Influence of the Interproximal Attrition of Teeth on the Formation of Neanderthal Retromolar Space

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Abstract Sixteen Neanderthal mandibles together with those of five European middle Pleistocene *Homo* specimens, and over one hundred prehistoric Jomon crania from Japan were examined to clarify whether the presence of large retromolar space, one of the unique facial features of Neanderthals, is at least in part a consequence of forward migration of the teeth caused by heavy interproximal attrition. When the Neanderthal and the Jomon samples were divided according to age or magnitude of tooth attrition, the reduction of molar teeth length and the enlargement of retromolar space with the advance of age or tooth attrition were indicated in both samples. The results suggest that the retromolar space is a morphological complex containing heterogeneous factors, one of which is the secondarily acquired one caused by forward migration of the postcanine dentition.

Keywords: retromolar space, teeth, interproximal attrition, forward migration, Neanderthals

Introduction

The retromolar space, one of the characteristic features of the Neanderthal face, is formed between the distal margin of the lower third molar and the anterior margin of the mandibular ramus. The first report of this feature was made by Martin (1926) for La Quina 5 specimen. Coon (1962) recognized the presence of a similar space in La Ferrassie 1 and suggested the association of this feature with facial prognathism of the Neanderthals. On the other hand, Suzuki (1970) pointed out that the relatively small lower molars might be a contributing factor for the formation of the space. Following these explanations, Howells (1975) argued that the characteristic Neanderthal facial feature was deeply related to the forwardly positioned dental arcade and the retromolar space was formed as a consequence of forwardly positioned molar teeth.

In the past few decades, a good number of attempts have been taken to understand

the morphology of facial skeleton of the Neanderthals, especially in terms of its implied biomechanics (for example, Trinkaus, 1984, 1987; Rak, 1986; Spencer and Demes, 1993). The two primary biomechanical models accounting for the Neanderthal facial morphology are Rak's *infraorbital plate* model (Rak, 1986) and Trinkaus' *zygomatic retreat* model (Trinkaus, 1987). Both models assumed that the total facial prognathism of the Neanderthals was caused by the frequent use of anterior dentition for paramasticatory purposes, which resulted in elevated and repetitive biomechanical stress through the facial skeleton.

Rak (1986) explained that the large retromolar spaces were seen as a consequence of the reduction in dental arcade length, with the posterior movement of the anterior ramal margin being a possible but minor contributing factor. On the other hand, the posterior movement of the masticatory muscle region relative to the dentition is at the core of Trinkaus' model for the formation of the retromolar space (Trinkaus, 1987). More recently, Spencer and Demes (1993) argued that an apparent separation of the masticatory muscles relative to the molar dentition suggested by the retromolar space was interpreted as the result of differential anterior migration of the molars and the masseter and temporalis muscles in terms of the efficiency of producing forces on the anterior dentition. Franciscus and Trinkaus (1995) demonstrated that the retromolar space was best seen as a combined result of the reduced dental arcade length and the reduced ramus breadth in the context of little reduction in overall mandibular length.

In the previous analysis of the first author, he noticed that the retromolar space of the Neanderthals is not remarkable in young adult specimens without heavy tooth attrition, but becomes prominent with the advance of age and the progress of tooth attrition as shown in Figure 1 (Nara, 1994). This raises a fundamental question as to whether the formation of the retromolar space is a secondary feature caused in part by the heavy attrition of teeth.

The present study was hence undertaken to examine the possible relationship between

Figure 1 Retromolar spaces of the young adult (a: Saint Césaire) and adult (b: La Ferrassie 1) Neanderthals.

tooth attrition and magnitude of the retromolar space for Neanderthals. Additionally, an examination of a prehistoric population in Japan, the Jomon, was performed as a further test of the above presumption for the formation of retromolar space.

Materials and Methods

In the present study, 5 specimens from the middle Pleistocene (isotopic stages 13-7) and 16 specimens from the late Pleistocene (isotopic stages 5e-3) (Stringer and Gamble, 1993) were examined. The information of the age classes and chronological stages of the specimens was obtained from the literature (Table 1).

