MtrBr
23	Symphyseal angle from the occlusal plane: angle formed between the occlusal plane and a line intersecting pogonion and infradental	SanOcc
24	Symphyseal angle from the basal plane: angle formed between the basal plane and a line intersecting pogonion and infradental	SanBas
25	Distance from supraspinous foramen to internal infradental	SspFiId
26	Distance from supraspinous foramen to interdigastric spine	SspIdsp
27	Digastric fossa length (mesiodistal)	DiFLn
28	Digastric fossa breadth (anteroposterior)	DiFBr
29	Internal symphyseal angle from occlusal plane: angle formed between the occlusal plane and the inclination of the planum alveolare	IsanOcc
30	Internal symphyseal angle from basal plane: angle formed between basal plane and the inclination of the planum alveolare	IsanBas
31	Retrolmolar Space	RmSp
32	Condylar breadth	CondBr
I9	Pogonion Projection Index: Infradental Projection (InfProj) ÷ Pogonion Projection (PogProj)	PPI

Measurements Number after Ahern and Smith

ment of the symphyseal angle in this study was made in relation to the occlusal plane, since the variable shape of the basal margin makes the use of the basal plane questionable.

The statistical analysis of this project consisted of two steps: 1) univariate tests of difference among the samples and 2) resampling simulation analysis of sample bias. Before sample bias can be addressed, the variables that significantly demonstrate the intermediacy of the Vindija mandibles in between Krapina and modern humans must be separated from those that do not. One-way analysis of variance (ANOVA) tests were used to test the null hypothesis of no difference among the three samples for each variable. Tukey-Kramer Multiple Comparisons tests were also used to test hypotheses of no-difference for each paired comparison for each variable. Variables for which the Vindija sample was significantly different from the Krapina sample and either not significantly different from the modern sample or signifantly different from the modern sample but intermediate between Krapina and the moderns were determined to be „intermediate« variables. These intermediate variables were selected for analysis of sample bias.

The argument that the differences between the Krapina and Vindija mandibular samples are due to sample bias can be stated as a testable hypotheses: both the Krapina and Vindija samples are examples of the same population. To test this hypothesis, we used a method that generated a normally distributed population, followed by resampling of a portion of this distribution to determine the probability that the observed metric differences can be explained by sample bias. Our method assumes that (1) age variation and sexual dimorphism are patterned in the same way (e.g., a female biased sample cannot be distinguished from a young-based population) and (2) all of the variables that we analyzed vary in some degree with sex and/or age. These assumptions are not »real-world« occurrences, but we make these assumptions to further support the null hypothesis and reduce the chance of Type I error in this analysis. The criticism of the transitional nature of the Vindija population is based upon the argument that the Vindija sample has an over-representation of females and/or young[11,12]. If we assume that a population consists of both old and young as well as an equal number of males and females, we could posit that half of the variation for a given trait would relate to females and young. With the assumption that males are generally larger than females, and that old individuals are generally larger than young individuals, the criticism from Bräuer[11] that the Vindija sample is from the smaller half of the population. If Krapina is assumed to be the random sample of a population, than this hypothesis states that Vindija could be equated to the lower half of the Krapina population.

As previously stated, our hypothesis assumes that all variables measured vary with age and/or sex. If this is not the case, then a female/ young population would not differ from an average population, and the differences between the Krapina and Vindija populations could not be explained as sample bias. We also assume that there is no overlap between old/male traits and young/female traits. This, again, is unrealistic, yet it further supports the null hypothesis by presuming that no old/male individuals would fall into the lower half of the distribution.

There are four types of sample bias that could explain the variation seen between the Krapina and Vindija samples (Figure 1). (1) The Krapina sample is normally distributed while the Vindija sample has an over-representation of young/females [Figure 1(b)]. (2) Both the Krapina and Vindija sample have an over-representation of young females, with the Vindija sample being more marked [Figure 1(c)]. (3) The Krapina sample has an over-representation of old/males, while the Vindija sample has an over-representation of young/ females [Figure 1(d)]. (4) The Krapina sample has an over representation of old/males, while the Vindija sample is normally distributed [Figure 1(e)].

