Dental Anthropology of the Madaklasht I: A Description and Analysis of Variation in Morphological Features of the Permanent Tooth Crown

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Key Words

ASU Dental Anthropology System, Dental Traits, Sex Dimorphism, Tooth-Trait Interactions

Introduction

Little is known of the biological history of ethnic groups occupying the Hindu Kush and Karakoram highlands of northern Pakistan. The inhabitants of Madaklasht live within the Shishi Koh Valley of Chitral District, the most northerly district of the Khyber Pakhtunkhwa Province of Pakistan (Fig. 1). This valley is well-known for its lush green appearance and the fertility of its soils, which yield rich agricultural produce. Much of the valley is inhabited by Gujars, whose traditional occupation is the tending of goats, sheep, and to a much lesser extent, cattle. Various passes connect the Shishi Koh Valley to other valleys, such as Porott Gol and Goreen Gol, which permit communication with populations in Dir Kohistan, while Dokwan, Ghochar and Radghali passes connect Shishi Koh to the Golain Valley.

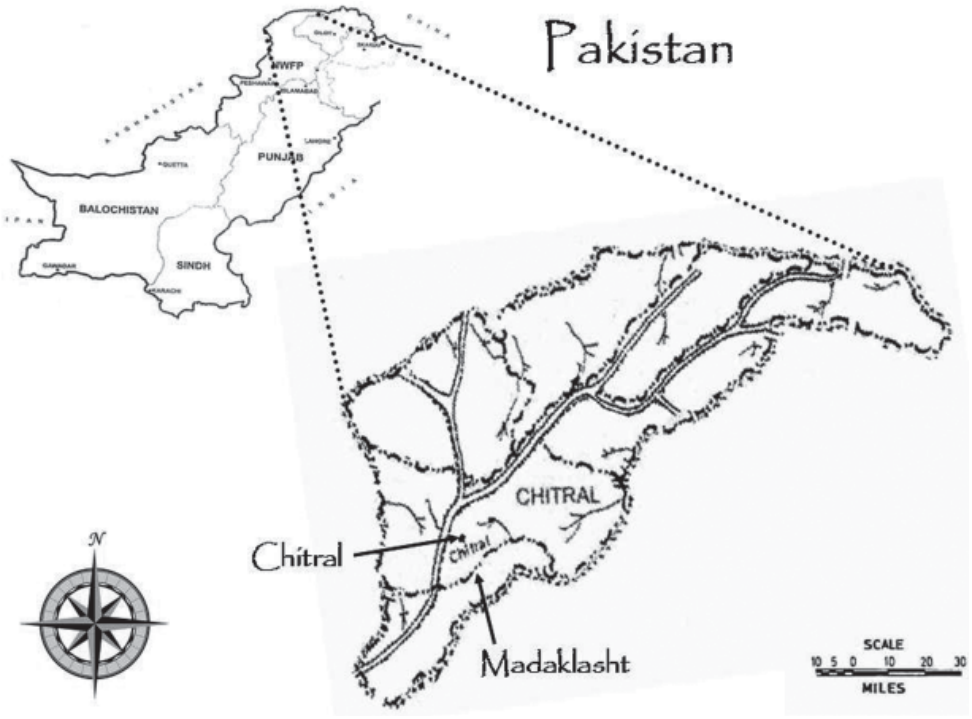

Fig. 1: Location of Madaklasht village within Chitral District, Khyber Pakhtunkhwa, Pakistan

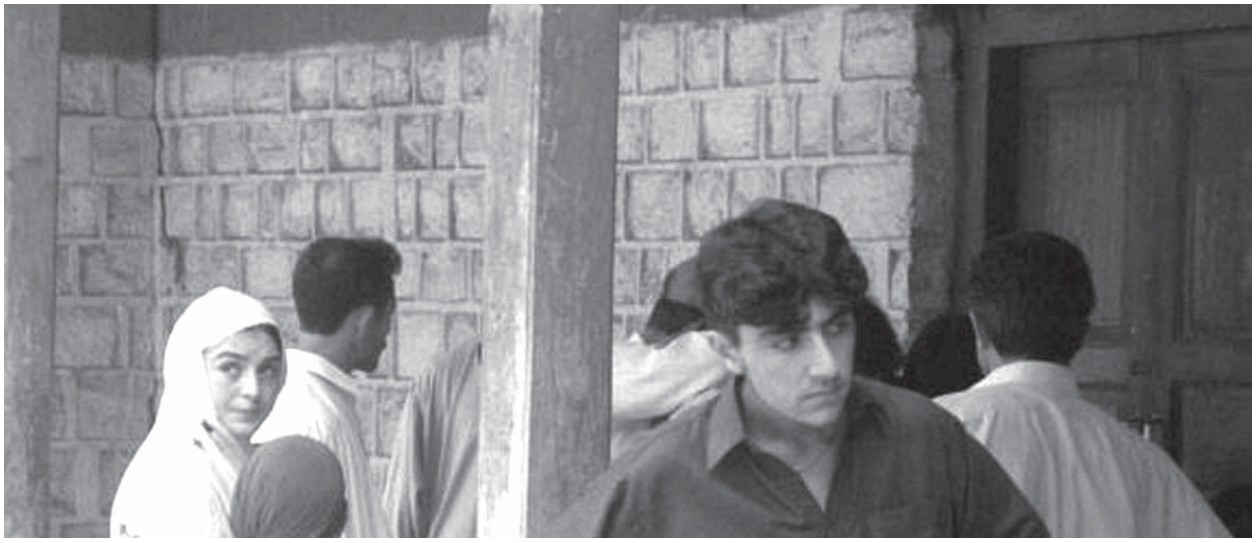

Fig. 2: Some of the volunteer villagers from Madaklasht

The village of Madaklasht is inhabited by one of the most unique ethnic groups in Chitral district the Badakhshis, (Fig. 2). According to oral tradition (Ghufran 1962), the Badakhshi tribe is named after their original homeland (Badakhshan), which is located in the northeastern region of Afghanistan. Oral tradition among the Madaklasht holds that they came to Chitral during the reign of the Katur Family in the 17th century, by whom they were recruited to the area because of their well-known artistry as armourers. Initially, these manufacturers of war material believed they would only remain in the region for a brief period of time, but the Katur ruler of Chitral, realizing their importance for strengthening the strategic position of his state, did not want to release them. So, due to the interest of the then ruler of Chitral, the ancestors of the present Badakhshi of Madaklasht decided to settle here permanently. Wahid Beg (1992:436) claims that it is likely the Sumbola of Garam Chashma, Chitral belong to the same ethnic group as the Madaklasht, for the Sumbola exhibit the same culture, speak the same language, and also have an oral tradition which claims their origins in the Badakhshan region of northeastern Afghanistan, followed by immigration to Chitral District during the 17th century.

The purposes of the current pair of studies are two-fold. First, scientific knowledge of morphological variation in the permanent tooth crown among ethnic groups of the Hindu Kush and Karakoram highlands is virtually unknown, for only two studies have described such variation in a single ethnic group, the Khowar of Chitral city (Blaylock 2008; Hemphill et al in press). Hence, the first study seeks to provide a comprehensive description and analysis of dental morphological variation among the Madaklasht. In the companion study, the pattern of morphological variation in the permanent tooth crown found among the Madaklasht is put into temporal and inter-regional perspective by contrasting a suite of dental morphology variables among the Madaklasht to a battery of prehistoric and living dental samples from western Central Asia, the Indus Valley and peninsular India.

Materials and Methods

The dental casts that form the database of the current study were collected on an impromptu basis in Madaklasht village and at the Aga Khan Diamond Jubilee School within that village over

a two day period in August 2007. The casts were collected by a team from the Department of Cultural Heritage and Tourism Management, Hazara University (Pakistan) under the direction of the author. A total of 205 individuals (101 males, 104 females) provided voluntary consent for plaster casts of their maxillary and mandibular teeth to be taken. Older adolescents and young adults (males: average (avg.) = 18.9, standard deviation (sd) = 6.9; females: avg. = 14.5, sd = 2.2) were specifically targeted for two reasons. First, such individuals have experienced eruption of all permanent teeth, except third molars. Second, these individuals have suffered minimally from dental disease (i.e., caries) or mechanical disorders (i.e., bruxism) that compromise the integrity of the permanent tooth crown.

The dental casts of each individual were assessed for 26 dental traits scored as 71 tooth-trait combinations in accordance with the Arizona State University Dental Anthropology (ASUDA) system (Turner et al 1991). Observations were made on both right and left antimeres. Frequencies of dental traits were calculated for each grade of expression according to the individual count method of Scott (1973; 1977; 1980; see also Scott and Turner 1997). This method not only compensates for the fluctuating asymmetric effects of environmental factors (Van Valen 1962; Staley and Green 1971; Sciulli et al 1979), but also maximizes sample sizes in dental series derived from archaeological sites where remains are often fragmentary or incomplete. While variation in trait morphology was scored along an ordinal scale among the Madaklasht, trait expression was dichotomized into presence/absence only for comparative purposes in both the current and companion study.

Dichotomized trait frequencies are contrasted in the current study by tooth (*i.e.,* trait expression in UM1 vs. UM2 vs. UM3) and by sex (females vs. males). For dichotomization, any degree of expression was considered a positive manifestation. The only exceptions were labial curvature of the central maxillary incisor, in which at least grade 2 curvature had to be present to be considered a positive expression, and hypocone size, where both grades 3.5 and 4 were considered full development of this cusp. Chi-square statistics were calculated to detect significant differences in specific trait frequencies by tooth and by sex among the Madaklasht. Sex-pooled trait frequencies among the Madaklasht were obtained by taking the average of male and female frequencies. This approach ensured that pooled trait frequencies were not skewed in favour of the sex represented by the most observations for a specific tooth-trait combination.

Intraobserver variation in morphological evaluations was assessed by repeated scoring of 35 tooth-trait combinations in a random sample of 50 plaster dental casts. Observation sessions were separated by a period of 18 months and observation differences were assessed according to the method of Nichol and Turner (1986). Intraobserver error was found to be well within acceptable limits (see Hemphill 1991).