The majority of specimens of the Jomon sample are from the middle to the final phases (ca. 5,000-2,500 years B.P.) excavated at various sites in Japan. The number of specimens examined was 87 males and 33 females. The examination was performed in fully adult

Table 1 The middle and late Pleistocene *Homo* specimens

Specimen	I.S.*	Age Class	State	Location**	References
Mauer	13	Young	Cast	Univ. Bx.I	Kraatz (1992)
Arago 2	12	Adult	Cast	Univ. Bx.I	Lumley and others (1982)
Arago 13	12	Young	Cast	Univ. Bx.I	Lumley and others (1982)
Atapuerca 1	8	Young	Cast	Univ. Bx.I	Aguirre and Lumley (1987)
Montmaurin	8-7	Young	Original	Mus. Hom.	Billy and Vallois (1977)
La Chaise 17	5e	Young	Cast	Univ. Bx.I	Debenath (1977)
Ehringsdorf F	5e	Adult	Cast	Univ. Bx.I	Vlček (1993)
Spy 1	4-3	Adult	Original	Ins. Belg.	Fraipont and Lohest (1886)
Spy 2	4-3	Young	Original	Ins. Belg.	Fraipont and Lohest (1886)
La Ferrassie 1	4-3	Adult	Original	Mus. Hom.	Heim (1976)
La Quina H5	4-3	Adult	Original	Mus. Hom.	Martin (1923)
La Quina H9	4-3	Young	Cast	Univ. Bx.I	Martin (1926)
Regourdou	4-3	Adult	Original	Mus. Per.	Piveteau (1963-1966)
Saint Césaire	4-3	Young	Original	Univ. Bx.I	Vandermeersch (1984)
Monte Circeo 3	4-3	Young	Cast	Univ. Bx.I	Sergi and Ascenzi (1955)
Krapina 59	4-3	Young	Cast	Univ. Bx.I	Wolpoff (1979)
Tabun 1	4-3	Adult	Cast	Univ. Bx.I	McCown and Keith (1939)
Tabun 2	4-3	Adult	Original	Nat. His. Mus.	McCown and Keith (1939)
Amud 1	4-3	Adult	Original	Roc. Mus.	Suzuki (1970)
Shanidar 1	4-3	Adult	Cast	Nat. His. Mus.	Trinkaus (1983)
Kebara 2	4-3	Adult	Original	Univ. Tel.	Tillier and others (1989)

*: I.S., Isotopic stage

**: Univ. Bx. I, Université de Bordeaux I

Mus. Hom., Musée de l'Homme, Paris

Ins. Belg., Institute Royal des Sciences Naturelles de Belgique

Mus. Per., Musée du Périgord

Nat. His. Mus., Natural History Museum, London

Roc. Mus., Rockefeller Museum

Univ. Tel., University of Tel-Aviv

specimens only. Complete fusion of the speno-occipital synchondrosis and fully erupted third molars were the two principal criteria employed to determine the adult status. Sex determination was based on visual inspection of the skulls, and pelvis if present. When possible, sex determinations made by previous investigators were consulted.

For estimating the magnitude of retromolar space numerically, two measurements were defined as shown in Figure 2. The length of retromolar space was defined as follows: the shortest length between the distal marginal ridge of the occlusal surface of the third molar and the line connecting the points on the anterior borders of the right and left mandibular rami marked at the same level of the occlusal surfaces of the third molars. The two points were connected by a thread to minimize possible intra-observer error (Figure 3). The

Figure 2 Occlusal and lateral views of the mandible showing the measurement items used in the present study: (1) retromolar space length, (2) retropremolar space length, and (3) lower more length (M80(3)).

Figure 3 The methods for measuring the retromolar space length (a) and the retropremolar space length (b).

second measurement is tentatively called “retropremolar space length” in the present study. This is the length perpendicular to the line described above from the anterior border of the first molar. The two measurements were recorded to the nearest 0.1mm on each side for individuals without any alveolar absorption caused by ante-mortem loss of teeth by dental and/or alveolar diseases, ritual tooth ablation, etc. In addition to the two measurements, one standard measurement, the lower molar length (M80(3); Bräuer, 1988), was recorded. For estimating the magnitude of retromolar space without possible effect of the absolute mandibular size, the “retromolar space index” [(retropremolar space length / lower molar length) *100] was calculated. In the present study, [(retromolar space length / lower molar length) *100] was not used as the retromolar space index, because the length of retromolar space usually gave a negative value in the Jomon cranial series.