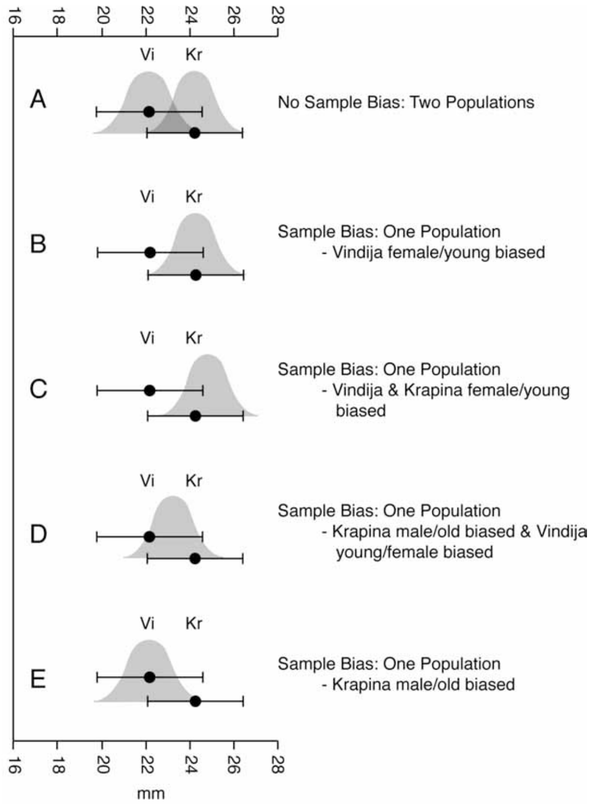

Fig. 1. Possible Cases of Sample Bias. From Ahern et al.[8]. Vi = Vindija Sample, Kr = Krapina Sample.

The first three scenarios are consistent with arguments of possible sample bias in the Vindija sample. The fourth scenario, while possible, is not likely as it would indicate that Neandertals shared many more similarities with Upper Paleolithic humans than has been previously posited. However, in order to disprove the null hypothesis, we must disprove all four scenarios indicated in Figure 1(b–e). For this analysis, we used three variant bootstraps: (1) a Krapina-based population, (2) a Vindija-based population, and (3) and intermediate population (see Table 3). The resampling procedure is that used by Ahern et al.[8]. The basic method comprises 1) drawing 10,000 samples of n = Vindija n (scenarios 1 & 2) or of n = Krapina n (scenario 3) from subsets of a simulated poulation based upon the criteria given in Table 3 and then 2) calculating the proportion of samples that have means smaller than the Vindija sample (scenarios 1 & 2) or larger than the Krapina sample (scenario 3).

Bootstrap scenario (1) tests the hypothesis that the Vindija sample has an over-representation of young/females while the Krapina sample is normally distributed or also an over-representation of young/females [see Fig-

TABLE 3
BOOTSTRAP SCENARIOS

Scenario	Basis for Simulated Population	Resampling Procedure
1. Krapina-based Sample	Krapina mean & *s*	Draw from lower half of simulated population
2. Intermediate-based Sample	Average of Vindija and Krapina mean and *s*	Draw from lower half of simulated population
3. Vindija-based Sample	Vindija mean and *s*	Draw from upper half of simulated population

TABLE 4
ANOVA AND TUKEY-KRAMER RESULTS FOR INTERMEDIATE VARIABLES

Variable	Anova Results		Tukey-Kramer Results		
	F	*p*	Kr. vs. Vi. *p*	Vi. vs. M. *p*	Kr. vs. M. *p*
2 – Maximum Corpus Thickness at C	8.593	<0.001	ns	ns	<0.01
6 – Alveolar Thickness at Mental Tubercle	23.398	<0.001	<0.05	<0.05	<0.001
10 – Alveolar Thickness at M_3	38.173	<0.001	<0.001	ns	<0.001
17 – Pogonion Projection	6.558	0.003	ns	ns	<0.01
18 – Infradental Projection	10.175	<0.001	<0.05	ns	<0.001
23 – Symphseal Angle	13.106	<0.001	ns	ns	<0.001
25 – Supraspinous foramen to internal Infradental	6.654	0.003	<0.01	ns	<0.01
27 – Digastric Fossa Mesiodistal Length	15.353	<0.001	<0.01	ns	<0.001
I9 – Pogonion Projection Index	32.928	<0.001	<0.01	ns	<0.001

ure 1(b) and 1(c)]. This scenario, referred to as the žKrapina-based population' simulation, refers to the scenario of a normally distributed sample based on the Krapina mean and standard deviation for each variable. From this normally distributed population, we measured the probability of drawing a measurement from the lower half of the simulated population.

