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Lower Third Premolar Rotation in the Krapina Dental Sample

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Abstract

This paper presents some new observations on the Krapina Neandertal dental sample. A number of lower third premolars from this site are rotated in comparison to their expected position relative to the other teeth. We developed a method for accurately describing the rotation for teeth, whether they are in mandibles, included in dental sets or isolated. We compare the frequencies of rotated P_3s in the Krapina sample with those observed in a modern human population and in the available Neandertal population specimens. It appears that the two latter have comparable frequencies of P_3 rotation whereas rotations found in the Krapina sample have a much higher frequency, whether in relation to the total number of teeth or the number of individuals. Bootstrapping in the comparative samples shows that the probabilities of finding the frequencies of rotated P_3s observed at Krapina within the modern and Neandertal lineage groups are very low, below the significance threshold. The Krapina sample thus appears to be unique in its proportion of rotated P_3s. After rejecting a mechanical hypothesis (i. e. lack of space) for explaining this condition, we propose a genetic origin for this condition. We discuss the implications of related individuals utilizing the cave over a long period of time.

INTRODUCTION

The Krapina Neandertal collection is one of the largest series of fossil hominids *(1, 2)*. It provides important information about both physical and behavioral characteristics of Upper Pleistocene European populations (e. g. *3, 4*). Many skeletal parts are well represented within the Krapina sample, and there are abundant dental remains. These have been studied in detail *(5)*, but here we report a special particularity that has received little attention. A number of lower left third premolars from Krapina are rotated clockwise; i.e. their crown's lingual face is turned in a distal direction compared to their expected position. This was first reported by Gorjanović-Kramberger *(3)* on one fossil and by Wolpoff *(5)* on another, but more can be described with an expression of this condition, which raises new questions and issues about the Neandertals from Krapina.

Very few studies have focused on the *in situ* rotation of human teeth. Two of these refer to maxillary and mandibular premolars and attempt the quantification of their relative rotation and growth pattern *(6, 7)*. Moreover, the exact etiology of tooth rotations is not clearly understood. Some authors distinguish rotation from other processes affecting teeth;

for instance Alt and Türp *(8)*, who tend to attribute malpositions to local and exogeneous factors while they refer to genetic explanations for rotated teeth. They base this distinction on the study of upper central incisor rotation by Iizuka *(9)* who showed heritable factors to be linked with this process. On the other hand, local dental conditions – such as late deciduous tooth loss or early loss of permanent teeth – have also been proposed to be the cause of rotated premolars *(10, 11)*. Mechanical and heritable hypotheses do not exclude each other and can be combined, which increases the difficulty of assessing the influence of each factor.

In this paper, we characterize our operational description of mandibular premolar rotation at Krapina and examine its frequency in two comparative samples: in a modern human population, and in the available Neandertal population sample, not including Krapina. Our aim is to estimate the probability of finding the frequency of rotated third premolars observed at Krapina within a modern population and within the Neandertal sample. We use bootstrapping to repeatedly draw random samples, with replacement, of the size preserved at Krapina from these comparative populations, and estimate this probability from the frequency distribution of rotated premolars in the samples. The question is whether the Krapina series can be explained as a random drawing from a population similar to our modern one, or from a broader Neandertal population. If these possibilities can be rejected, the Krapina pattern of premolar rotation is unique to the Neandertals from this site.