Regarding the fossil samples, metric database was formed for well-preserved specimens belonging to the two chronological and taxonomic groups: 1) the middle Pleistocene fossil *Homo* sample, and 2) the late Pleistocene Neanderthal sample. In order to analyze the relationship between the magnitude of retromolar space and age, the young adult and adult specimens were separately grouped. Among the Neanderthal sample, statistical comparison was performed combining both sexes in order to minimize the possible preponderance of either males or females (Turbon and others, 1997). This also produces an increase in intra-group variability that would reinforce the conclusion about any inter-group differences, if present. Regarding the middle Pleistocene sample, no statistical analyses were attempted because of the small sample size.

The male and female specimens were separately analyzed in the Jomon sample. Moreover, three groups were classified based on the magnitude of wear of the lower first molar as: Stage 1, enamel or dentine-dots; Stage 2, dentine-lines; and Stage 3, dentine-plane. These stages correspond respectively to the categories of (1)-(3+), (4)-(4+) and (5)-(6) in Miles (1963).

One way analysis of variance (one way ANOVA) was performed to evaluate the differences in the magnitude of retromolar space between the different stages of age or tooth attrition. In the present study, the analyses were based on total left plus right side measurements. Since the null hypothesis of normal distribution was not rejected at the 5% level in any series of the retromolar space indices, ANOVA was also applied to test the differences of these indices.

All the figures for comparisons of the measurements and indices were drawn using the box and whisker chart method which represents the variate values of the 10th percentile, lower quartile, median, upper quartile, and 90th percentile.

Results

Table 2 gives individual data of the three measurements and one index in the fossil specimens. Although the retromolar space appears in one adult specimen, Arago 2, it is absent or not prominent in the middle Pleistocene young adult specimens. On the contrary, in the late Pleistocene Neanderthal group, all the specimens treated here exhibit the

retromolar space. The adult specimens have generally larger retromolar spaces than the young adult specimens. However, it is noteworthy that the retromolar space is not restricted to the late Pleistocene Neanderthals but also observable in the earlier fossil specimens.

The basic statistics for the Neanderthals of the young adult and adult groups are separately presented in Table 3. Statistical assessments of the magnitude of retromolar

Table 2 Individual metric data on the retromolar space in the fossil specimens

Specimen	R/L ¹⁾	RMS ²⁾	RPS ³⁾	M80(3) ⁴⁾	RMS-Index ⁵⁾	Young/Adult
Mauer	R	0.6	-	-	-	Young
	L	0.0	-	-	-	
Arago 2	R	6.0	-	-	-	Adult
Arago 13	R	-4.6	34.6	42.1	82.19	Young
Atapuerca 1	R	2.8	-	-	-	Young
Montmaurin	R	0.0	35.6	35.1	101.42	Young
	L	0.0	35.1	35.6	98.60	
La Chaise 17	R	7.8	41.1	34.0	120.88	Young
	L	5.6	38.0	32.5	116.92	
Ehringsdorf F	R	8.0	42.1	34.8	120.98	Adult
Spy 1	R	10.0	41.5	32.9	126.14	Adult
	L	8.8	42.8	32.8	130.49	
Spy 2	R	3.2	38.0	34.1	111.44	Adult
	L	5.7	41.1	35.8	114.80	
La Ferrassie 1	R	14.1	45.5	32.4	140.43	Adult
	L	11.0	43.1	35.9	127.89	
La Quina H5	R	8.3	43.3	34.2	126.61	Adult
	L	4.6	40.0	35.9	111.42	
La Quina H9	L	5.2	44.4	35.6	124.72	Young
Regourdou	R	9.0	42.7	33.1	129.00	Adult
Saint Cesaire	R	6.2	39.8	34.0	117.06	Young
Monte Circeo 3	R	3.6	34.8	31.2	111.54	Young
Krapina 59	R	8.0	41.6	34.8	119.54	Young
Tabun 1	R	4.0	36.7	31.2	117.63	Adult
	L	3.0	36.0	33.1	108.76	
Tabun 2	R	6.7	39.9	34.0	117.35	Adult
	L	5.8	38.5	33.0	116.67	
Amud 1	R	12.5	48.5	33.8	143.49	Adult
	L	10.5	43.8	31.8	137.74	
Shanidar 1	R	10.7	41.3	30.8	134.09	Adult
	L	11.5	41.2	30.5	135.08	
Kebara 2	R	10.0	42.6	35.7	119.33	Adult
	L	9.5	41.2	35.2	117.05	

