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WHO WERE THE NATUFIANS? A DENTAL ASSESSMENT OF THEIR BIOLOGICAL COHERENCY

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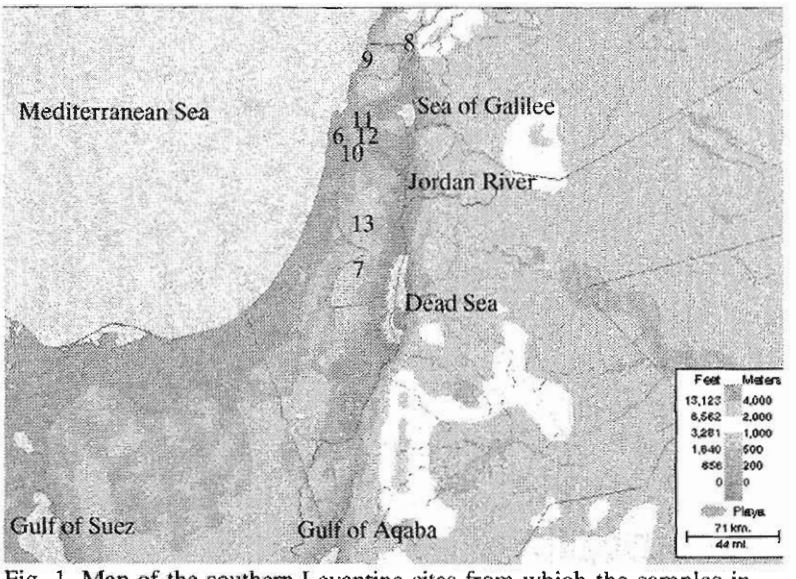

Fig. 1. Map of the southern Levantine sites from which the samples in this study originated. Key: 6-El-Wad, 7-Erq el-Ahmar, 8-Eynan, 9-Hayonim Cave and Terrace, 10-Kebara, 11-Nahal Oren, 12-Rakefet, 13-Shukba.

ABSTRACT The Natufians were complex, semi-sedentary hunter-gatherers who intensively exploited wild plant resources in the southern Levant 12,800 to 10,200 BP. They represent the human culturo-behavioral transition from simple, mobile hunter-gathers to fully sedentary agriculturalists. The Natufians have been the subject of much archaeological and biological study because of their pivotal position in human prehistory. Previous studies of Natufian population biology, which employed osteometrics, craniometrics, and odontometrics, qualitatively supported the following archaeologically-defined hypothesis. Every human skeletal sample found at each Natufian site belonged to a biologically coherent population.

The present study tests the hypothesis of Natufian biological coherency by analyzing their dental morphology. The data were collected from nearly all available Natufian dental material, using the Arizona State University Dental Anthropology System. The results of the multivariate Mean Measure of Divergence statistical analysis support the biological coherency of the Natufian population.

INTRODUCTION

The Natufian techno-complex (C_{14}-dated between 12,800 and 10,200 BP) (Henry, 1989) represents an unprecedented change in the human lifestyle in the southern Levant from highly mobile, simple hunting and gathering to semi-sedentary, complex hunting and gathering. The transition likely involved the movement of people to new areas, as well as the fusion of more numerous, smaller, and more mobile groups (from the period preceding the Natufian) into less numerous, larger, and more sedentary groups (in the Natufian). Therefore, this period in the

TABLE 1. Natufian dental samples.

Sample Site Name	Date BP[1]	N[2]	Facility
El-Wad	11,920	90	HVD
Erq el-Ahmar	12,800-10,500	3	TAU
Eynan	11,500	14	TAU
Hayonim Cave	12,175	90	TAU
Hayonim Terrace	11,920	12	TAU
Kebara	11,150	26	HVD
Nahal Oren	10,046	44	TAU
Rakefet	10,780	8	TAU
Shukba	12,800-10,500	4	HVD

[1]Dates are based on either published absolute dates (Bar-Yosef, 1980; Henry, 1989; Hovers and Marder, 1991) or archaeologically derived dates.
[2]Sample size estimates are based on the number of individuals dentally represented. HVD is the Peabody Museum, Harvard University. TAU is the Department of Anatomy and Anthropology, Tel Aviv University.

southern Levant may well have involved some momentous changes in human population relationships.