MATERIAL

The Krapina sample

The observed Krapina sample that preserves third premolars includes seven mandibles. They are presented in Table 1 and Figure 1. Note that Krapina 59 (KDP 13) is not listed. It is an almost complete mandible with all teeth except both P_3s and the left M_3 (post-mortem loss). This specimen can not be directly included in the discussion because its two anterior premolars are absent. However it was necessary to identify the cause of this loss. As direct observation does not allow any conclusions because shellac and calculus cover the premolars area, we examined the CT images. They show that the right P_3 is broken away with only the lingual half of its root pre-

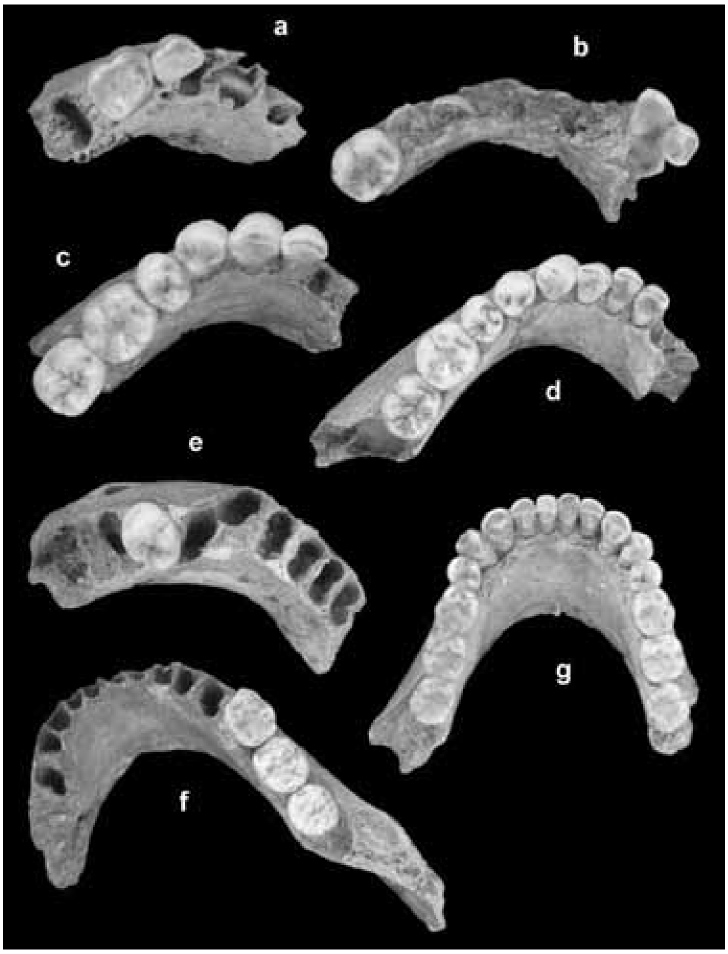

Figure 1. *Mandibles from Krapina in occlusal view (not to scale): a) Krapina 51, b) Krapina 52, c) Krapina 54, d) Krapina 55, e) Krapina 56, f) Krapina 57, g) Krapina 58. Pictures by L. Mjeda – Croatian Natural History Museum/TNT.*

TABLE 1

List of the Krapina mandibles included in the discussion of third premolar rotation.

Krapina mandible	KDP	See figure #	Observations
Krapina 51	7	1a	Fragments of immature mandibular corpus preserving the left premolars germs inside their alveolus; the P_3 position is not measured on these specimens since the premolars are still in the process of erupting. Krapina 51 and 52 bring important information though, and are considered in the discussion section.
Krapina 52	8	1b	
Krapina 54	4	1c	Fragment of left mandibular corpus preserving the left dental set from I_2 to M_2; all the preserved teeth seem to be in a "theoretical" position except for the P_3.
Krapina 55	10	1d	Mandibular fragment including the right I_1, and all the left teeth except the M_3 which alveolus is partly preserved; the left P_3 of Krapina 55 looks rotated clockwise. The other teeth are in their expected position except for the left canine that seems to be slightly rotated.
Krapina 56	11	1e	Fragment with the left P_4 and the alveoli of all incisors, and of the left C, P_3 and M_1; this specimen shows a similar disposition as Krapina 55.
Krapina 57	12	1f	Partial mandible with all right molars and the alveoli of both right and left I_1s to P_4s; the orientation of both P_3s socket looks normal.
Krapina 58	6	1g	Mandibular corpus preserving its complete teeth set including both M_3s; beside the left strongly rotated P_3, all the teeth are well aligned.