1) R/L, Right side or left side

2) RMS, Retromolar space (mm)

3) RPS, Retropremolar space (mm)

4) M80(3), Lower molar length (mm)

5) RMS-Index, Retromolar space index

space in the two groups are illustrated in Figure 4a using the box and whisker charts. Testing for difference between the two groups by one way ANOVA discloses that the spaces are significantly larger in adult group than in young adult group. Although the differences are not significant, the retropremolar space increases, and the lower molar length decreases with age. The retromolar space indices of the Neanderthal sample are summarized in the same table, and Figure 4b represents the box plot showing distribution of the indices. The retromolar space index, which eliminates possible influence of the absolute size difference of the mandible, is significantly larger in the adult than in the young adult group.

Table 4 summarizes the comparisons of the three measurements and the retromolar space index between the three groups of different stages of tooth attrition for male and female Jomon samples, respectively. Figure 5 illustrates the distribution of retromolar space lengths in three different stages of tooth attrition for each sex. The retromolar space is almost entirely absent in all the stages of attrition of the occlusal surface of M1 in both male and female samples. However, reduction of the lower molar length, and enlargements

Table 3 Summary statistics and results of ANOVA for comparisons between the young adult and adult groups in the Neanderthal sample

Sample	N	RMS		RPS		M80(3)		RMS-Index	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Young adult	8	5.66	1.7262	39.85	2.9091	34.00	1.5372	117.11	4.5760
Adult	18	8.78	2.9944	41.71	2.9441	33.27	1.5758	125.56	10.0618
F-value		7.444*		2.215 (n.s.)		1.198 (n.s.)		5.082*	

*: $P < 0.05$

n.s.: not significant

Figure 4 Box and whisker charts showing the distributions of the retromolar space length (a) and the retromolar space index (b) in the young adult and adult Neanderthal groups. The horizontal lines of the box indicate the variate values of the 1st quartile, median, and 3rd quartile from below to above. The lowest point of the vertical line indicates the value of the 10th percentile, and the highest point the value of the 90th percentile.

of the retromolar and retropremolar space lengths, and the retromolar space index with the advance of tooth attrition are evident in both sexes. With the exception of the lower molar length of the female Jomon, one way ANOVA tests give the results of significant differences ($P<0.001$) in the mean values of the three measurements and the retromolar space index among the three stages of tooth attrition.

When the attrition of the lower third molar is advanced to Stage 3, the line connecting the right and left points on the anterior borders of mandibular rami moves forwards, because at this occlusal level of the third molar the anterior border of the ramus acutely curves forwards to continue with the oblique line of the mandibular body. Consequently,

Table 4 Summary statistics and results of ANOVA for comparisons among three groups of male and female Jomon samples respectively, classified on the basis of the magnitude of M₁ attrition

Sample	N	RMS		RPS		M80(3)		RMS-Index	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Male									
Stage 1	53	-4.05	2.0880	27.48	2.2892	32.29	1.1225	85.14	7.2999
2	49	-2.19	1.8634	28.75	2.0144	31.57	1.2815	91.12	5.5844
3	46	-1.56	1.7036	28.88	1.7931	31.18	1.3702	92.67	5.3806
F-value		23.98***		7.14***		9.73***		20.14***	
Female									
Stage 1	27	-5.04	1.5883	25.20	2.4972	31.04	1.7308	81.09	5.6809
2	18	-2.22	0.7705	28.03	1.3258	30.82	1.1865	90.96	3.1209
3	11	-1.38	1.2464	28.43	2.8800	30.11	1.9544	94.25	4.4653
F-value		41.83***		12.12***		1.27 (n.s.)		42.39***	

***: $P<0.001$
n.s.: not significant

Figure 5 Box and whisker charts representing the distributions of retromolar space length in the three groups of Jomon sample, classified on the basis of the magnitude of M₁ attrition (a: male, b: female).