Results

Dental Morphology Trait Variation among the Madaklasht as a Whole

Maxillary Anterior Teeth

Trait presence by grade of expression, frequencies and number of observations for each of the 38 tooth-trait combinations in the maxillary dentition are provided in Table 1. The Madaklasht possess maxillary incisors that commonly feature shovelling of the labial margins, albeit at rather low grades

Table 1: Morphological Variations of Permanent Maxillary Teeth among the Madaklasht by Sex

Females								Males						
Shovel Shape (SHOV)								Shovel Shape (SHOV)						
	I1		I2		C				I1		I2		C	
Grade	n	Pct.	n	Pct.	n	Pct.		Grade	n	Pct.	n	Pct.	n	Pct.
0	24	25.3	51	55.4	57	62.6		0	32	38.6	40	49.4	48	63.2
1	29	30.5	19	20.7	25	27.5		1	20	24.1	25	30.9	20	26.3
2	30	31.5	18	19.6	9	9.9		2	20	24.1	13	16.0	8	10.5
3	12	12.6	2	2.2	0	0.0		3	10	12.0	2	2.5	0	0.0
4	0	0.0	0	0.0	0	0.0		4	1	1.2	1	1.2	0	0.0
5	0	0.0	1	1.1	0	0.0		5	0	0.0	0	0.0	0	0.0
6	0	0.0	1	1.1	0	0.0		6	0	0.0	0	0.0	0	0.0
Total	95	100.0	92	100.0	91	100.0		Total	83	100.0	83	100.0	83	100.0

Double Shovel (DSHOV)									Double Shovel (DSHOV)							
	I1		I2		C		P3		I1		I2		C		P3	
Grade	n	Pct.	n	Pct.	n	Pct.	n	Pct.	n	Pct.	n	Pct.	n	Pct.	n	Pct.
0	73	76.8	85	90.4	86	92.5	94	97.9	65	79.3	71	86.6	80	96.4	81	96.4
1	13	13.7	8	8.5	5	5.4	1	1.0	13	15.9	11	13.4	3	3.6	3	3.6
2	8	8.4	1	1.1	2	2.2	1	1.0	3	3.7	0	0.0	0	0.0	0	0.0
3	1	1.1	0	0.0	0	0.0	0	0.0	1	1.2	0	0.0	0	0.0	0	0.0
Total	95	100.0	94	100.0	93	100.0	96	100.0	82	100.0	82	100.0	83	100.0	84	100.0

Interruption Groove (IGRV)				
	I1		I2	
Grade	n	Pct.	n	Pct.
0	94	100.0	75	83.3
1	0	0.0	3	3.3
2	0	0.0	10	11.1
3	0	0.0	0	0.0
4	0	0.0	2	2.2
Total	94	100.0	90	100.0

Interruption Groove (IGRV)				
	I1		I2	
Grade	n	Pct.	n	Pct.
0	83	98.8	59	72.8
1	1	1.2	8	9.9
2	0	0.0	10	12.3
3	0	0.0	1	1.2
4	0	0.0	3	3.7
Total	84	100.0	81	100.0

Median Lingual Ridge (MLR)						
	I1		I2		C	
Grade	n	Pct.	n	Pct.	n	Pct.
0	27	28.7	59	61.5	53	57.6
1	27	28.7	18	18.8	12	13.0
2	27	28.7	15	15.6	20	21.7
3	11	11.7	4	4.2	6	6.5
4	2	2.1	0	0.0	1	1.1
Total	94	100.0	96	100.0	92	100.0

Median Lingual Ridge (MLR)						
	I1		I2		C	
Grade	n	Pct.	n	Pct.	n	Pct.
0	26	31.0	55	67.9	37	48.7
1	13	15.5	12	14.8	7	9.2
2	26	31.0	12	14.8	19	25.0
3	17	20.2	1	1.2	8	10.5
4	2	2.4	1	1.2	5	6.6
Total	84	100.0	81	100.0	76	100.0

Table 1 Continued.....

Females

Labial Curvature (LC) I1		
Grade	n	Pct.
0	11	11.6
1	35	36.8
2	36	37.9
3	13	13.7
4	0	0.0
Total	95	100.0

Distal Accessory Ridge (DAR) C		
Grade	n	Pct.
0	45	47.4
1	15	15.8
2	28	29.5
3	6	6.3
4	1	1.1
Total	95	100.0

Males

Labial Curvature (LC) I1		
Grade	n	Pct.
0	16	18.8
1	25	29.4
2	29	34.1
3	14	16.5
4	1	1.2
Total	95	100.0

Distal Accessory Ridge (DAR) C		
Grade	n	Pct.
0	47	60.3
1	12	15.4
2	13	16.7
3	4	5.1
4	2	2.6
Total	78	100.0

Accessory Buccal Cusp (PCSP)	P3		P4	
Grade	N	Pct.	n	Pct.
0	90	93.8	86	92.5
1	6	6.3	7	7.5
Total	96	100.0	83	100.0

Accessory Buccal Cusp (PCSP)	P3		P4	
Grade	N	Pct.	n	Pct.
0	77	92.8	73	92.4
1	7	7.2	6	7.6
Total	84	100.0	79	100.0

Accessory Ridges (PRDG)	P3		P4	
Grade	N	Pct.	n	Pct.
0	53	55.8	30	32.3
1	42	44.2	63	67.7
Total	95	100.0	93	100.0

Accessory Ridge (PRDG)	P3		P4	
Grade	N	Pct.	n	Pct.
0	50	64.1	31	40.3
1	28	35.9	46	59.7
Total	84	100.0	77	100.0

Metacone Size (META)	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	0	0.0	0	0.0	0	0.0
1	0	0.0	1	1.2	1	50.0
2	0	0.0	0	0.0	0	0.0
3	0	0.0	0	0.0	0	0.0
3.5	0	0.0	0	0.0	0	0.0
4	1	1.0	18	21.2	1	50.0
5	95	99.0	66	77.6	0	0.0
Total	96	100.0	85	100.0	2	100.0

Metacone Size (META)	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	0	0.0	0	0.0	1	3.7
1	0	0.0	0	0.0	0	0.0
2	0	0.0	0	0.0	1	3.7
3	0	0.0	2	2.6	3	11.1
3.5	0	0.0	0	0.0	1	3.7
4	2	2.4	21	27.6	14	51.9
5	85	97.6	53	69.7	7	25.9
Total	87	100.0	76	100.0	27	100.0

Females Hypocone Size (HYPO)	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	0	0.0	22	27.5	2	100.0
1	0	0.0	30	37.5	0	0.0
2	0	0.0	11	13.8	0	0.0
3	0	0.0	9	11.3	0	0.0
3.5	1	0.0	4	5.0	0	0.0
4	95	1.0	4	5.0	0	0.0
Total	96	100.0	80	100.0	2	100.0

Males Hypocone Size (HYPO)	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	0	0.0	17	24.3	12	46.2
1	0	0.0	20	28.6	5	19.2
2	0	0.0	1	1.4	5	19.2
3	0	0.0	13	18.6	3	11.5
3.5	2	2.4	8	11.4	0	0.0
4	83	97.6	11	15.7	1	3.8
Total	85	100.0	70	100.0	26	100.0

Table 1 Continued.....

Metaconule Size (MTCLE)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	93	96.9	69	89.6	2	100.0
1	2	2.1	7	9.1	0	0.0
2	1	1.0	0	0.0	0	0.0
3	0	0.0	1	1.3	0	0.0
Total	96	100.0	77	100.0	2	100.0

Metaconule Size (MTCLE)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	80	97.6	61	87.1	21	80.8
1	2	2.4	7	10.0	4	15.4
2	0	0.0	2	2.9	1	3.8
3	0	0.0	0	0.0	0	0.0
Total	82	100.0	70	100.0	26	100.0

Carabelli's Trait (CARA)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	25	26.0	67	75.3	3	100.0
1	15	15.6	12	13.5	0	0.0
2	12	12.5	4	4.5	0	0.0
3	15	15.6	4	4.5	0	0.0
4	3	3.1	0	0.0	0	0.0
5	10	10.4	2	2.2	0	0.0
6	7	7.3	0	0.0	0	0.0
7	9	9.4	0	0.0	0	0.0
Total	96	100.0	89	100.0	3	100.0

Carabelli's Trait (CARA)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	22	26.2	68	86.1	28	100.0
1	17	20.2	6	7.6	0	0.0
2	14	16.7	2	2.5	0	0.0
3	12	14.3	1	1.3	0	0.0
4	3	3.6	0	0.0	0	0.0
5	7	8.3	1	1.3	0	0.0
6	4	4.8	1	1.3	0	0.0
7	5	6.0	0	0.0	0	0.0
Total	84	100.0	79	100.0	28	100.0

Parastyle (PARA)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	95	100.0	86	100.0	2	100.0
1	0	0.0	0	0.0	0	0.0
Total	95	100.0	86	100.0	2	100.0

Parastyle (PARA)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	84	100.0	76	100.0	23	95.8
1	0	0.0	0	0.0	1	4.2
Total	84	100.0	76	100.0	24	100.0

Females Pegging (PEG)				
	12		M3	
Grade	n	Pct.	n	Pct.
Absent	87	90.6	3	75.0
Present	9	9.4	1	25.0
Total	96	100.0	4	100.0

Males Pegging (PEG)				
	12		M3	
Grade	n	Pct.	n	Pct.
Absent	80	94.1	27	93.1
Present	5	5.9	2	6.9
Total	85	100.0	29	100.0

Congenital Absence (CABS)						
	12		P4		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	95	99.0	93	100.0	5	100.0
Present	1	1.0	0	0.0	0	0.0
Total	96	100.0	77	100.0	5	100.0

Congenital Absence (CABS)						
	12		P4		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	84	96.6	84	100.0	26	92.9
Present	3	3.4	0	0.0	2	7.1
Total	87	100.0	84	100.0	28	100.0

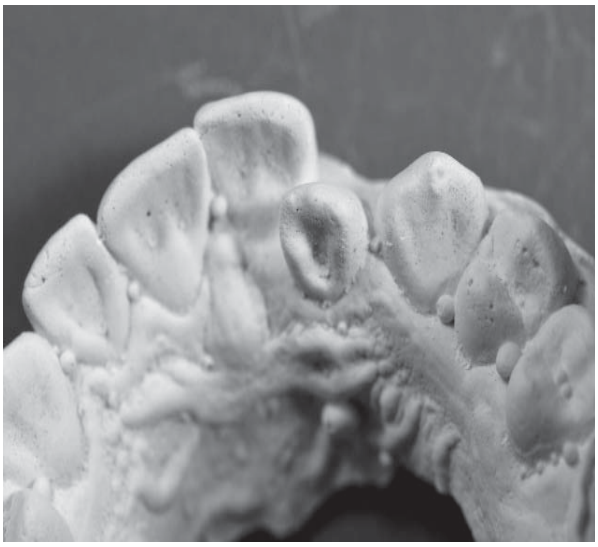

Fig. 3: Shovelling of ULI2, Specimen MDK-184, Grade 5.

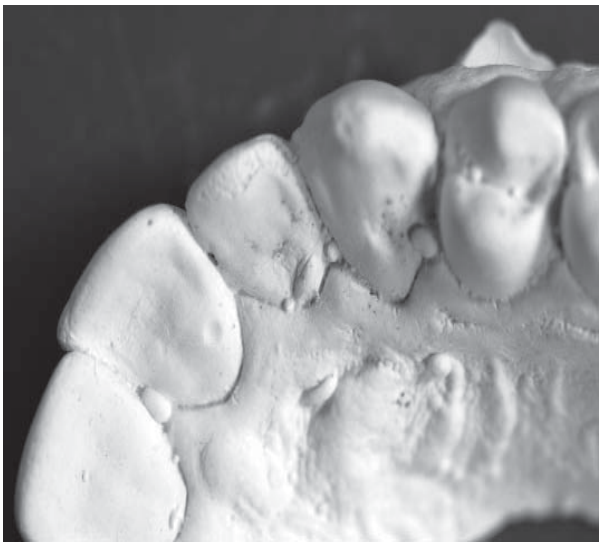

Fig. 4: Interruption groove found on the lingual aspect of ULI2, Specimen MDK-031.

(1-2) of expression. In fact, about half (50.8%) of all maxillary anterior teeth (I1, I2, C) that could be observed for shovelling express this morphological trait. In a few cases, a pronounced degree of shovelling occurs on the lateral incisor (Fig. 3). Shovelling is most common on UI1 (68.5%), is less common on UI2 (48.0%), and is rarest on UC (35.6%).