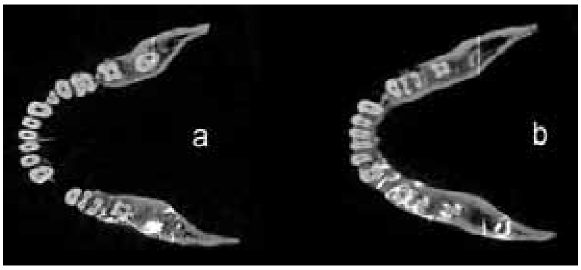

Figure 2. *CT scan of Krapina 59 seen from above illustrating the loss of both P_3s. a) Section showing the preserved mesial fragment of the right P_3's root; b) Section showing the breakage of the mandibular corpus in the left P_3 area. CT images courtesy of J. Radovčić – Croatian Natural History Museum / TNT.*

served (see Figure 2a) while the absence of the left P_3 can be explained by the breakage of this area of the mandible (see Figure 2b). That the tooth was originally present is confirmed by slight interproximal wear facets on both the left canine and fourth premolar. These observations are in agreement with Gorjanović-Kramberger's observation of a break in the mandible at the level of the left P_3 (*3*, p. 159) and of the erosion of the right P_3 from which only a stub remains *in situ* (*3*, p. 161).

Given the explanation above, we observe that none of the Krapina specimens shows evidence of lower P_3 agenesis. This is obvious on the mandibles preserving these teeth and on mandibles preserving the P_3 alveoli. It was also checked on the radiographs of younger specimens for which premolars formation is not fully achieved *(12)*. We examined isolated lower canines and fourth premolars for interproximal wear facets as well, respectively on their distal and mesial faces.

Thus, while the isolated lower third premolars from Krapina are included in our study, only those that were

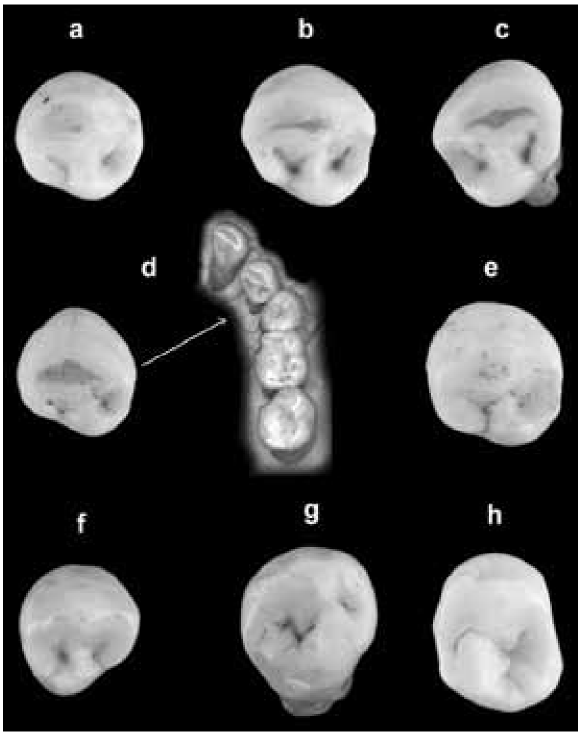

Figure 3. *Isolated mandibular premolars from Krapina in occlusal view (not to scale): a) Krapina 29, rP_3; b) Krapina 25, rP_3; c) Krapina 27, lP_3; d) Krapina 28, rP_3 and arcade of KDP 18 reconstructed; e) Krapina 34, rP_3; f) Krapina 33, lP_3; g) Krapina 32, lP_4; h) Krapina 35, rP_4. Pictures by L. Mjeda – Croatian Natural History Museum/TNT, except KDP 18 arcade reconstruction by MHW.*

erupted and showed interproximal wear facets at the time of death are taken into account in our metrical analysis (Figure 3a-f). We noted the position of the facets since they provide an indication of the position of the tooth in the dental arcade. For example, the lower right P_3 Krapina #29 (ex-KDP 34*) that shows an »asymmetry« facet of the position of its facets (Figure 3a). The distal one is located at the distolingual corner of the crown and the mesial one on the mesial face. We interpret these positions to show that Krapina #29 was rotated counter-clockwise. Its large occlusal wear facet extending onto the buccal face is similar to the condition seen on KDP 18 (see below), though more moderate.