The Natufians have been hypothesized to represent a coherent archaeological entity and biological population (Vallois, 1936; Smith, 1970; Bar-Yosef et al., 1971-72; Arensberg, 1973; Bar-Yosef, 1981; Henry, 1989; Bar-Yosef and Belfer-Cohen, 1989; Belfer-Cohen, 1991). That is, as classified on the basis of archaeological and biological criteria, the Natufians represent a natural and logical grouping. According to biological analyses, the Natufians were not an amalgam of individuals from various contemporaneous, but biologically distinct populations.

Jolly and White (1995; p.52) define a Mendelian population as, ". . . a group of organisms whose members are *more likely* (their italics) to mate with each other than with outsiders." They also note that large Mendelian populations can include smaller ones that exchange genes by interbreeding.

The present study will classify the Natufians, if and where appropriate, as a biologically coherent population. Members of this population were more likely to mate with each other than with non-Natufians, and were comprised of smaller populations among whom interbreeding occurred. Given the state of biological classification today, this may most accurately classify the Natufians and explain how they have been viewed by the scholars who have studied them.

The present study tests the hypothesis of the Natufian population's biological coherency by quantifying the dental relationships between the skeletal samples from Natufian sites.

MATERIALS AND METHODS

The samples (Table 1, Fig. 1) are comprised of nearly all the Natufian dentitions currently available. The Natufian data for this study come from Lipschultz (1996). Data collection followed the standard method described by Turner et al. (1991), using the dental trait, ranked-scale plaster plaques and definitions of the Arizona State University Dental Anthropology System (ASU DAS), for scoring the dental morphology of the adult human dentition. Data were collected for all 42 scoreable dental traits of the ASU DAS.

STATISTICAL ANALYSIS

C.A.B. Smith's multivariate Mean Measure of Divergence (MMD) statistic, employing the Freeman and Tukey angular transformation (Berry and Berry, 1967; Sjovold, 1973; Green and Suchey, 1976) to correct for small sample sizes, was used. The MMD statistic offers a quantitative measure of biological divergence between samples, based on the degree of phenetic similarity for the entire suite of dental traits. A higher MMD value indicates a greater degree of phenetic dissimilarity (and thus genetic distance) than does a lower value. Using the MMD statistic, it is assumed that phenetic similarity closely approximates an underlying cladistic relationship (Scott et al., 1983).

To determine if MMD values are statistically significant, each MMD value is compared to its standard deviation. If the MMD value is greater than two times its standard deviation, then the null hypothesis of the samples being identical is rejected at the 0.025 significance level (Sjovold, 1977). Conversely, an insignificant MMD value indicates that it is impossible to distinguish between the two samples because (1) the samples are phenetically indistinguishable because they are from the same populations or are from two populations with the same dental trait distribution, or (2) the size of one or both samples is small, which can result in an excessively large standard deviation (Sjovold, 1977).

In the Natufian inter-sample MMD comparison, trait selection included 25 of the 29 dental traits of the ASU DAS that Turner (1987) has found to best differentiate between populations at different levels of geographic comparison. Trait presence/absence break-point selection also followed Turner (1987). The data and presence/absence frequencies are given in Table 2.The MMD analysis includes the maximum number of dental traits common to *all* the samples in a given matrix.

TABLE 2. Frequencies of 25 dental morphological traits used in the Natufian inter-sample MMD's in Table 4.