Bootstrap scenario (2) tests the hypothesis that the Vindija sample has an over-representation of young/females while the Krapina sample has an over-representation of old/males [see Figure 1(d)]. This scenario will be called the žIntermediate-based Sample' and will refer to the scenario of a normally distributed sample based on an average of the Krapina and Vindija means and standard deviations for each variable. From this normally distributed population, we measured the probability of drawing a measurement from the lower half of the simulated population.

Bootstrap scenario (3) tests the hypothesis that the Krapina sample has an over-representation old/males [see Figure 1(e)]. This scenario will be referred to as the žVindija-based Sample' and will refer to the scenario of a normally distributed population based on the Vindija mean and standard deviation for each variable. From this normally distributed population, we measure the probability of drawing a measurement from the upper half of the simulated population. All three of the simulated scenarios can be seen in Table 3.

Results

Summary statistics for all of the measurements are given in Table 5. ANOVA and Tukey-Kramer multiple comparison tests were used to test the null hypotheses of no difference between the Vindija and Krapina samples and between the Vindija and modern human samples. Significant results of these analyses are given in Table 4 and the sample means and two standard deviations for the significant variables are plotted in Figures 2–4. Eight variables (seven chords and one index), for which the Vindija sample fell intermediate between the Krapina and modern samples (significantly different from both), or was not significantly different from the modern sample while the Krapina sample was, were regarded as intermediate variables. Only these variables were analyzed for sample bias.

Bootstrap Scenario 1 (Figure 5). For five of the nine intermediate variables, the probability that the Vindija sample represents a young/female biased subset of a

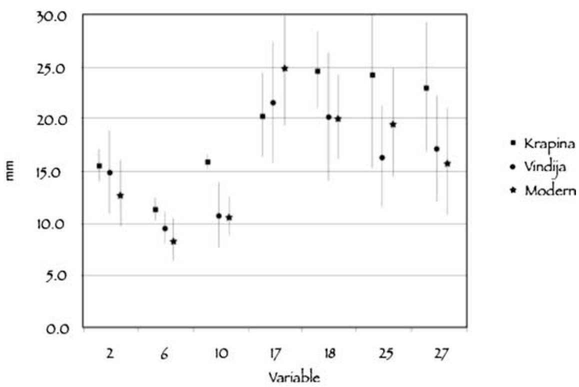

Fig. 2. Plot of sample means and two standard deviations for significant intermediate chord variables.

TABLE 5
SUMMARY STATISTICS

SUMMARY STATISTICS – SIGNIFICANT VARIABLES

Measure-ment	Krapina			Vindija			Modern Humans		
	n	mean	St. Dev.	n	mean	St. Dev.	n	mean	St. Dev.
2	6	15.78	1.18	4	14.74	1.971	32	12.73	1.860
6	5	11.51	0.84	4	9.48	0.749	43	7.99	1.182
10	3	16.40	0.53	4	14.28	5.556	42	10.68	1.066
17	6	20.72	3.13	4	21.53	2.891	43	25.22	3.347
18	6	24.79	2.86	4	20.11	3.035	43	20.02	2.326
23	5	110.73	3.39	4	99.50	5.916	42	88.16	10.541
25	5	24.13	7.15	4	16.31	2.400	43	19.43	3.038
27	6	23.63	4.88	4	17.06	2.511	45	15.99	2.957
I9	7	1.20	0.12	4	0.95	0.173	43	0.80	0.116