By contrast, development of labial marginal ridges, or double shovelling, is fairly rare among the Madaklasht, occurring only on 10.4% of all maxillary teeth for which the trait could be assessed. This trait only occurs with any degree of commonality on UI1 (22.0%) and, to a lesser degree, UI2 (11.4%). Like shovelling, double shovelling also exhibits a pattern of decreased frequency as one moves distally from UI1, to UI2, to UC (5.7%), to UP3 (2.8%).

Interruption grooves (Fig. 4), which either divide the mesial or distal aspects of the cingulum or bisect the basal eminence on the lingual aspect of UI1, UI2, and UC are also rather uncommon among the Madaklasht, for such grooves were only found on 10.9% of maxillary incisors that could be assessed for this trait. However, in this case, the pattern of prevalence is reversed relative to that seen for shovelling and double shovelling. Instead of featuring a reduction in frequency from mesial to distal, interruption groves are far more common in UI2 (21.6%: 37/171) than in UI1 (0.6%: 1/178).

Median lingual ridge development, or *tuberculum dentale*, are flame-like, finger-like, or tubercular extensions of the cingulum found on the lingual surface of UI1, UI2 or UC (Fig. 5). Such extensions of the cingulum affect the same proportion of maxillary teeth (50.9%) that could be assessed for this trait as shovelling. However, the patterning of expression is quite different, and this difference is expressed in two ways. First, while shovelling is usually manifested at rather low grades of development, median lingual ridges often occur at more marked levels (>3), especially in UI1 (18.0%). Second, whereas shovelling occurs with less frequency from UI1 to UC, median lingual ridge development features frequencies that are highest for UI1 (70.2%), intermediate for UC (46.4%), and lowest for UI2 (35.6%).

Fig. 5: Medial lingual ridge development on the lingual surface of URI1, Specimen MDK-062, Grade 4

Fig. 6: Distal accessory ridge present on the lingual surface of URC, Specimen MDK-074, Grade 4

Curvature of the labial surface of UI1 is commonly found among the Madaklasht (85.8%), yet in the overwhelming majority of cases (76.7%) of those expressing the condition, the amount of curvature is quite modest (grades 1-2).

The distal accessory ridge occurs on the lingual surface of UC between the medial ridge and the distal marginal ridge (Morris 1965; Scott 1977) (Fig. 6). Such ridges occur among nearly half (46.8%) of the individuals for whom this trait could be assessed. Like shovelling, the preponderance of positive manifestations (68/81= 84%) tend to be low-grade (grades 1-2) expressions.

Maxillary Posterior Teeth

Accessory buccal cusps are rarely found on the maxillary premolars of the Madaklasht and they tend to be slightly more common on UP4 (13/162 = 8.2%) than UP3 (13/180 = 7.2%). By contrast, accessory ridges on the buccal cusps are not only much more common overall (51.3%), but are found much more often on UP4 (64.1%) than UP3 (39.1%).

The maxillary molars of the Madaklasht exhibit very little reduction of the metacone, for both UM1 and UM2 fail to exhibit a single case of such reduction despite sample sizes of 183 and 161, respectively. Only for UM3 is there any substantial reduction of the metacone, but even with sample size limited to 29 observations, such reduction is only seen in roughly one-fifth of cases (6/29= 20.7%).

The hypocone, found in the distolingual quadrant of the crown, exhibits a markedly different pattern of reduction among the Madaklasht (Fig. 7). While UM1 appears resistant to a reduction of this cusp (0/181= 0%), this cusp has been reduced in an overwhelmingly majority of cases on both UM2 (87.3%) and UM3 (89.3%).

The metaconule is somewhat rare among the Madaklasht, for it is only found among 7.6% of the maxillary molars for which observations could be made. The frequency of the metaconule forms an interesting pattern in that it trends in the opposite direction from incisor shovelling. That is, instead of decreasing in frequency from mesial to distal, the presence of the metaconule increases from a low on 2.8% on UM1, to 11.6% on UM2, to highest levels on UM3 (17.9%), despite the limited number of observations for this latter tooth (n= 28).

Fig. 7: Hypocone reduction. Specimen MDK-073, No reduction present on URM1, (Grade 4 development), complete reduction on URM2, (Grade 0 development)

Carabelli's trait occurs with moderate frequency among the Madaklasht (43.8%) and two aspects of its manifestation merit comment. First, in direct opposition to the presence of the metaconule, Carabelli's trait follows the same pattern in reduction in frequency from mesial to distal noted for shovelling; but for Carabelli's, the fall-off in occurrence is much more severe, with Carabelli's being very common on UM1 (73.9%), of low occurrence on UM2 (19.6%), and completely non-existent on UM3. Second, the degree of expression of Carabelli's trait by grade spans the seven grade range of the ASUDA system. Low grade (grades 1-3) expressions tend to be more common (68.7%) than high grade (grades 4-7) expressions (31.3%), but the latter (Fig. 8) are nevertheless well represented, especially on UM1 (21.8% of all positive manifestations).

Parastyles are nearly completely absent from the maxillary molars of the Madaklasht. Out of a total of 367 tooth-trait observations for this feature, it was found only once, on a UM3 (0.3%) (Fig. 9).

Pegging, or marked reduction of the mesiodistal dimension of the tooth crown (Fig. 10), occurs with low frequency (7.9%) among the Madaklasht. Pegging of UI2 was found in 7.7% of cases, while pegging of UM3 occurred in 7.9% of cases.

Congenitally absent teeth appear to be quite rare among the Madaklasht, although it must be pointed out that dental casts can only identify teeth that are missing at the time the cast is made. Consequently, while it is often quite easy to distinguish between antemortem tooth loss and congenital absence of all teeth mesial to M3 in the absence of sophisticated orthodontic intervention, dental casts cannot distinguish between teeth that are missing due to congenital absence from those that have failed to erupt due to impaction. With this caveat in mind, the overall absence of missing maxillary teeth among the Madaklasht is 6.1%. Non-antemortem absence appears highest for UM3 (2/33 = 6.1%), followed by UI2 (4/183 = 2.2%), while no UP4s (0/161) were found to be missing.

Fig. 8: Carabelli's trait on ULM1, Specimen MDK-062, Grade 7

Mandibular Anterior Teeth

Trait presence by grade of expression, frequencies and number of observations for each of the 33

Fig. 9: Paracone development on ULM3, Specimen MDK-015, Grade 5

tooth-trait combinations in the mandibular dentition is provided in Table 2. Only a modest minority of the mandibular anterior teeth among the Madaklasht exhibit lingual marginal development, for such development was found in only 20.7% of individuals and, when found, consisted only of the most minimal grade of expression.

Development of a distal accessory ridge on the mandibular canine is much more rare (9.8%) among the Madaklasht than upon its isomer (46.8%), a finding consistent with that found worldwide by Scott and Turner (1997:33). However, unlike shovelling, development of the distal accessory ridge, when present, is often expressed as stronger grades of development (8/17 positive manifestations= 47.1%).

Mandibular Posterior Teeth

The modal number of lingual cusps on the mandibular incisors is one. However, LP3 often exhibits complete reduction of the lingual cusp and sometimes this tooth and its counterpart, LP4, are marked by two lingual cusps (Kraus and Furr 1953; Ludwig 1957). Assessment of lingual cusp number among the mandibular premolars of the Madaklasht reveals that departures from the modal single lingual cusp occur in 33.7% of mandibular premolars. When considered by tooth, departures from modality occur nearly twice as often in LP3 (44.8%) than in LP4 (22.5%). Further, the nature of the departure differs dramatically between LP3 and LP4. In the former, the overwhelming majority of departures are due to complete elimination of the lingual cusp (91.4%), while very few are due to an accessory lingual cusp (8.6%). By contrast, in the latter (LP4) all departures are the result of two lingual cusps. Not surprisingly, LP3s and LP4s differ markedly in the frequency of lingual cusp fusion to the buccal cusp, occurring far more often in those LP3s that possess a lingual cusp (61/107 = 57.0%) than those LP4s that also possess a lingual cusp (8/178 = 4.5%).

The lingual surface of the mandibular premolars may be divided by a groove. This groove may occur mesial to the apex of the buccal cusp, distal to the apex, or grooves may be found both mesially and distally. Overall, 42.9% (153/357) of mandibular premolars among the Madaklasht feature lingual surfaces marked by grooving. The distribution of grooves by position is most common mesial of the buccal cusp apex (38.6%), followed by a distal position (32.0%), with grooves on both

Fig. 10: Pegging of ULI2, Specimen MDK-103

sides least common (29.4%). Overall, grooves are far more common on the lingual surface of LP3 (69.6%) than LP4 (15.3%). The position of the grooves differs between these two teeth, with LP3s most often featuring a groove mesial to the apex of the buccal cusp (44.4%), with remaining grooves evenly distributed between those mesial to the buccal apex (27.8%) and those featuring grooves both mesial and distal to this cuspal apex (27.8%). In marked contrast, grooves occurring mesial to the buccal cusp apex are *least* common in LP4, grooves distal to the apex are the most common (51.9%), while the frequency of grooves both mesial and distal to the buccal apex occur with intermediate frequency (37.0%).

The anterior fovea is commonly found on LM1 among the Madaklasht, for 88.3% of those teeth for which this trait could be assessed for this trait possessed an anterior fovea.

The presence of the Y-occlusal groove occurs on about half (50.5%) of mandibular molars among the Madaklasht for which an assessment of this trait could be made. Presence of the Y-occlusal groove is highest for LM1 (81.0%) and sequentially decreases in frequency distally from LM2 (26.4%) to LM3 (16.0%).

The most common number of cusps on the mandibular molars of the Madaklasht is five (54.7%), followed closely by four (41.1%), with very few possessing six cusps (4.2%). However, when the molars are considered individually, it is clear there is great variation from one to the next. Five-cusped molars dominate LM1s (84.7%), with rather few possessing four cusps (10.2%) and even fewer with six (5.1%). By contrast, four-cusps are the modal occurrence for LM2 (77.5%), followed by those with five cusps (21.3%), with very few possessing six cusps (1.3%). Yet another pattern emerges among LM3s. Once again, five-cusps are the norm (59.1%), but there is near-parity between four- (22.7%) and six-cusped (18.2%) expressions.

Deflecting wrinkles occur with rather low frequency (17.6%) on the occlusal surfaces of the mandibular molars among the Madaklasht and virtually all of these occurrences are confined to LM1 (37.0% of all LM1s; 93.8% of all positive manifestations).

Protostylids, a cingular derivative found on buccal surface of the protoconid (Fig. 11), occur with low frequency on the mandibular molars of the Madaklasht (12.5%) and the overwhelming majority of occurrences are buccal pits (grade 2: 10.9% of all mandibular molars; 87.5% of all positive manifestations).

The hypocunulid (Cusp 5), when present on the mandibular molars among the Madaklasht, tend to be rather well-developed, for manifestations rated in the three highest grades (3-5) dominate positive expressions of this trait (96.7%). Intriguingly, unlike many other morphological traits, the size of the hypoconulid, when present, does not differ markedly among the mandibular molars, with only LM2 showing a moderate decrease in the frequency of marked expressions (88.9%) relative to LM1 (98.1%) and LM3 (100.0%).