P_3s #25 and 27 are respectively reported to be the right and left teeth of the same individual (KDP 23 – 1,5). They both show interproximal facets situated on their mesial and distal faces, and approximately parallel to each other (Figure 3b,c). There is, then, no hint of rotation for these teeth.

Krapina #28, a right P_3 associated with isolated right canine #145 and P_4 #31 in KDP 18, seems to show the same disposition as on mandible Krapina 55 (Figure 1d) but on the right side (Figure 3d). The right P_3 has a distal interproximal facet situated almost at the distolingual angle of its crown, and no mesial facet, although one would be expected considering its wear stage. We contend that Krapina #28 was shifted lingually and rotated counterclockwise (in this case and others as seen from above), as was previously noted by Wolpoff *(5)*. This explains the absence of contact with the right canine, which shows no distal facet. The right P_4 has a distal interproximal facet at the distolingual angle of the crown and a mesial one almost at the mesiolingual angle. KDP 18's P_4 is thereby slightly shifted buccally compared to M_1 and slightly rotated counterclockwise (Figure 3d). Both P_3 and P_4 show a peculiar occlusal wear with oblique facets that extend on the buccal face of P_3, and that are oblique mesiolingually on both cusps of P_4. The observed positional anomalies of the mandibular teeth lead to contact anomalies with the maxillary teeth, which also show peculiar occlusal wear (see also the description of individual N in Wolpoff *(5)*).

Krapina #34 is the isolated right P_3 associated with the left mandibular fragment Krapina 56 (KDP 11). The right P_3 preserves a distal wear facet located on its crown's distal face and a mesial facet on its mesial face (Figure 3e). The buccal cusp shows a large occlusal wear facet tending to extend on the buccal face. There is no trace of peculiar occlusion for this tooth, and no evidence of rotation.

Krapina #33 is the lower left P_3 of KDP 27 (Figure 3f). It is not fully erupted. It is therefore considered in the discussion section but not included in the metrical analysis.

The Neandertal sample

The Neandertal sample is comprised of all the preserved mandibles or mandible fragments available, plus isolated lower third premolars. Specimens attributed to the whole Neandertal population are considered, except of course those from Krapina. Observations are made on figures published in the literature or original pictures of the specimens. Table 2 lists all the sites where fossils included in this study come from. Note that the Malarnaud 1 mandible has not been included in our Neandertal sample since two of its incisors (central or lateral) are congenitally absent. There has been bone remodeling that can apparently be linked to rotation of both fourth premolars (see pictures in *(13)* and Figure 4). Since we do not know to what extent this process has affected the original position of the P_3s, we rejected this specimen from our comparative sample.

TABLE 2

List of sites from which Neandertal lineage fossils are included in this study.

Amud	La Quina
Arago	Le Moustier
Arcy-sur-Cure	Mauer
Atapuerca – SH	Monsempron
Ehringsdorf	Ochoz
Genay	Regourdou
Goyet	Saint-Césaire
Guattari	Shanidar
Hortus	Spy
Kébara	Tabun
La Chaise – BD	Vindija