Traits	Grades +	El-Wad			Eynan			Hayonim			Nahal Oren			AHKRS			Natufians (all)		
		N	K	%	N	K	%	N	K	%	N	K	%	N	K	%	N	K	%
Winging UI1	1	13	0	0.0	8	0	0.0	1	0	0.0	5	0	0.0	14	0	0.0	31	0	0.0
Shoveling UI1	3-7	16	0	0.0	22	0	0.0	14	1	7.7	3	0	0.0	4	0	0.0	59	1	1.9
Double-shovel UI1	2-6	26	3	11.5	30	1	3.3	25	4	16.0	9	2	22.2	10	2	20.0	12	100	12.0
Interruption groove UI2	1	31	2	6.4	24	1	4.2	19	7	36.8	9	0	0.0	9	2	22.2	92	12	13.0
Tuberculum dentale UI2	1-6	23	23	100.0	19	16	84.2	11	11	100.0	4	4	100.0	4	4	100.0	61	58	88.5
Mesial ridge UC	1-3	18	1	5.6	22	6	27.3	10	1	10.0	5	0	0.0	3	0	0.0	58	8	13.8
Uto-Aztecan UP1	1	36	0	0.0	31	0	0.0	22	0	0.0	10	0	0.0	10	0	0.0	109	0	0.0
Hypocone UM2	2-5	51	50	98.0	39	36	92.3	25	22	88.0	16	16	100.0	16	15	93.7	147	136	94.5
Cusp 5 UMI	1-5	60	1	1.7	54	5	9.2	34	5	14.7	18	1	5.5	23	2	8.7	189	14	7.4
Carabelli's trait UM1	2-7	23	19	82.6	28	23	82.1	19	13	68.4	8	7	87.5	12	11	91.7	90	30	81.1
Parastyle UM3	1-6	51	0	0.0	31	1	3.2	20	0	0.0	14	0	0.0	17	0	0.0	133	1	0.7
Enamel Extension UM1	2-3	49	0	0.0	46	0	0.0	31	0	0.0	14	0	0.0	16	0	0.0	156	0	0.0
>-root UP1	1	6	1	16.7	5	3	60.0	13	6	46.1	3	1	33.3	6	0	0.0	33	11	33.3
3-root UM2	3	7	6	85.7	16	14	87.5	13	13	100.0	3	3	100.0	7	7	100.0	46	43	93.5
Peg/reduced UM3	1-2	51	22	43.1	31	18	58.1	20	10	50.0	14	7	50.0	18	10	55.5	134	167	50.0
Odontome U/L P1/P2	1	50	0	0.0	47	1	2.1	28	0	0.0	16	0	0.0	20	0	0.0	161	1	0.6
>1 lingual cusp LP2	2-9	28	18	64.3	23	12	52.2	24	13	54.2	14	8	88.9	9	8	88.9	98	59	60.2
Y groove pattern LM2	Y	47	17	36.2	37	11	29.7	32	8	25.0	24	8	33.3	14	3	21.4	154	47	30.5
6-cusp LM1	6	50	6	12.0	43	8	18.6	24	7	29.2	18	4	22.2	21	6	28.6	156	31	19.9
4-cusp LM2	4	51	36	61.0	44	32	72.7	32	19	5934	25	9	36.0	16	8	50.0	176	104	59.1
Deflecting wrinkle LM1	3	9	0	0.0	12	0	0.0	9	0	0.0	2	0	0.0	5	0	0.0	37	0	0.0
Distal trigonid crest	1	35	0	0.0	32	0	0.0	23	0	0.0	12	0	0.0	17	0	0.0	119	0	0.0
Protostylid LM1	1-7	49	7	14.3	39	5	12.8	20	3	15.0	16	3	18.7	22	3	13.6	146	21	14.4
Cusp 7 LM1	1-5	54	2	3.7	42	3	7.1	32	0	0.0	21	0	0.0	21	0	0.0	170	8	4.7
1-root LM2	1	3	0	0.0	8	0	0.0	7	0	0.0	4	0	0.0	11	0	0.0	33	0	0.0

Abbreviations: N is the number of observable dentitions with at least one tooth containing trait. K is the number of dentitions with trait, based on the tooth with the high grade of the trait in cases of unequal antimere expression. UI1 is maxillary central incisor. UI2 is maxillary lateral incisor. UC is maxillary canine. UP1 is maxillary first molar. UM1 is maxillary first molar. UM2 is maxillary second molar. UM3 is maxillary third molar. U/L is upper/lower. P1/2 is first/second. LP2 is mandibular second premolar. LM1 is mandibular first molar. LM2 is mandibular second molar.

TABLE 3. Frequencies of 26 dental morphological traits used in the Natufian-Nubian MMD's in Table 5.