The entoconulid (Cusp 6), a supernumerary cusp found on the distal aspect of the crown interposed between the hypoconulid and the entoconid (Fig. 12), occurs with very low frequency on the mandibular molars of the Madaklasht (15/363 = 4.1%) and when found always occurs at rather low levels (grades 1-2) of development. The presence of the entoconulid is most common on LM3 (4/21 = 19.0%), is less common on LM1 (9/177 = 5.1%), followed by LM2 (2/165 = 1.2%). The

markedly higher frequencies for the entoconulid on LM3 may be a consequence of the small number of observations available for this tooth.

The metaconulid (Cusp 7), a supernumerary cusp found interposed between the metaconid and entoconid on the lingual aspect of the crown (Fig. 13) occurs even more rarely (13/362 = 3.6%) upon the mandibular molars of the Madaklasht than the entoconulid. Like the entoconulid, the metaconulid occurs most frequently on LM3 (2/21 = 8.7%), followed by LM1 (10/176 = 5.7%), with occurrence least common on LM2 (1/163 = 0.6%). Intriguingly, the only moderate degrees of expression (grade 3) of this trait are confined to LM3.

Table 2: Morphological Variations of Permanent Mandibular Teeth among the Madaklasht by Sex

Females

Shovelling (SHOVA) Anterior Teeth		
Grade	n	Pct.
0	80	82.5
1	17	7.5
2	0	0.0
Total	97	100.0

Dist. Acc. Ridge (DAR) C		
Grade	n	Pct.
0	91	93.8
1	3	3.1
2	3	3.1
3	0	0.0
4	0	0.0
Total	97	100.0

Males

Shovelling (SHOVA) Anterior Teeth		
Grade	n	Pct.
0	62	5.6
1	19	3.2
2	1	1.2
Total	82	100.0

Dist. Acc. Ridge (DAR) C		
Grade	n	Pct.
0	65	5.5
1	6	7.9
2	3	3.9
3	1	1.3
4	1	1.3
Total	76	100.0

Lingual Cusp Number (LCSP)	P3		P4	
Grade	n	Pct.	n	Pct.
0	36	37.9	0	0.0
1	55	57.9	75	78.9
2	4	4.2	20	21.1
3	0	0.0	0	0.0
Total	95	100.0	95	100.0

Lingual Cusp Number (LCSP)	P3		P4	
Grade	n	Pct.	n	Pct.
0	38	44.2	0	0.0
1	45	52.3	63	75.9
2	3	3.5	19	22.9
3	0	0.0	1	1.2
Total	86	100.0	83	100.0

Lingual Cusp Fusion (LCF)	P3		P4	
Grade	n	Pct.	n	Pct.
Absent	25	42.4	90	94.7
Present	34	57.6	5	5.3
Total	59	100.0	95	100.0

Lingual Cusp Fusion (LCF)	P3		P4	
Grade	n	Pct.	n	Pct.
Absent	21	43.8	80	96.4
Present	27	56.2	3	3.6
Total	48	100.0	83	100.0

	Lingual Grooves (LGRV) P3		P4		Ant. Fovea (AF) M1		
Grade	n	Pct.	n	Pct.	Grade	n	Pct.
Absent	26	26.8	80	85.1	0	10	10.8
Mesial	33	34.0	2	2.1	1	1	1.1
Distal	20	20.6	7	7.4	2	60	64.5
Both	18	18.6	5	5.3	3	22	23.7
Total	97		94	100.0	Total	93	100.0

	Lingual Grooves (LGRV) P3		P4		Ant. Fovea (AF) M1		
Grade	n	Pct.	n	Pct.	Grade	n	Pct.
Absent	29	34.5	69	84.1	0	9	13.0
Mesial	23	27.4	1	1.2	1	2	2.9
Distal	15	17.9	7	8.5	2	42	60.9
Both	17	20.2	5	6.1	3	16	23.2
Total	84	100.0	82	100.0	Total	69	100.0

Table 2 Continued.....

Y Occlusal Groove Pattern (YGRV)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	15	19.7	56	70.9	3	75.0
Present	61	80.3	23	29.1	1	25.0
Total	76	100.0	79	100.0	4	100.0

Y Occlusal Groove Pattern (YGRV)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	12	18.2	50	76.9	18	85.7
Present	54	81.8	15	23.1	3	14.3
Total	66	100.0	65	100.0	21	100.0

Females Cusp Number (CSPN)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
4	12	12.6	67	77.6	0	0.0
5	77	81.1	18	21.2	2	66.7
6	6	6.3	0	0.0	1	33.3
Total	95	100.0	85	100.0	3	100.0

Males Cusp Number (CSPN)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
4	6	7.4	57	76.0	5	26.3
5	72	88.9	16	21.3	11	57.9
6	3	3.7	2	2.7	3	15.8
Total	81	100.0	75	100.0	19	100.0

Deflecting Wrinkle (DWKL)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	61	67.0	90	98.9	4	100.0
1	3	3.3	0	0.0	0	0.0
2	21	23.1	1	1.1	0	0.0
3	6	6.6	0	0.0	0	0.0
Total	91	100.0	91	100.0	4	100.0

Deflecting Wrinkle (DWKL)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	41	57.7	77	97.5	21	100.0
1	2	2.8	1	1.3	0	0.0
2	18	25.4	1	1.3	0	0.0
3	10	14.1	0	0.0	0	0.0
Total	71	100.0	79	100.0	21	100.0

Protostylid (PROTO)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	84	87.5	87	92.6	3	75.0
1	1	1.0	1	1.1	0	0.0
2	11	11.5	5	5.3	1	25.0
4	0	0.0	0	0.0	0	0.0
7	0	0.0	1	1.1	0	0.0
Total	96	100.0	94	100.0	4	100.0

Protostylid (PROTO)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	68	80.0	74	88.1	20	95.2
1	2	2.4	0	0.0	0	0.0
2	15	17.6	10	11.9	0	0.0
4	0	0.0	0	0.0	1	4.8
7	0	0.0	0	0.0	0	0.0
Total	85	100.0	84	100.0	21	100.0

Hypoconulid Size (CS)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	12	12.6	71	79.8	0	0.0
1	0	0.0	1	1.1	0	0.0
2	0	0.0	1	1.1	0	0.0
3	15	15.8	9	10.1	1	25.0
4	47	49.5	4	4.5	3	75.0
5	21	22.1	3	3.4	0	0.0
Total	95	100.0	89	100.0	4	100.0

Hypoconulid Size (CS)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	6	7.4	58	76.3	5	26.3
1	0	0.0	0	0.0	0	0.0
2	3	3.7	2	2.6	0	0.0
3	12	14.8	6	7.9	4	21.1
4	41	50.6	7	9.2	4	21.1
5	19	23.5	3	3.9	6	31.6
Total	81	100.0	76	100.0	19	100.0

Table 2 Continued.....

Females Entoconulid Size (CS)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	89	93.7	89	100.0	2	66.7
1	2	2.1	0	0.0	1	33.3
2	4	4.2	0	0.0	0	0.0
Total	95	100.0	89	100.0	3	100.0

Males Entoconulid Size (CS)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	79	96.3	74	97.4	15	83.3
1	1	1.2	1	1.3	1	5.6
2	2	2.4	1	1.3	2	11.1
Total	82	100.0	76	100.0	18	100.0

Metaconulid Size (C7)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	92	97.9	82	100.0	4	100.0
1	2	2.1	0	0.0	0	0.0
2	0	0.0	0	0.0	0	0.0
3	0	0.0	0	0.0	0	0.0
Total	94	100.0	82	100.0	4	100.0

Metaconulid Size (C7)						
	M1		M2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
0	74	90.2	80	98.8	17	89.5
1	6	7.3	0	0.0	0	0.0
2	2	2.4	1	1.2	0	0.0
3	0	0.0	0	0.0	2	10.6
Total	82	100.0	81	100.0	19	100.0

Congenital Absence (CABS)						
	I1		P2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	98	100.0	96	100.0	6	100.0
Present	0	0.0	0	0.0	0	0.0
Total	98	100.0	96	100.0	6	100.0

Congenital Absence (CABS)						
	I1		P2		M3	
Grade	n	Pct.	n	Pct.	n	Pct.
Absent	87	100.0	85	100.0	27	100.0
Present	0	0.0	0	0.0	0	0.0
Total	87	100.0	85	100.0	27	100.0

Congenital absence was assessed for three mandibular teeth: LI1, LP4, and LM3. Although observations could be made for 185, 181, and 33 individuals, respectively, not a single case of non-antemortem loss was observed among these mandibular teeth.

Dichotomized Trait Frequencies

When trait expressions are dichotomized into categories of presence/absence only, it is clear that marked differences in trait expression occur between the various teeth that express the individual traits. Chi-square analysis reveals that 22 of the 34 maxillary tooth-trait combinations (64.7%) for which multiple teeth may be scored for a specific trait differ significantly by dental element (Table 3). Every contrast in trait frequency by tooth for shovelling, interruption grooves, median lingual ridge, ridging of the buccal cusp on the premolars, and Carabelli's trait is significant. Such results indicate that when maxillary tooth trait frequencies of the Madaklasht are compared, either by sex, or to samples of individuals of other ethnic groups, frequencies of these traits must be considered separately by tooth.

No significant differences in trait frequencies were found by tooth for the parastyle (completely absent among the Madaklasht), for pegging, or for congenital absence (except between UP4 and UM3). Such results suggest these traits are likely to be of little utility for comparative purposes. Remaining maxillary traits not found to differ significantly in frequency by tooth include full hypocone development and the presence of the metaconule on UM2 and UM3. Such results are likely the

consequence of small sample size for UM3, due to the sampling strategy used in the collection of dental casts. The lack of significant differences in buccal cusp number between UP3 and UP4, and in double shovelling between UI2 and UC as well as between UC and UP3, suggests that these traits are also unlikely to be of much use for detecting biological differences between the Madaklasht and other samples.

Chi-square analysis of dichotomized frequency differences in mandibular trait expressions by tooth yield similar results to those obtained for the maxilla. A total of 11 dental traits were scored as 27 tooth-trait combinations in which multiple teeth could be scored for a specific trait. Of these 27 tooth-trait combinations, 18 (66.7%) were found to differ significantly by tooth (Table 3). Every contrast in trait frequency by tooth for lingual cusp number, lingual cusp fusion and grooving among the mandibular premolars is significant. Similar results were obtained for the presence of the deflecting wrinkle, hypoconuild (Cusp 5) and entoconulid (Cusp 6). By contrast, none of the contrasts in frequency by tooth for the protostylid or congenital absence are significant. Remaining contrasts found to yield insignificant differences by tooth include the Y-occlusal groove on LM2 and LM3, cusp number on LM2 and LM3 and the presence of the metaconulid (Cusp 7) on LM1 and LM2.

Taken as a whole, the results obtained from contrasts of dichotomized trait frequencies indicate that trait expression must be considered by tooth to have any biological meaning. This is true for the overwhelming majority of traits considered. Hence, when trait expression among the Madaklasht is compared, either between males and females, or between the Madaklasht and samples of individuals from other ethnic groups, these comparisons must be performed not only by trait, but also by the tooth on which that trait is expressed.