SUMMARY STATISTICS – OVERALL

Measure-ment	Krapina			Vindija			Modern Humans		
	n	mean	St. Dev.	n	mean	St. Dev.	n	mean	St. Dev.
1	5	15.74	3.967	4	16.55	2.066	45	14.49	3.807
2	6	15.78	3.972	4	14.74	1.971	32	12.73	3.568
3	6	14.73	3.838	4	14.56	1.858	33	13.01	3.606
4	6	14.79	3.845	4	14.90	1.445	46	15.39	3.923
5	5	10.12	3.181	4	9.16	0.183	41	5.88	2.426
6	5	11.51	3.392	4	9.48	0.749	43	7.99	2.827
7	6	14.26	3.776	3	15.09	1.272	44	15.09	3.884
8	6	14.97	3.869	4	14.30	1.788	46	13.71	3.703
9	3	10.23	3.198	4	11.05	1.440	43	8.97	2.995
10	3	16.40	4.050	4	14.28	5.556	42	10.68	3.268
11	4	37.06	6.088	4	31.38	3.338	40	33.29	5.770
12	6	33.47	5.785	4	30.45	3.249	42	32.79	5.726
13	4	30.54	5.526	3	30.04	3.371	45	29.50	5.431
14	6	32.89	5.735	4	30.44	3.161	42	33.00	5.744
15	5	34.89	5.907	4	30.79	2.951	41	33.55	5.792
16	6	21.46	4.633	3	22.36	3.329	43	16.17	4.022
17	6	20.72	4.552	4	21.53	2.891	43	25.22	5.022
18	6	24.79	4.979	4	20.11	3.035	43	20.02	4.475
19	6	33.84	5.817	3	33.06	1.319	46	28.76	5.362
20	6	17.58	4.193	3	12.79	1.899	48	15.84	3.980
21	5	19.18	4.379	4	18.29	1.978	45	20.74	4.554
22	5	24.80	4.980	2	20.68	3.217	42	22.65	4.759
23	5	110.73	10.523	4	99.50	5.916	42	88.16	9.389
24	5	100.30	10.015	4	96.75	6.461	44	70.43	8.392
25	5	24.13	4.912	4	16.31	2.400	43	19.43	4.407
26	6	19.00	4.359	3	17.12	1.229	46	16.29	4.037
27	6	23.63	4.861	4	17.06	2.511	45	15.99	3.998
28	6	8.95	2.991	3	7.82	1.075	45	7.78	2.789
29	4	125.00	11.180	2	124.00	2.121	18	110.06	10.491
30	4	118.63	10.892	2	115.50	0.707	18	98.58	9.929
31	7	4.76	2.183	5	3.74	1.447	41	0.38	0.617
32	7	24.21	4.921	1	21.30	–	36	21.08	4.591
I1	4	0.94	0.048	4	0.97	0.034	24	0.97	0.047
I2	4	0.83	0.111	3	0.95	0.012	24	0.90	0.043
I3	4	0.53	0.110	3	0.56	0.064	27	0.49	0.047
I4	4	0.42	0.067	4	0.48	0.027	25	0.44	0.048
I5	5	0.68	0.076	4	0.62	0.061	26	0.39	0.059
I6	5	0.75	0.070	4	0.67	0.078	26	0.66	0.132
I7	2	1.73	0.091	4	1.30	0.458	28	1.39	0.426
I8	5	0.56	0.064	3	0.48	0.029	27	0.56	0.042
I9	7	1.20	0.121	4	0.95	0.173	28	0.85	0.107

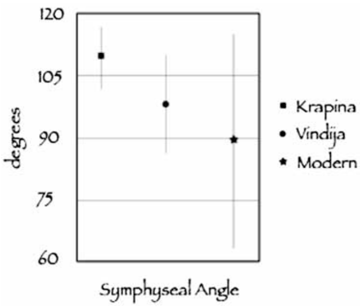

Fig. 3. Plot of the sample means and two standard deviations for the significant intermediate variable symphyseal angle (#23).

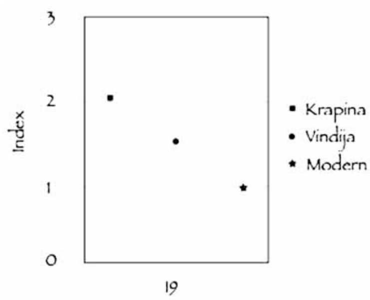

Fig. 4. Plot of the sample means and two standard deviations for the significant intermediate variable pogonion projection index (#I9).

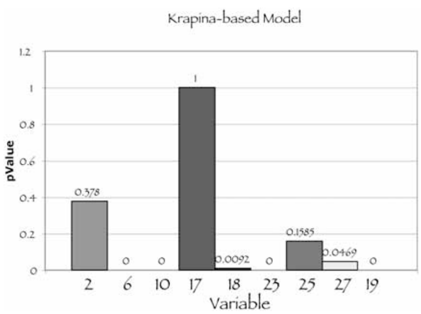

Fig. 5. Analysis of sample bias results: Scenario 1. P Values given in the plot are the proportion of 10,000 random, n = Vindija n samples with a mean less than the observed Vindija mean. For each variable, the 10,000 samples are drawn from the lower half a simulated population based upon the Krapina sample's mean and standard deviation.