Figure 6 Box and whisker charts representing the distributions of retromolar space index in the three groups of Jomon sample, classified on the basis of the magnitude of M1 attrition (a: male, b: female).

we can expect a decrease of the retromolar space length in individuals with heavy attrition of the molar teeth. On the contrary, however, enlargements of the retromolar and retropremolar space lengths are observable in the advance of tooth attrition from Stage 2 to Stage 3 in both sexes (Table 4, and Figure 5).

The box plot showing the distribution of retromolar space indices in each sex is presented in Figure 6. Almost the same pattern of increase with the advance of tooth attrition is observed. These results indicate that there is a clear patterning of enlargement of the retromolar space with the progress of tooth attrition.

Discussion

As summarized by Franciscus and Trinkaus (1995), several explanations relating the variation in Neanderthal dentofacial morphology to the high frequency of retromolar space have been put forward (Coon, 1962; Howells, 1975; Rak, 1986; Trinkaus, 1987; Spencer and Demes, 1993; Franciscus and Trinkaus, 1995). These arguments emphasize that some selective forces that produce the prognathic facial features have worked in particular fashion for the formation of retromolar space of the Neanderthals. From these perspectives, biomechanical causes have been suggested (Rak, 1986; Trinkaus, 1987; Spencer and Demes, 1993; Franciscus and Trinkaus, 1995).

The present study reconfirms that the retromolar space is not a specific feature for the "classic" Neanderthals. It occurs more strongly and frequently in the Neanderthals than in the earlier Pleistocene *Homo* in Europe. The present study, moreover, demonstrates that the magnitude of the retromolar space is greater in the adult group than in the young adult group in the same Neanderthal lineage. The observed difference between the young adult and adult groups cannot be ascribed to the absolute size of the mandible as indicated by the consistently different pattern of the retromolar space index.

It is clear that tooth attrition is in general an age-affected phenomenon. Slight movement between neighboring teeth during clenching of the jaws produces wear facets around the

contact points (interproximal attrition), which results in the anterior migration of the postcanine dentition (Hillson, 1996). According to Wolpoff (1970), extensive interproximal wear is seen in all hominids, living and extinct. In a study of American Indians, Hinton (1982) found heavier interproximal wear in archaic than in recent populations, and considered such wear to be a particular feature of hunter-gatherer subsistence. It is well known, moreover, that the Neanderthals show severe tooth attrition (for example, Brace, 1962; Wallace, 1975).

Taking this into account, together with the enlargement of the retromolar space with the advance of age or tooth attrition, the anterior migration of postcanine dentition caused by heavy interproximal attrition can not be ignored for the formation of retromolar space in Neanderthals. The existence of relatively large retromolar space even in the young adult Neanderthal specimens may support the view that the formation of the space is one of the morphological complex explainable mainly in biomechanical terms. At the same time, however, the retromolar space may be regarded at least in part as a secondary feature caused by the heavy attrition of teeth. If this is true, such subsistence-induced changes during life must be observed not only in the Neanderthal lineage but also in recent human populations with the teeth subjected to heavy use.

Begg (1954) reported a remarkable attritional reduction of the length of whole dental arch in Australian Aborigines. The present examination of Jomon people, the prehistoric hunter-gatherers in Japan, further demonstrates the relationship between the enlargement of retromolar space and the forward migration of postpremolar dentition caused by heavy tooth attrition.

Taking all of these into account, the retromolar space, often regarded as an autapomorphic feature of the Neanderthals (Stringer and others, 1984), may be a morphological complex not entirely explainable from the biomechanical context, but containing more heterogeneous factors. The forward migration of the postcanine dentition caused by heavy interproximal attrition must be at least one of these factors.

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