Dental Morphology Trait Variation among the Madaklasht by Sex

It has often been claimed that one of the great advantages of dental morphology variation is that the large number of genes contributing to their manifestation (Nichol 1989; Townsend et al. 1988; 1992; 1994) results in an absence of sex dimorphism in both the degree and frequency of trait expression (Scott and Turner 1997). It is this quality that facilitates use of this system of biological variation for assessment of biological affinities of populations of the past, especially in those areas where extraction of ancient DNA has been rendered impossible due to depositional circumstances (Hemphill 2009).

Maxillary Anterior Teeth

Trait frequencies dichotomized into presence/absence only between males and females among the Madaklasht are presented in Table 4. Females exhibit shovelling more often (74.7%) than males (61.4%) on the lingual margins of UI1, but males (50.6%) have greater frequencies than females (44.6%) for UI2, while the sexes express shovelling with nearly equal frequency on UC (females = 37.4%, males = 36.8%). Chi-square analyses indicate that while the difference in shovelling frequency between males and females for UI1 approaches statistical significance, differences between males and females for shovelling on the other two teeth do not.

Females exhibit slightly higher frequencies of labial marginal ridge development, or double shovelling, than males for UI1 (females = 23.2%, males = 20.7%) and UC (females = 7.5%, males = 3.6%), but males possess slightly greater frequencies for UI2 (females= 9.6%, males= 13.4%) and

Fig. 11: Protostylid on LLM2, Specimen MDK-106, Grade 7

Fig. 12: Presence of the entoconulid (C6) on LRM1, Specimen MDK-039, Grade 2

UP3 (females = 2.1%, males = 3.6%). Not surprisingly, chi-square analyses indicate that none of these differences comes close to approaching statistical significance.

There is little difference in the frequency of interruption grooves by sex for UI1 (females= 0.0%, males= 1.2%), but males exhibit greater frequencies of this trait on UI2 (27.2%) than females (16.7%). Nevertheless, chi-square analyses reveal that neither of these differences is statistically significant.

Median lingual ridge development occurs with somewhat greater frequency among females for UI1 and UI2 than males (UI1: females= 71.3%; males= 69.0%; UI2: females= 38.5%, males= 32.1%), but in UC this relationship is reversed, with males (51.3%) exhibiting ridge development more often than females (42.4%). Chi-square analyses indicate that none of these differences are significant.

Males and females exhibit development of labial curvature of UI1 in nearly the same frequencies (males= 51.8%; females= 51.6%). This is not the case for development of the distal accessory ridge on UC, for expression of this ridge occurs more often among females (52.6%) than among males (39.7%). However, chi-square analysis indicates that neither this trait nor labial curvature of UI1 differs significantly in frequency between the two sexes.

Fig. 13: Presence of the metaconulid (C7) on LLM1, Specimen MDK-001, Grade 2

Maxillary Posterior Teeth

Presence of accessory buccal cusps on UP3 (females= 6.3%, males= 7.2%) and UP4 (females= 7.5%, males= 7.6%) occur with very similar frequencies by sex among the Madaklasht. By conttrast, differences between the two sexes are more marked

for the presence of ridges on the occlusal surfaces of the buccal cusp on these same teeth. In both cases, females exhibit these ridges with greater frequency than males (UP3: females= 44.2%, males= 35.9%; UP4: females= 67.7%, males: 59.7%). Nevertheless, chi-square analyses fail to identify any significant differences by sex for these traits.

Full expression of the metacone occurs with ubiquity and near ubiquity among both males and females for UM1 (males= 100.0%, females= 100.0%) and UM2 (males= 98.8%, females= 97.4%), respectively. By contrast, reduction of the metacone is commonly found on UM3, with males exhibiting somewhat higher frequencies (70.4%) than their female counterparts (66.7%). None of the differences in metacone frequencies between the sexes are statistically significant.

A somewhat different pattern emerges for reduction of the hypocone. Like the metacone, both males and females are marked by ubiquitous retention of a fully developed hypocone on UM1 (males= 100.0%, females= 100.0%). By contrast to the metacone, however, both males and females exhibit a high frequency of hypocone reduction on UM2. This reduction is more common among females, for full expressions of the hypocone nearly three times rarer among females (10.0%) than among males (27.1%). Males and females exhibit near ubiquitous (3.8%) or ubiquitous (0.0%) reduction of the hypocone on UM3. While chi-square tests reveal no significant differences by sex for hypocone reduction on either UM1 or UM3, the much great frequency of hypocone reduction in females on UM2 is statistically significant.

As noted above, metaconules are quite rare among the Madaklasht and this rarity is expressed with near equality by sex, with females (3.1%) exhibiting slightly higher frequencies than males (2.4%) for UM1, but males (12.9%) possessing slightly higher frequencies than females (10.4%) for UM2. However, males and females differ with respect to the presence of this cusp on UM3. The metaconule is universally absent among Madaklasht females (0/2= 0.0%), but is found among nearly one-fifth of males (5/26= 19.2%) among whom this trait could be scored. Nevertheless, despite this disparity, chi-square analysis fails to find any significant differences in metaconule frequency between the two sexes. For UM3, this likely reflects the impact of extremely small sample sizes, especially for females.

Carabelli's trait is very commonly found on the mesiolingual cusp of UM1 and occurs with virtually identical frequency among males (73.8%) and females (74.0%). By contrast, Carabelli's trait is universally absent on UM3s, regardless of sex. It is for UM2, however, that males and females among the Madaklasht differ in Carabelli's trait presence, for females express this trait nearly twice as often (24.7%) as their male counterparts (13.9%). Nevertheless, chi-square analysis fails to identify any significant differences in Carabelli's trait frequencies by sex among the Madaklasht.

The parastyle is extremely rare among the Madaklasht, for this accessory cusp, found on the buccal aspect of the maxillary molars, is entirely absent from the UM1s and UM2s of both males and females. The only example of this accessory cusp was found on a UM3 of a male. Not surprisingly, chi-square analysis fails to identify any significant sex differences in parastyle frequency among males and females from Madaklasht.

Extensive reduction of the mesiodistal dimension of the tooth crown, or pegging, occurs for both UI2 and UM3 among Madaklasht males and females. Pegging of UI2 is more common among females (9.4%) than among males (5.9%), and the same holds for UM3 (females= 25.0%; males= 6.9%). In

Table 3: Chi-square Analysis of Dichotomized Trait Frequencies among the Madaklasht by Tooth

Maxilla							
		T1[1]		T2			
Trait	Contrast	Pres.	n	Pres.	n	X^2	Prob.
SHOV	I1 vs. I2	122	178	84	175	7.227	0.007
SHOV	I1 vs. C	122	178	62	174	38.191	0.000
SHOV	I2 vs. C	84	175	62	174	11.442	0.001
DSHOV	I1 vs. I2	40	177	20	176	7.896	0.005
DSHOV	I1 vs. C	40	177	10	176	20.773	0.000
DSHOV	I1 vs. P3	40	177	5	180	31.827	0.000
DSHOV	I2 vs. C	20	176	10	176	3.644	0.056
DSHOV	I2 vs. P3	20	176	5	180	10.047	0.002
DSHOV	C vs. P3	10	176	5	180	1.859	0.173
IGRV	I1 vs. I2	1	178	37	171	39.926	0.000
MLR	I1 vs. I2	125	178	63	177	42.726	0.000
MLR	I1 vs. C	125	178	78	168	20.183	0.000
MLR	I2 vs. C	63	177	78	168	4.187	0.041
PCSP	P3 vs. P4	13	180	13	162	0.078	0.780
PRDG	P3 vs. P4	70	179	109	170	21.833	0.000
META	M1 vs. M2	183	183	158	161	1.622	0.203
META	M1 vs. M3	183	183	6	29	154.704	0.000
META	M2 vs. M3	158	161	6	29	118.316	0.000
HYPO	M1 vs. M2	181	181	27	150	236.188	0.000
HYPO	M1 vs. M3	181	181	1	28	191.948	0.000
HYPO	M2 vs. M3	27	150	1	28	2.697	0.101
MTCLE	M1 vs. M2	5	178	17	147	9.780	0.002
MTCLE	M1 vs. M3	5	178	5	28	8.828	0.003
MTCLE	M2 vs. M3	17	147	5	28	0.372	0.542
CARA	M1 vs. M2	133	180	33	168	102.498	0.000
CARA	M1 vs. M3	133	180	0	31	61.962	0.000
CARA	M2 vs. M3	33	168	0	31	7.300	0.007
PARA	M1 vs. M2	0	179	0	162	0.000	1.000
PARA	M1 vs. M3	0	179	0	26	0.000	1.000
PARA	M2 vs. M3	0	162	0	26	0.000	1.000
PEG	I2 vs. M3	14	181	3	33	0.000	1.000
CABS	I2 vs. P4	4	183	0	161	1.913	0.167
CABS	I2 vs. M3	4	183	2	33	0.451	0.502
CABS	P4 vs. M3	0	161	2	33	4.814	0.028

Table 3 Continued.....

Mandible							
		T1		T2			
Trait	Contrast	Pres.	n	Pres.	n	X^2	Prob.
LCSP	P3 vs. P4	81	181	40	178	19.936	0.000
LCF	P3 vs. P4	61	107	8	178	107.324	0.000
LGRV	P3 vs. P4	126	181	27	176	100.441	0.000
YGRV	M1 vs. M2	115	142	38	144	85.667	0.000
YGRV	M1 vs. M3	115	142	4	25	43.832	0.000
YGRV	M2 vs. M3	38	144	4	25	1.231	0.267
CSPN	M1 vs. M2	158	176	36	160	155.439	0.000
CSPN	M1 vs. M3	158	176	5	22	55.887	0.000
CSPN	M2 vs. M3	36	160	5	22	0.000	1.000
DWKL	M1 vs. M2	60	162	3	170	67.124	0.000
DWKL	M1 vs. M3	60	162	0	25	13.634	0.000
DWKL	M2 vs. M3	3	170	0	25	7.464	0.006
PROTO	M1 vs. M2	29	181	17	178	3.364	0.067
PROTO	M1 vs. M3	29	181	2	25	0.567	0.451
PROTO	M2 vs. M3	17	178	2	25	0.000	1.000
C5	M1 vs. M2	158	176	36	165	160.350	0.000
C5	M1 vs. M3	158	176	14	23	12.131	0.000
C5	M2 vs. M3	36	165	14	23	15.769	0.000
C6	M1 vs. M2	9	177	2	165	4.114	0.043
C6	M1 vs. M3	9	177	4	21	3.907	0.048
C6	M2 vs. M3	2	165	4	21	13.699	0.000
C7	M1 vs. M2	10	176	1	163	6.924	0.009
C7	M1 vs. M3	10	176	2	23	0.011	0.916
C7	M2 vs. M3	1	163	2	23	3.985	0.041
CABS	I1 vs. P4	0	185	0	181	0.000	1.000
CABS	I1 vs. M3	0	185	0	33	0.000	1.000
CABS	P4 vs. M3	0	181	0	33	0.000	1.000

1. T1 and T2 stand for the first and second members of a tooth contrast by trait, respectively.

neither case is the difference in frequency significant. In the latter case, this is largely a consequence of small sample sizes, especially for females (n= 4).