Krapina-based population is less than 0.02 (Figure 5). In other words, random, n = Vindija n, samples with means less than the observed Vindija sample were drawn less than 200 times out of 10,000 attempts from the simulated Krapina population. Such sample bias is also an unlikely explanation for Vindija's digastric fossa length (#27) intermediacy with only 4.7% of the random samples exhibiting means smaller than the observed Vindija mean being drawn from the simulated Krapina population. On the other hand, Vindija's intermediacy for three of the variables (#2, #17, and #25) could possibly be explained by young/female sample bias.

Bootstrap Scenario 2 (Figure 6). Only Vindija's intermediacy for one variable (#10) is not likely due to sample bias of the sort where Vindija is young/female biased while Krpaina is old/male biased. Analysis of sample bias using an intermediate-based population yielded probabilities higher than 0.10 for six of the remaining eight variables and higher than 0.05 for variables #6 and #23.

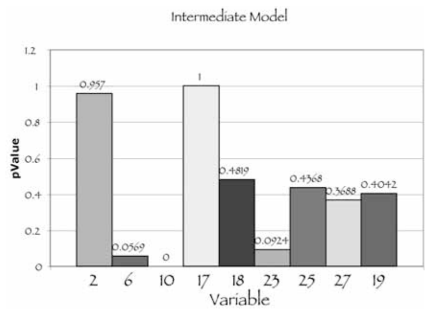

Fig. 6. Analysis of sample bias results: Scenario 2. P Values given in the plot are the proportion of 10,000 random, n = Vindija n samples with a mean less than the observed Vindija mean. For each variable, the 10,000 samples are drawn from the lower half of a simulated population based upon an average of Vindijažs and Krapina's means and standard deviations.

Bootstrap Scenario 3 (Figure 7). A scenario where Krapina is male/old biased while Vindija is not biased is the most improbable of the three possibilities tested in this paper. While analysis of this scenario yieled high probabilities for two of the variables (#2 and #17), the remaining seven variables yielded probabilities of less than 0.004.

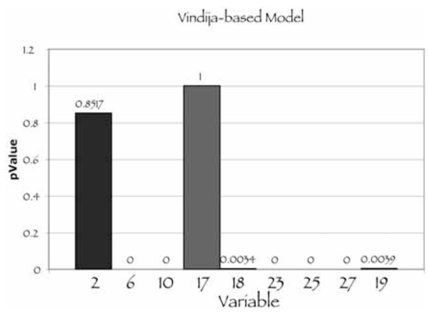

Fig. 7. Analysis of sample bias results: Scenario 3. P Values given in the plot are the proportion of 10,000 random, n = Krapina n samples with a mean greater than the observed Krapina mean. For each variable, the 10,000 samples are drawn from the upper half of a simulated population based upon Vindijažs mean and standard deviation.

Discussion and Conclusion

The results of this study show that the intermediate appearance of the Vindija mandibular sample can only be attributed to sample bias under the extreme scenario where Vindija is young/female biased while Krapina is old/male biased. However, previous analyses[8,17,19,20] of the age and sex compositions of the Krapina sample indicate that it likely contains an overrepresentation of females and young. Given this, even bootstrap scenario 3, where Krapina is assumed to be unbiased, likely overestimates the probability that sample bias could explain the Krapina – Vindija differences. Thus, this analysis undermines the argument made by Bräuer[11] and Stringer and Bräuer[12] that the transitional appearance of the Vindija specimens is a result of sample bias. Coupled with past studies of sample bias in the Vindija sample[8,9,20], the transitional appearance of the Vindija cave Neandertals cannot be explained solely as sample bias.

One possibility for the anatomical intermediacy of the Vindija hominids is that Neandertals were changing in response to selection acting on gene flow from cospecific hominids outside of western Eurasia[1,21,22]. Although we tentatively concure with this scenario, it is also possible that the similarities between Vindija sample and modern humans are homoplasic. Under this latter scenario, the similarities between Vindija and modern humans could possibily be due to similar selection acting on different hominid species. Additionally, all but one (I9) of the variables reflect size rather than shape. Thus is is possible that the Vindija Neandertals were smaller in their mandibular dimensions and this, superficially, makes them resemble modern humans. While this study does not prove genetic contribution from Neandertals to modern human population in Europe, it does rule out one possible explanation for the transitional appearance of the Vindija late Neandertal sample.

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