Traits	Grades +	El-Wad			Eynan			Hayonim Cave			Nahal Oren			AHKRS			Nubians		
		N	K	%	N	K	%	N	K	%	N	K	%	N	K	%	N	K	%
Winging UI1	1	13	0	0.0	8	0	0.0	1	0	0.0	5	0	0.0	4	0	0.0	25	8	32.0
Shoveling UI1	2-7	16	4	25.0	22	0	0.0	14	1	7.1	3	0	0.0	4	1	25.0	22	13	59.1
Double-shovel UI1	2-6	26	3	11.5	30	1	3.3	25	4	16.0	9	2	22.2	10	10	20.0	20	0	0.0
Interruption groove UI2	1	31	2	6.4	24	1	4.2	19	7	36.8	9	0	0.0	9	2	22.2	25	4	16.0
Tuberculum dentale UI2	2-6	23	23	100.0	19	16	84.2	11	11	100.0	4	4	100.0	4	4	100.0	18	7	38.9
Mesial ridge UC	1-3	18	1	5.6	22	6	27.3	10	1	10.0	5	0	0.0	16	15	93.7	23	1	4.3
Hypocone UM2	3-5	51	50	98.0	39	33	84.6	25	20	80.0	16	16	100.0	16	14	93.7	27	25	92.6
Cusp 5 UMI	2-5	60	0	0.0	54	1	1.8	34	4	11.8	18	0	0.0	23	1	4.3	14	4	28.6
Carabelli's trait UM1	2-7	23	19	82.6	28	23	82.1	19	13	68.4	8	7	87.5	12	11	91.7	13	6	46.2
Parastyle UM3	2-6	51	0	0.0	31	0	0.0	20	0	0.0	14	0	0.0	17	0	0.0	34	0	0.0
Enamel Extension UM1	1-3	49	1	2.0	46	2	4.3	31	1	3.2	14	0	0.0	16	2	12.5	35	21	60.0
>-root UP1	2-3	6	5	83.3	5	2	40.0	13	7	53.8	3	2	66.7	6	6	100.0	28	20	71.4
Root # UM2	3-4	7	6	85.7	16	14	87.5	13	13	100.0	3	3	100.0	7	7	100.0	25	18	72.0
Peg/reduced UI2	1-2	37	2	54.0	22	4	18.2	20	10	50.0	9	1	11.1	10	5	50.0	32	1	3.1
>1 lingual cusp LP2	2-9	28	18	64.3	23	18	54.2	24	13	54.2	14	8	57.1	9	8	88.9	15	14	93.3
Y groove pattern LM2	Y	47	17	36.2	37	11	29.7	32	8	25.0	24	8	33.3	15	4	26.7	27	16	59.3
6-cusp LM1	6	50	6	12.0	43	8	18.6	24	7	29.2	18	4	22.2	21	6	28.6	30	9	30.0
5-cusp LM2	5	51	15	29.4	34	2	5.9	27	8	28.6	16	7	43.7	10	0	0.0	33	31	93.9
Deflecting wrinkle LM1	2-3	9	1	11.1	12	0	0.0	9	1	11.1	2	0	0.0	5	2	40.0	10	3	30.0
Distal trigonid crest	1	35	0	0.0	32	0	0.0	23	0	0.0	12	0	0.0	17	0	0.0	14	0	0.0
Protostylid LM1	1-7	49	7	14.3	39	5	12.8	20	3	15.0	16	3	18.7	22	3	13.6	21	6	28.6
Cusp 7 LM1	2-5	54	1	1.8	42	1	2.4	32	3	9.4	21	0	0.0	21	0	0.0	28	1	3.6
Root # LM2	2-3	3	3	100.0	8	8	100.0	7	7	100.0	4	4	100.0	11	11	100.0	36	31	86.1
Palatine torus	2-4	5	1	20.0	4	0	0.0	1	0	0.0	4	1	25.0	2	1	50.0	22	2	9.1
Rocker jaw	1	12	1	8.3	9	2	22.2	7	1	14.3	14	4	28.6	6	1	16.7	38	0	0.0

Abbreviations are the same as those in Table 2. Nubian data are from Turner and Irish (1990).

The MMD statistic is a measure of relative phenetic similarity/dissimilarity, and in addition to an inter-sample comparison among the Natufian sites, it is important to compare each Natufian sample with an outgroup to which they could conceivably be more dentally similar, instead. The best available outgroup in this case is the late Pleistocene Nubian dental sample (18,000-12,000 BP) from Irish and Turner (1990). The Nubian sample is broadly contemporaneous with and geographically proximate to the Natufian samples, and the archaeological evidence suggests the possibility that late Pleistocene Nubian-derived gene flow may have augmented the Natufian gene pool (Lipschultz, 1996).