Non-antemortem missing teeth are generally quite rare in this sample of adolescents and young adults from Madaklasht. Indeed, the sampling strategy was designed to achieve this very end (see also Hemphill 1991; Hemphill et al. 1991; 1994, in press). Nevertheless, likely congenital absence was observed for both UI2 and UM3, but no cases of likely congenital absence of UP4 were observed. Likely congenital absence of UI2, although rare, occurs more than three times more often among males

(5/85= 3.6%) than among females (1/95= 1.0%). Likely congenital absence of UM3 was not observed in this sample of Madaklasht females, but was observed in two cases (2/28= 7.1%) among males.

Mandibular Anterior Teeth

The development of ridges along the lingual surfaces of the mesial and distal margins (*i.e,* shovelling) of mandibular anterior teeth is far less common than among their maxillary isomers (see Scott and Turner 1997). These ridges occur at moderate to low frequency among the Madaklasht and are more common among males (24.4%) than females (17.5%). A similar pattern holds for the distal accessory ridge on the mandibular canine. That is, frequencies are far lower than among their maxillary counterparts and frequencies are markedly higher among males (14.5%) than females (6.2%). Although the difference in the distal accessory ridge frequency approaches statistical significance (X^2= 3.303, p= 0.069), neither this trait nor shovelling of the anterior teeth differs significantly between males and females.

Mandibular Posterior Teeth

As noted for the Madaklasht overall, the model number of lingual cusps for LP3 is one, but often the lingual cusp is completely absent. In a similar fashion, the modal number of cusps for LP4 is also one, but a second lingual cusp occurs regularly, albeit rarely (see Kraus and Furr 1953; Ludwig 1957). Departures from the model number of a single lingual cusp on the mandibular premolars occur quite often among the Madaklasht. Males exceed females in such departures from modality in both teeth (LP3: males= 47.7%; females= 42.1%; LP4: males= 24.1%; females= 21.1%), but these differences are small and are not significant statistically.

A somewhat different pattern emerges for fusion of the lingual cusp apex to the apex of the buccal cusp. Madaklasht males and females exhibit near identity in expression of this trait in LP3 (males= 56.9%, females= 56.8%), but in LP4 females are affected more often (5.3%) than males (3.6%). In neither case do chi-square analyses indicate any significant differences in the expression of this trait by sex.

The presence of a groove, or grooves, on the lingual surface of the mandibular premolars was found on LP3 and LP4 among both males and females from Madaklasht. Females exhibit this trait more often (73.2%) than males (65.5%) on LP3, but for LP4 the relationship is reversed with males exhibiting grooves slightly more often (15.9%) than females (14.9%). Once again, chi-square analyses fail to detect any significant difference in expression of this trait by sex for either LP3 or LP4.

The anterior fovea is commonly expressed on LM1 among the Madaklasht. Trait expression is only slightly more common among females (89.2%) than among males (87.0%). The difference between the two sexes is not statistically significant.

Both males and females among the Madaklasht exhibit decreasing frequencies of the Y-occlusal groove pattern from LM1 to LM2 to LM3. Frequencies of the Y-occlusal groove on LM1 are nearly identical for males (81.8%) and females (80.3%), but females exhibit this groove pattern more often than males on both LM2 (females= 29.1%; males= 23.1%) and LM3 (females= 25.0%; males= 14.3%). Chi-square analyses indicate that none of these differences in Y-occlusal groove frequency are significant between the two sexes.

Table 4. Chi-square Analysis of Dichotomized Trait Frequencies among the Madaklasht by Sex.

Maxilla							
		Females		Males			
Trait	Tooth	Pres.	n	Pres.	n	X^2	Prob.
SHOV	I1	71	95	51	83	3.269	0.057
SHOV	I2	41	92	41	81	0.633	0.426
SHOV	C	34	91	28	76	0.005	0.945
DSHOV	I1	22	95	17	82	0.151	0.698
DSHOV	I2	9	94	11	82	0.641	0.423
DSHOV	C	7	93	3	83	0.629	0.428
DSHOV	P3	2	96	3	84	0.023	0.880
IGRV	I1	0	94	1	84	0.003	0.955
IGRV	I2	15	90	22	81	2.769	0.096
MLR	I1	67	94	58	84	0.105	0.745
MLR	I2	37	96	26	81	0.796	0.372
MLR	C	39	92	39	76	1.333	0.248
LC	I1	49	95	44	85	0.001	0.980
DAR	C	50	95	31	78	2.857	0.091
PCSP	P3	6	96	6	83	0.068	0.794
PCSP	P4	7	93	6	79	0.000	0.987
PRDG	P3	42	95	28	78	1.229	0.268
PRDG	P4	63	93	46	77	1.172	0.279
META	M1	96	96	85	85	0.000	1.000
META	M2	84	85	74	76	0.010	0.922
META	M3	2	3	19	27	0.000	1.000
HYPO	M1	96	96	85	85	0.000	1.000
HYPO	M2	8	80	19	70	7.433	0.006
HYPO	M3	0	2	1	26	0.000	1.000
MTCLE	M1	3	96	2	82	0.000	1.000
MTCLE	M2	8	77	9	70	0.218	0.640
MTCLE	M3	0	2	5	26	0.000	1.000
CARA	M1	71	96	62	84	0.001	0.982
CARA	M2	22	89	11	79	3.090	0.079
CARA	M3	0	3	0	28	0.000	1.000
PARA	M1	0	95	0	84	0.000	1.000
PARA	M2	0	86	0	76	0.000	1.000
PARA	M3	0	2	1	24	0.000	1.000
PEG	I2	9	96	5	85	0.771	0.380
PEG	M3	1	4	2	29	0.064	0.800
CABS	I2	1	96	3	84	0.367	0.545
CABS	P4	0	93	0	84	0.000	1.000
CABS	M3	0	5	2	28	0.000	1.000

Table 4 Continued.....

		Mandible					
		Females		Males			
Trait	Tooth	Pres.	n	Pres.	n	X^2	Prob.
SHOVA	Ant.	17	97	20	82	1.277	0.258
DAR	C	6	97	11	76	3.303	0.069
LCSP	P3	40	95	41	86	0.566	0.452
LCSP	P4	20	95	20	83	0.236	0.627
LCF	P3	42	74	37	65	0.000	0.984
LCF	P4	5	95	3	83	0.028	0.867
LGRV	P3	71	97	55	84	0.799	0.371
LGRV	P4	14	94	13	82	0.031	0.860
AF	M1	83	93	60	69	0.201	0.654
YGRV	M1	61	76	54	66	0.055	0.814
YGRV	M2	23	79	15	65	0.669	0.413
YGRV	M3	1	4	3	21	0.000	1.000
CSPN	M1	83	95	75	81	1.300	0.254
CSPN	M2	18	85	18	75	0.182	0.670
CSPN	M3	3	3	14	19	0.073	0.788
DWKL	M1	30	91	30	71	1.475	0.225
DWKL	M2	1	91	2	79	0.015	0.902
DWKL	M3	0	4	0	21	0.000	1.000
PROTO	M1	12	96	17	85	1.885	0.170
PROTO	M2	7	94	10	84	1.021	0.312
PROTO	M3	1	4	1	21	0.131	0.717
C5	M1	83	95	75	81	1.300	0.254
C5	M2	18	89	18	76	0.288	0.592
C5	M3	3	3	14	19	0.073	0.788
C6	M1	6	95	3	82	0.211	0.646
C6	M2	0	89	2	76	0.682	0.211
C6	M3	1	3	3	18	0.000	1.000
C7	M1	2	94	8	82	3.439	0.064
C7	M2	0	82	1	81	0.000	1.000
C7	M3	0	4	2	19	0.000	1.000
CABS	I1	0	98	0	87	0.000	1.000
CABS	P4	0	96	0	85	0.000	1.000
CABS	M3	0	6	0	27	0.000	1.000

Possession of high cusp number, due to retention of the hypoconulid, follows the same pattern among Madaklasht males and females in which frequencies are lowest for LM2. Males tend to retain the hypoconulid more often in both LM1 (92.6%) and LM2 (24.0%) than females (LM1= 87.4%; LM2= 21.2%), but in LM3 this relationship is reversed (females= 100.0%; males= 73.7%). This reversal is a likely consequence of the low number of observations for this trait on the LM3 of Madaklasht

females. Chi-square analyses reveal no significant differences in cusp number by sex among any of the mandibular molars among the Madaklasht.

Presence of the deflecting wrinkle exhibits the same decline in frequency from mesial to distal members of the mandibular molars as described for the Y-occlusal groove above. However, unlike the Y-occlusal groove, Madaklasht males exceed their female counterparts in deflecting wrinkle frequencies for both LM1 (males= 42.3%; females= 33.0%) and LM2 (males= 2.5%; females= 1.1%). The deflecting wrinkle is completely absent from LM3 among both males and females. Chi-square analyses indicate that there are no significant differences in deflecting wrinkle frequencies by sex among the Madaklasht.

As noted above, the protostylid is rather uncommon among the Madaklasht and, when present, is nearly always expressed as a buccal pit (grade 2). Males feature higher frequencies of the protostylid on LM1 (20.0 %) and LM2 (11.9%) than females (LM1= 12.5%; LM2= 7.4%), but for LM3 this relationship is reversed (females= 25.0%; males= 4.8%). Chi-square analyses indicate that none of these differences between males and females are significant.

Presence of the hypoconulid follows the pattern for mandibular molar cusp number described above. However, since the latter includes all molars that possess *either* a hypocomunlid or an entoconulid as a positive manifestation (but not the metaconulid, see Turner et al 1991), the frequencies for C5 among males and females are somewhat different. The hypoconulid is commonly found on LM1 among both males and females, but is more often absent on LM2. In both cases, males retain the hypoconulid more often than their female counterparts (LM1: males= 92.6%, females= 87.4%; LM2: males= 23.7%, females= 20.2%). The hypoconulid occurs far more often on LM3, reaching unity among females (100.0%), but not among males (73.7%). None of these differences in the frequency of hypoconulid presence are significantly different between males and females.

Development of the hypocone (C5), as reflected by the size of this cusp, exhibits a similar pattern for both sexes for LM1. Both Madaklasht males and females most commonly possess a slightly diminished expression (grade 4) of this cusp (males= 50.6%, females= 49.5%), followed by full expression (males= 23.5%, females= 22.1%), and then by a moderate degree (grade 3) of expression (males= 14.8%, females= 15.8%). Low expressions (grades 1-2) are rare among Madaklasht males (3.7%) and are completely absent among females. Some minor differences distinguish hypocone development in Madaklasht males and females. For males, the most common manifestation is a slightly diminished expression (grade 4= 9.2%), followed closely by moderate expressions (grade 3= 7.9%). By contrast, this relationship is reversed among females (grade 3= 10.1%, grade 4= 4.5%). Both sexes are marked by similar frequencies of full (grade 5: males= 3.9%; females= 3.4%) and low expressions (grades 1-2: males= 2.6%; females= 2.2%). Chi-square tests indicate that there are no significant differences in the frequency of fully developed expressions of the hypocone between Madaklasht males and females.