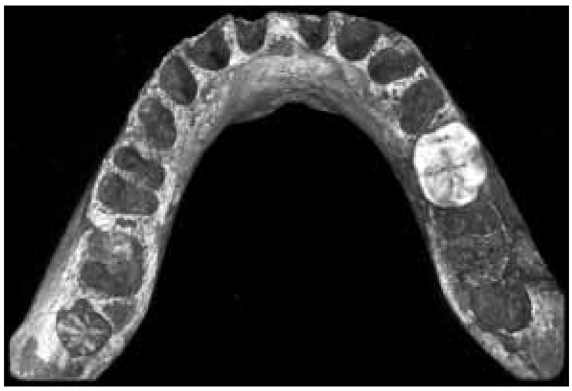

Figure 4. *The Malarnaud 1 mandible in upper view (not to scale) showing bone remodeling of the dental arcade.*

The modern sample

Our modern comparative sample is from within the series from the Coxyde cemetery (Belgium). This collection has excellent preservation *(14)* and premolars are well represented. The selection of the mandibles included in this study was based on several criteria:

* During our study of the collection in September 2005, we determined that the teeth Krapina #29 and #35, previously associated and assigned to the same individual (KDP 34), did not match, and this dental individual was suppressed.

1) Each mandible preserves both lower premolars so that we can compare the bilateral relationship of premolar rotation;

2) Mandibles that show minimal displacement (overlap, diastema,...) within the dental arches and/or rotation of teeth other than the premolars;

3) Mandibles that show no bony rearrangement due to loss of any tooth;

4) Mandibles that show no apparent pathology.

The selected mandibles present all the stages of maturation for M_3s – from absent to fully erupted and functional, on one or both sides. Since we wanted to check whether the development of this molar influenced the position of the other teeth, in particular the rotation of the anterior premolars, we scored three stages for the M_3: absence, presence, erupting.

METHODS

Method for dental sets

The measurement method used to describe rotated vs. not rotated P_3s was adapted from McMullan and Kvam *(6)*. However, these authors developed a method using a standardized arch form that can not be applied to many (fragmentary) fossils. Instead we drew the dental arch shape of each specimen, but we followed McMullan and Kvam's determination of the rotation direction *(6)*; i. e., the lingual face of a tooth being turned clockwise as seen from above, or distally, is labeled as a negative rotation. The two axes we defined are 1) the tangent to the dental arch on the P_3 crown (labeled (1) on Figure 5), and 2) the long axis of the P_3 crown, or the axis along which the buccolingual diameter is taken (labeled *(2)* on Figure 5). To determine these axes, zenithal pictures of the mandibles were printed, and the two axes were drawn manually (as is shown on Figure 5). We defined an orientation angle between the perpendicular to the first axis (dotted line on Figure 5) and the second axis. If the second axis points distally to the perpendicular, the angle value is negative; if it points mesially, the angle is positive.

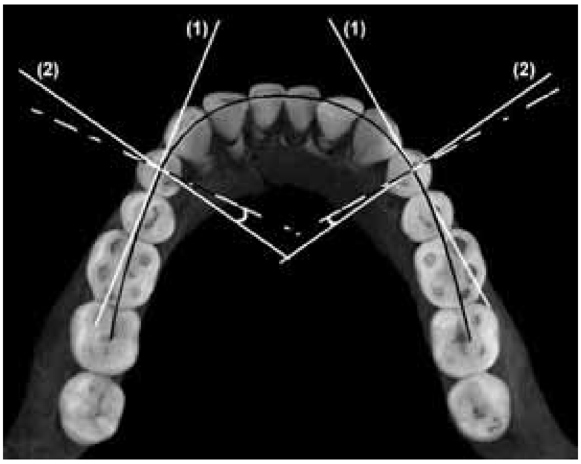

Figure 5. *Representation of the rotation measurement of P_3s: the angle is measured between the perpendicular (dotted line) to axis (1) taken as the tangent to the dental arch on the P_3 crown and axis (2) representing the long axis of the P_3 crown. Note that for isolated teeth, axis (1) is substituted by the axis drawn between the middle of the mesial and distal wear facets of the considered P_3.*

For dental sets, each measurement was taken independently by two of us on both sides of thirty seven mandibles. The inter-observer error was calculated with statistical formula as the difference in our angle determinations for the same tooth. This was ±5° with a 95% confidence interval. McMullan and Kvam *(6)* used Dahlberg's formula ($15 - \Sigma d^2/2n$) to evaluate their method's error. Using the same formula, we obtain a value of 3.5° which is close to the one calculated by McMullan and Kvam (op. cit.: 2.95°). We therefore consider our measurement method for teeth rotation as accurately reproducible.