The Nubian sample thus represents a reasonable outgroup for comparative purposes. Furthermore, the data from the two studies (Irish and Turner, 1990; Lipschultz, 1996) are comparable because the present author was trained in the use of the ASU DAS by Turner, who collected the late Pleistocene Nubian data found in Irish and Turner (1990). Also, to make the Natufian and late Pleistocene Nubian dental data more directly comparable, trait and presence/absence break-point selection followed Irish and Turner (1990). Of the 31 traits Irish and Turner (1990) use, all but torsomolar angle for the lower third molar were scored. Of these these 30 traits, 26 were scoreable for the late Pleistocene Nubian sample and all of the Natufian samples. The data for these 26 traits are given in Table 3.

TABLE 4. Mean measure of divergence values between Natufian dental samples.

Sample	El-Wad	Eynan	Hayonim Cave	Nahal Oren	AHKRS
El-Wad		-0.016	-0.026	-0.133	-0.074
Eynan	(0.038)		-0.029	-0.078	0.026
Hayonim Cave	(0.056)	(0.054)		-0.111	-0.076
Nahal Oren	(0.066)	(0.062)	(0.077)		-0.148
AHKRS	(0.053)	(0.050)	(0.070)	(0.080)	

Values in parentheses are standard deviations. AHKRS represents pooled Natufian samples from the sites of Erq-el-Ahmar, Hayonim Terrace, Kebara, Rakefet, and Shukba. Natufian data are from Lipschultz (1996).

TABLE 5. Mean measure of divergence values between Natufian and late Pleistocene Nubian dental samples.

Sample	El-Wad	Eynan	Hayonim Cave	Nahal Cave	AHKRS	Late Pleistocene Nubians
El-Wad		0.047	-0.045	-0.113	-0.049	0.412
Eynan	(0.044)		-0.022	-0.064	0.124	0.490
Hayonim Cave	(0.072)	(0.072)		-0.105	-0.043	0.354
Nahal Oren	(0.068)	(0.065)	(0.089)		-0.043	0.346
AHKRS	(0.062)	(0.032)	(0.090)	(0.085)		0.446
Late Pleistocene Nubians	(0.034)	(0.032)	(0.062)	(0.057)	(0.052)	

Underlined MMD values are statistically significant. Values in parentheses are standard deviations. Late Pleistocene Nubian data are from Irish (1993). AHKRS represents pooled Natufian samples from the sites of Erq-el-Ahmar, Hayonim Terrace, Kebara, Rakefet, and Shukba. Natufian data are from Lipschultz (1996).

MMD RESULTS

Comparison of the Natufian site dental data with one another shows that all but one of the resulting MMD values are negative (-0.148 to -0.026) and all are statistically insignificant (Table 4). The average MMD value between the Natufian dental samples is 0.003. Caution must be exercised when interpretations of population similarity are based upon negative MMD values, as this can result from the small sample size of one or both of the samples. Despite the fact that the MMD statistic is designed to contend with small sample size, via the Freeman and Tukey angular transformation (Berry and Berry, 1967; Sjovold, 1973; Green and Suchey, 1976), the possibility for error resulting from small sample size should always be explicitly stated, especially when negative MMD values result.

Given this, negative MMD values can generally be treated as being equivalent to a value of 0.000, which indicates no phenetic dissimilarity between samples (Turner, 1994). In the present comparison, the Natufian dental samples are considered to large enough to warrant the interpretation that the negative MMD values between them represent the absence of phenetic dissimilarity.

Including Irish and Turner's (1990) late Pleistocene Nubian dental sample in the analysis, all but one of the Natufian inter-sample MMD values are statistically insignificant, all are small, and all but two are negative (Table 4). Each Natufian/late Pleistocene Nubian comparison yields a statistically significant and large MMD value, especially

relative to the Natufian inter-sample MMD values. The average MMD value between the Natufian and late Pleistocene Nubian dental samples is 0.410.

CONCLUSIONS

First, the dental samples from each Natufian site are phenetically similar to, and are statistically indistinguishable from one another when compared using the multivariate MMD statistic. Second. the close Natufian inter-sample dental relationship is supported when each is compared with an out-group, the late Pleistocene Nubians. All of the Natufian dental samples are significantly different from the late Pleistocene Nubian dental sample. Third, the phenetic similarity between the Natufian dental samples supports the hypothesis, defined by previous archaeological and biological investigations, that the Natufians are a biologically coherent population.

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