As noted above for the Madaklasht as a whole, the entoconulid (C6) is rare in this population. Frequencies among both males and females tend to be highest on LM3, but this may be a consequence of the lesser number of observations made for the trait on this tooth. Females tend to exhibit the entoconulid more often on LM1 (6.3%) than males (3.7%), but this relationship is reversed

for LM2 (males= 2.6%; females= 0.0%). None of these differences in entoconulid frequency by tooth are significant between Madaklasht males and females.

The metaconulid (C7) also occurs rarely among the Madaklasht, but unlike the entoconulid described above, the distribution of the metaconulid reflects a distinctive distribution by sex. Frequencies of the metaconulid are higher among males for all three mandibular molars. The metaconulid is found in 9.8%, 1.2%, and 11.1% of LM1s, LM2s, and LM3s, respectively, for which observations could be made among Madaklasht males. By contrast, metaconulid frequencies among females are 21.3%, 0%, and 0% for these same teeth. Although none of these differences in frequency are significant, the difference in metaconulid frequency on LM1 approaches statistical significance (X^2= 3.439, p= 0.064, see Table 4).

Despite nearly 400 observations, not a single example of non-antemortem tooth loss was observed among the Madaklasht for either LI1, LP4, or LM3. Consequently, there is no difference by sex in the occurrence of such absences.

Discussion

Morphology of the Maxillary Teeth

A total of 38 maxillary tooth-trait combinations were scored among the Madaklasht. Traits range in frequency from complete fixation (100%) to complete absence. The most commonly expressed maxillary traits among the Madaklasht are retention of a fully expressed metacone (cusp 3) and hypocone (cusp 4) on UM1, which were found in every individual where these traits could be assessed. Four traits were completely absent among the Madaklasht. These include the presence of Carabelli's trait on UM3, the parastyle on UM1 and UM2, and non-antemortem absence of UP4.

For purposes of discussion, the remaining 32 tooth-trait combinations are trichotomized into high, medium, and low frequency traits. High frequency traits are those found in more than half of the cases available for analysis, medium frequency traits occur in 10 to 49.9% of cases, and low frequency traits occur in less than 10% of cases. When trichotomized in this fashion, the Madaklasht exhibit seven, 13, and 12 high, medium, and low frequency tooth-trait combinations in the maxilla, respectively.

The most commonly non-fixed tooth-trait combination found in the maxillary teeth of the Madaklasht is a fully expressed metacone on UM2 (98.1%). This is followed by the presence of Carabelli's trait on UM1 (73.9%), the median lingual ridge on UI1 (70.2%), and retention of a fully expressed metacone on UM3 (68.5%). However, with respect to the last of these traits, the relatively low number of observations (n= 29) renders the high frequency found among the Madaklasht somewhat questionable. Other traits found in rather high frequencies include shovelling of UI1 (68.1%), accessory ridges on the occlusal surface of UP4 (63.7%) and curvature of the labial surface of UI1 (51.7%).

Tooth-trait combinations found with moderate frequencies among the Madaklasht can be further divided into those found in high-moderate frequencies, defined as those found between one-fourth and one-half of those Madaklasht individuals for whom these traits could be assessed, and those found in low-moderate frequencies, which is defined here as those found among greater than 10%, but less than 25% of the Madaklasht.

A total of six maxillary tooth-trait combinations are found in high-moderate frequencies. The most common are shovelling of UI2 (47.6%), development of the median lingual ridge on UC (46.9%), and the presence of a distal accessory ridge on this same tooth (46.2%). Somewhat less common is the presence of an accessory ridge on the occlusal surface of UP3 (40.1%), shovelling on UC (37.1%) and median lingual ridge development on UI2 (35.3%).

Seven maxillary tooth-trait combinations occur with low-moderate frequency among the Madaklasht. The most common of these are double shovelling on UI1 and interruption grooves on UI2, both of which are found at identical frequencies (21.9%). Somewhat less common is Carabelli's trait on UM2 (19.3%), followed by the presence of a fully developed hypocone and by the presence of the metaconule on this same tooth, the latter of which occur with the same frequency (18.6%) among the Madaklasht. The least common tooth-trait combinations that occur with low-moderate frequency are pegging of UM3 (15.9%) and double shovelling on UI2 (11.5%).

Some 12 tooth-trait combinations are present among the Madaklasht at low frequencies. The most common of these are the presence of the metaconule on UM3 (9.6%), pegging of UI2 (7.6%), the presence of accessory cusps on UP4 (7.6%) and UP3 (6.7%), and double shovelling of UC (5.6%). Somewhat less common are non-antemortem absence of UM3 (3.6%), double shovelling of UP3 and the presence of the metaconule on UM1, both of which affected the same proportion of Madaklast dentitions (2.8%) that could be assessed for these traits. The least common tooth-trait combinations found in the maxillary teeth of the Madaklasht are non-antemortem loss of UI2 (2.3%), the presence of the parastyle (2.1%) and a fully developed hypocone (1.9%) on UM3, and the presence of an interruption groove on the lingual surface of UI1 (0.6%).

Morphology of the Mandibular Teeth

A total of 33 mandibular tooth-trait combinations were scored among the Madaklasht. Unlike their maxillary counterparts, none of these tooth-trait combinations were found to reach fixation in the mandible. However, as seen in the maxilla four tooth-trait combinations were completely absent from the Madaklasht dentition. These include the presence of the deflecting wrinkle on LM3, and non-antemortem absence of LI1, LP4, and LM3. Classification of the remaining 29 mandibular tooth-trait combinations frequencies into the high, medium and low frequency categories defined for maxillary variations yields six combinations that occur with high frequency, 14 that occur at medium frequency and 13 that occur at low frequency.

The most common mandibular tooth-trait combination found among the Madaklasht is retention of the hypoconulid (90.0%) on LM1. This is followed by the presence of the anterior fovea on this same tooth (88.1%), retention of the hypoconulid on LM3 (86.8%), and the presence of the Y-groove on LM1 (81.0%). Somewhat less common in the Madaklasht mandibular dentition is the lingual groove (69.3%) on LP3 and fusion of the lingual cusp to the buccal cusp (56.8%) on those LP3s marked by a free-standing lingual cusp.

As in the maxilla, mandibular tooth-trait combinations found with moderate frequencies can be further divided into those found in high-moderate frequencies, defined as those found between one-fourth and one-half of those Madaklasht individuals for whom these traits could be assessed,

and those found in low-moderate frequencies, defined as those found among greater than 10%, but less than 25% of the Madaklasht. While such a division results in a fairly balanced division of moderately occurring tooth-trait combinations in the maxilla (six, high-moderate, seven low-moderate), this is not the case for mandibular tooth-trait combinations. Instead, only four tooth-trait combinations can be considered to be of high-moderate frequency, while 10 are of low-moderate frequency. The difference reflects the fact that the average of moderate frequency traits is higher for maxillary tooth-trait combinations (29.3%) than for their mandibular counterparts (22.5%).

The four tooth-trait combinations found with high-moderate frequencies among the Madaklasht include deviations from the normative cusp number on LP3 (44.9%) and presence of the deflecting wrinkle on LM1 (37.6%), as well as a Y-groove on LM2 (26.1%) and the presence of the entoconulid on LM3 (25.0%).

The most commonly occurring tooth-trait combinations found at low-moderate frequency among the Madaklasht are full expressions of the hypoconulid on LM1 (22.8%), retention of this cusp on LM2 (22.6%), and shovelling of the anterior teeth (21.0%). Somewhat less common are the Y-groove on LM3 (19.6%), the protostylid on LM1 (16.3%), retention of the hypoconulid on LM3 (15.8%), a groove on the lingual surface of LP4 (15.4%), the protostylid on LM3 (14.9%), and the presence of a distal accessory ridge on LC (10.3%).

Nine tooth-trait combinations are found in rather low frequencies among the mandibular teeth of the Madaklasht. The most common of these is the protostylid on LM2, which is found in nearly one out of ten (9.7%) individuals whose teeth could be scored for this trait. The next most common tooth-trait combinations are the presence of the metaconulid (C7) on LM1 (5.9%) and LM3 (5.3%). These are followed in frequency by the presence of the entoconulid (C6) on LM1 (5.0%) fusion between the lingual and buccal cusps on LP4 (4.4%) and the presence of fully developed hypoconulids on LM2 (3.7%). The least frequent tooth-trait combinations found among the mandibular teeth of the Madaklasht are the presence of the deflecting wrinkle (1.8%), entoconulid (1.3%) and metaconulid (0.6%) on LM3.

Dental Morphology of the Madaklasht in Continental Perspective

Taken as a whole, the dental morphology of the Madaklasht may be described as follows. The Madaklasht possess maxillary teeth that universally retain full expressions of the metacone and hypocone on UM1, almost always possess full expressions of the metacone, but only a minority of cases feature full expression of the hypocone on UM2. By contrast, the metacone is fully expressed on UM3 among a majority of the Madaklasht. The maxillary teeth also commonly express Carabelli's trait on UM1, albeit at rather low grades of expression, but this trait occurs only among one out of five Madaklasht individuals on UM2 and never on UM3. Median lingual ridges and low grades of shovelling are present on UI1 in just over two-thirds of Madaklasht, while these traits are much less common on UI2. Just under two-thirds of UP4s exhibit accessory ridges on the buccal cusp, while about half of the Madaklasht are marked by curvature of the labial surface of UI1 and by distal accessory ridges on UC. A considerable minority of Madaklasht maxillary dentitions feature accessory ridges on the buccal cusp of UP3 and shovelling of UC, while only about one in five are marked by double shovelling of UI1, interruption grooves on the lingual surface of UI2, and by Carabelli's

trait, full expression of the hypocone and the presence of the metaconule on UM2. Metaconules on UM3, pegging of UI2, accessory buccal cusps on UP3 and UP4, double shovelling of UC, and non-antemortem loss of UM3 appear occasionally in the maxilla of the Madaklasht, while double shovelling of UP3, the metaconule on UM1, non-antemortem loss of UI2, the presence of the parastyle and full expression of the hypocone on UM3 and an interruption groove in the lingual surface of UI1 rarely occur among the Madaklasht.

The mandibular teeth of the Madaklasht are marked by retention of the hypoconulid on LM1 and LM3, but not on LM2. Anterior foveae are commonly found on LM1 as is the Y-groove, while Y-grooves are found only in a minority of LM2s and LM3s. Fusion between lingual and buccal cusps, departures from normative cusp number, and grooves in the lingual surface are commonly present on the lingual surface of LP3, but none of these three traits are as common on LP4. Deflecting wrinkles are commonly found on LM1, but not on LM2, and are never present in LM3. Protostylids are not common among the Madaklasht, but when found tend to be more common on LM3 and LM1 than on LM2. About one in ten Madaklasht dentitions is marked by a distal accessory ridge on the canine, while accessory cusps, apart from the entoconulid on LM3 are only occasionally encountered. Deflecting wrinkles on LM3 and non-antemortem tooth loss of LI1, LP4, and LM3 do not occur among the Madaklasht.

Scott and Turner (1997) provide some comparative data on tooth-trait combination frequencies in regional populations throughout the world. These data can be used to place the dental morphological profile of the Madaklasht into world perspective. Comparative data are available for nine tooth-trait combinations, with three from the maxilla and six from the mandible. For brevity, comparative data from only six of these regions is considered here. These include modern Western Europeans, Southeast Asians, Southern Siberians and Chinese-Mongolians from Scott and Turner's dataset, as well as data on modern Indians and Indo-Iranians. The first four dental series were scored by Turner, while frequencies for the latter two were taken from the literature.