The relation between the obtained angle value and the macroscopic observation of rotated vs. not rotated P_3s

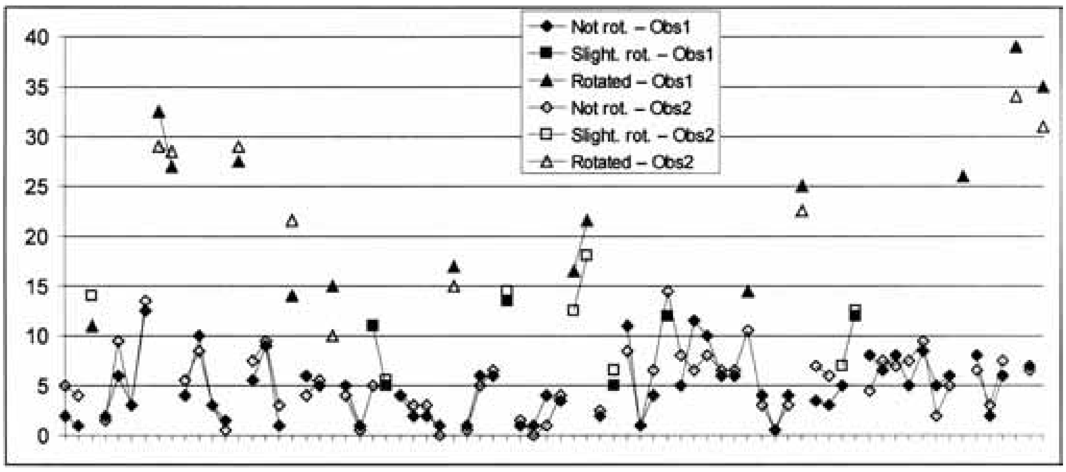

Figure 6. *Measurements of the third premolars rotation of 37 mandibles from our modern comparative sample taken by two of us (observer 1 – Obs1, observer 2 – Obs2) and compared to the corresponding macroscopic appreciation of the rotation (not rotated – Not rot., slightly rotated – Slight. rot., rotated – Rotated).*

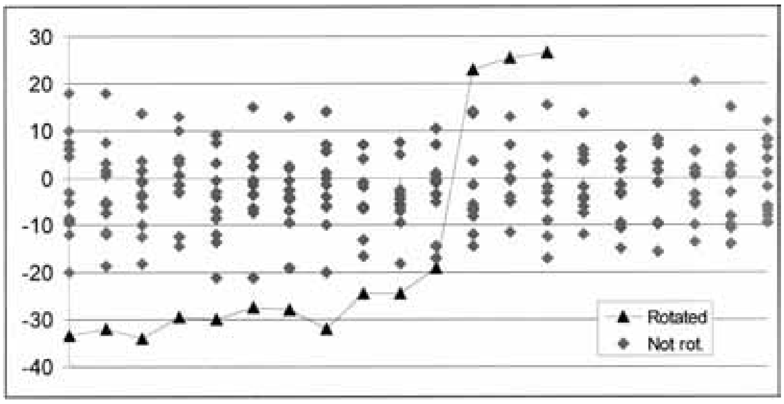

Figure 7. *Measurements of third premolars rotation using the »isolated teeth method« (see text) compared to the measurements taken with the »dental set method« and for which the condition rotated vs. not rotated (Not rot.) has been determined.*

allows us to identify what we define as a rotated premolar. Figure 6 shows that for an absolute value > 22°, both observers consistently agree on recognizing the corresponding tooth as rotated. Based on this result, and to be conservative in our observations, we consider rotated premolars as having an absolute value angle > 22°.