Beginning with the maxilla, Scott and Turner (1997) opt to report data for moderate to strong expressions (grades 3 and above) of shovelling on UI1 for comparative purposes. Frequencies across these six comparative samples range from a high of 72.0% among Chinese-Mongolians to a low of 2.7% among Western Europeans. Moderate to strong expressions of shovelling occurs with a frequency of 12.3% among the Madaklasht. This frequency is very similar to that seen among modern Indians (12.6%) and Indo-Iranians (12.7%), but is much more divergent from that seen in modern Southeast Asians (34.9%) and Southern Siberians (34.9%).

Likewise, for comparative purposes, expressions of Carabelli's trait were limited to tubercular and cuspal expressions (grades 5-7). Frequencies across the six comparative samples range from a high of 27.3% among Western Europeans to a low of 14.0% among Southern Siberians. The Madaklasht have a frequency of tubercular and cuspal manifestation of Carabelli's trait of 23.1% As such, they appear most similar to modern Indians (22.8%), followed by Indo-Iranians (17.6%), with Western Europeans (27.3%) and Southeast Asians (20.8%) somewhat more divergent. The Madaklasht are least like southern Siberians and Chinese-Mongolians (16.2%) for Carabelli's trait.

Complete elimination of the hypocone in UM2, resulting in a 3-cusped molar, varies in frequency across the six comparative samples from a high of 27.4% among Indo-Iranians to a low of 10.8% among Chinese-Mongolians. Complete elimination of the hypocone on UM2 occurs with a frequency of 26% among the Madaklasht. As a result, the Madaklasht are most similar to Indo-Iranians, nearly equally divergent from Western Europeans and modern Indians (22.7%), but markedly divergent from Southern Siberians (14.2%), Southeast Asians (11.5%) and Chinese-Mongolians.

Turning now to the mandible, Scott and Turner (1997) provide comparative data for the same six populations (modern Western Europeans, Southeast Asians, Southern Siberians, Chinese-Mongolians, Indians and Indo-Iranians). Unfortunately, this comparative data is limited to traits found on the molars.

Retention of the conservative Y-groove on LM2 varies from lows of 7.0% and 7.6% among modern Indians and Chinese-Mongolians, respectively, to a high of 27.2% among modern Western Europeans. The Madaklasht, featuring a frequency of 26.1% for this trait, are most similar to these Western Europeans, followed by Southern Siberians (22.2%), Southeast Asians (17.5%) and Indo-Iranians (10.0%).

Presence of the deflecting wrinkle on the occlusal surface of LM1 was found to be rather common among the Madaklasht, occurring among 37.6% of individuals for whom this trait could be assessed. This trait is of remarkably greater frequency in this population than reported by Scott and Turner for the six comparative populations. For in these latter samples, frequencies of the deflecting wrinkle range from a high of 16.9% among modern Indians and Southern Siberians to a low of 5.2% among Western Europeans. This strong departure in the occurrence of the deflecting wrinkle among the Madaklasht could be the product of two potential factors. The first is that if Madaklasht origins are as asserted by the Madaklasht themselves, in which a relatively small founding population entered their current location and then embarked on several centuries of reproductive isolation from other groups, this could easily lead to over- and under-representation of specific genetically controlled anatomical features, such as the deflecting wrinkle (Hamilton 2009; Hartl and Clark 2006; Hedrick 2000; Templeton 2006). Alternatively, such high values may merely reflect a difference in scoring between the author and Turner, despite all efforts to adhere to the guidelines set forth in the ASU Dental Anthropology System (Scott and Turner 1997; Turner et al 1991).

Retention of the hypoconulid (C5) on the occlusal surface of the mandibular molars is considered the conservative condition among members of the superfamily *Hominoidea* (Gregory and Hellman 1926; Swindler 1976). However, in the later stages of human evolution, especially after the development of agricultural production, there appears to have been a trend towards mandibular molar cusp reduction and loss of the hypoconulid results in a four-cusped molar (Gregory 1922; Hellman 1928). Scott and Turner report frequencies of hypoconulid loss in both LM1, where such loss is relatively rare, and in LM2, where loss of the hypoconulid is common.

Loss of the hypoconulid on LM1 ranges across the six comparative samples from a high of 15.1% among modern Indians to a low of 0.2% among Chinese-Mongolians. Loss of the hypoconulid on LM1 among the Madaklasht is relatively common, with 10.0% of individuals exhibiting such loss. As such, frequencies of hypoconulid loss among the Madaklasht are most similar to Indo-Iranians

(13.4%) and Western Europeans (7.8%), with modern Indians somewhat more divergent. The Madaklasht differ strongly from Southern Siberians (2.2%), Southeast Asians (0.7%) and Chinese-Mongolians with respect to this trait.

When loss of the hypoconulid on LM2 is considered, frequencies of such loss differ dramatically across the six comparative samples. Loss of the hypoconulid is most common among modern Indians (84.4%), followed closely by Indo-Iranians (82.0%), with frequencies somewhat lower among Western Europeans (71.1%) and lower still among Southern Siberians (54.2%). By contrast, loss of the hypoconulid on this tooth is relatively rare among Southeast Asians (30.3%) and especially Chinese-Mongolians (20.8%). The Madaklasht feature loss of the hypoconulid with a rate of 78.0%, which places them intermediate in frequency between Indo-Iranians on the one hand, with modern Indians somewhat more distantly removed, and Western Europeans on the other.

The entoconulid (C6) is an accessory cusp found on the mandibular molars. Scott and Turner report frequencies of this cusp on LM1. Frequencies across the six comparative samples range from a high of 35.9% among Chinese-Mongolians to a low of 4.0% among Indo-Iranians. The Madaklasht rarely exhibit this trait on any of the mandibular molars and LM1 is no exception (5.0%). Hence, frequencies of the entoconulid on LM1 among the Madaklasht are very similar to frequencies found among modern Indians (6.0%) and Indo-Iranians, somewhat more divergent from frequencies found in Western Europeans (8.3%) and markedly divergent from Southern Siberians (20.5%), Southeast Asians (32.5%) and Chinese-Mongolians.

The metaconulid (C7) is another accessory cusp found on the mandibular molars and for which Scott and Turner provide frequencies on LM1. Less variation in frequency occurs across the six comparative samples for this trait, for frequencies are universally modest ranging from a high of 9.9% among Southern Siberians to a low of 1.6% among Indo-Iranians. The Madaklasht are marked by the presence of the metaconulid on LM1 with a frequency of 5.9%. As such, the Madaklasht possess nearly identical frequencies of this trait as that found among modern Indians (5.8%) and are somewhat more divergent from Western Europeans (4.5%). The Madaklasht are further distinguished from Southeast Asians (7.3%) and Chinese-Mongolians (7.9%), and stand dramatically apart from Indo-Iranians and southern Siberians with respect to this trait.

A rank-order comparison of differences in the maxillary traits for which comparisons could be made between the Madaklasht and the regional data provided by Scott and Turner indicate that modern Indians are most similar, followed by modern Indo-Iranians and Western Europeans. Modern Indians are closest to the Madaklasht for two traits, shovelling of UI1 and Carabelli's trait on UM1, but are only third-most common for the presence of a fully reduced hypocone on UM2. The Madaklasht appear to be equally distinguished from modern Indo-Iranians and Western Europeans. Modern Indo-Iranians are most similar to the Madaklast for expression of hypocone reduction on UM2, but rank second-most similar and fourth most similar for shovelling of UI1 and expression of Carabelli's trait on UM1, respectively. Western Europeans rank second-most common to the Madaklasht for expression of Carabelli's trait and reduction of the hypocone on UM2, but are third-most similar to the Madaklasht for shovelling of UI1.

A comparison of maxillary trait frequencies clearly identifies Chinese-Mongolians as the most divergent of the comparative samples from the Madaklasht, followed by Southern Siberians and then by Southeast Asians. Chinese-Mongolians stand apart as the most divergent in shovelling frequencies for UI1 and presence of a fully reduced hypocone on UM2, and they are next to the most divergent for Carabelli's trait expression on UM1. Southern Siberians are the most divergent sample from the Madaklasht for expression of Carabelli's trait on UM1, next most divergent for shovelling of UI1, and fourth-most divergent in full reduction of the hypocone on UM2. Southeast Asians on the other hand, are next to the most divergent for full reduction of the hypocone on UM2, are fourth-most divergent for shovelling of UI1, and are just third-most divergent for expression of Carabelli's trait on UM1.

Five traits could be compared by rank order between the Madaklasht and the six regional samples provided by Scott and Turner. The deflecting wrinkle was not considered given its markedly higher presence among the Madaklasht (see discussion in text above). Similar to results obtained from the maxillary teeth, it is clear that the Madaklasht share closer affinities to modern Indians, Indo-Iranians and Western Europeans than to Southeast Asians, Southern Siberians or Chinese-Mongolians. In the former group, rank order comparisons identify Western Europeans as most similar to the Madaklasht, followed by modern Indians, and then by Indo-Iranians. This proximity to Western Europeans appears to be fuelled by similarities in the presence of the Y-groove on LM2 and by the presence of the hypoconulid on LM2. Conversely, the more distant position of modern Indians relative to the Madaklasht yielded by this comparison of mandibular features relative to that seen in the maxilla is solely the consequence of the profoundly lower rate of retention of the Y-groove on LM2 (7.0%) relative to that seen among the Madaklasht (26.1%). By contrast, the more peripheral position of modern Indo-Iranians to the Madaklasht appears to be a consequence of both the lower retention of the Y-groove on LM2 (10.0%) as well as a far lower presence of the metaconulid on LM1 (1.6%; Madaklasht= 5.9%).

Once again, Southeast Asians, Southern Siberians and Chinese-Mongolians are identified as possessing the most distant affinities to the Madaklasht. Chinese-Mongolians, are clearly the most different, possessing the most divergent frequencies for three tooth-trait combinations (C5 on LM1, C5 on LM2, C6 on LM1) and next-most divergent for the other two (Y-groove on LM1, C7 on LM1). South Siberians, with a rank order score of 20 are identified as only slightly more similar to the Madaklasht than are Southeast Asians with a rank order score of 20.5.

Overall, such results indicate that it is to peninsular India, to Indo-Iranians and to Western Europeans that the relatives of the Madaklasht are to be found and not to Southern Siberians, Southeast Asians, or to Chinese-Mongolians. However, this is a very crude comparison involving samples of rather broadly defined provenance. It is unknown to what degree interobserver differences between the author, Turner, and those whose work was drawn from the literature by Scott and Turner (1997) for such a comparison.

The companion paper addresses these shortcomings by providing an in-depth examination of the phenetic affinities possessed by the Madaklasht through a multivariate statistical comparison between the Madaklasht and 1,738 individuals from 19 additional samples that include both prehistoric and living individuals from the Hindu Kush highlands, the Indus Valley, southern Central Asia and peninsular

India. Since all of these samples were either scored by the author or were scored by Lukacs, with whom insignificant levels of differences in scoring were found, this comparison is unlikely to suffer any significant ill-effects due to interobserver differences.

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