Note that a few fossils, including Krapina mandible #57 (Figure 1f), preserved only their P_3 alveoli. In these cases we substituted the tooth's long axis with the long axis of the alveolus, and kept the 22° criterion that we judge relevant. In these cases, we compared the measured angle and corresponding macroscopic observation to make sure the proposed result (rotated vs. not rotated) was coherent.

Method for isolated teeth

The previous measurement method is only applicable to dental sets and not to isolated specimens. We wanted to include isolated teeth as well since they are often the only remains of fossil individuals. To do so in a comparable manner we developed the following method. We based our assessments on the orientation of interproximal wear facets, since they are the only evidence of the position of an isolated tooth. The measurement is taken between the perpendicular to an axis drawn between the middle of the mesial and distal wear facets of the tooth (instead of axis *(1)* defined for the »dental set method«) and the long axis of the premolars (same as the second axis defined for the previous method, see Figure 5). Negative angles indicate distally rotated teeth, positive ones mesially rotated teeth.

We took this measurement on all the third premolars of the modern sample and checked our results for concordance with the results of the first method. We looked for significant differences between the angles obtained for teeth we consider rotated following the first method, and for not rotated teeth. Figure 7 shows that the method developed for isolated teeth provided equivalent and comparable results for rotated teeth, since the teeth observed as rotated in accordance the first method are distinguished here as well. The angle limit discriminating rotated premolars with the present method appears to be the same as for the previous one, i. e. 22° in absolute value (Figure 7). The facts that interproximal facets change with wear severity and increased age at death, and contacts between adjacent teeth are variable because they depending on the position of the other teeth do not have a critical influence on our angle measurement method for isolated teeth.

The two methods proposed for measuring rotated teeth are comparable and repeatable. Angles superior to 22° in absolute value relate for rotated premolars both in dental sets and for isolated premolars. In the following, only the deduced disposition rotated vs. not rotated is taken into account and discussed.

TABLE 3

Proportions of rotated P_3s with regard to the total number of teeth and individuals in the Krapina, Neandertal population and Coxyde samples.

		Krapina			Neandertal population			Modern sample		
		Left	Right	Total	Left	Right	Total	Left	Right	Total
Teeth	Rotations number	4	0	4	3	0	3	10	4	14
	Total number	6	5	11	26	24	50	112	112	224
	Rotation %	66.7%	0.0%	36.4%	11.5%	0.0%	6.0%	8.9%	3.6%	6.3%
Individuals	Rotations number	–	–	4	–	–	3	–	–	13
	Total number	–	–	7	–	–	34	–	–	112
	Rotation %	–	–	57.1%	–	–	8.8%	–	–	11.6%

RESULTS

Using the methods described above, we determined the proportion of rotated third mandibular premolars in the different samples (Table 3). In the Coxyde sample, 6.3% of the lower P_3s are rotated. This corresponds to 11.6% of the Coxyde individuals. We used a Fisher exact test (two-tailed) for assessing whether there is a difference in P_3 rotation between the left and right sides. Though left P_3s are more often rotated than their right counterparts, the difference (p=0.166) is not statistically significant. The same result is obtained with a Chi^2 test (p=0.098) on the data. Note that this is the only comparison in the present study where the sample sizes are sufficient to use a Chi^2 test. In the following, only the two-tailed Fisher exact test will be applied.

We determined whether there is a relationship between P_3 rotation and the eruption of lower M_3s. In the Coxyde population, 50.0% of the hemi-archs with rotated P_3 show a fully erupted M_3 (7 out of 14 cases) whereas the proportion is 68.6% for the hemi-archs which P_3 is not rotated (144 out of 210 cases). If considering both fully erupted and erupting M_3s, the proportions become respectively 64.3% and 77.2%. In both cases, the differences as shown by a two-tailed Fisher exact test are not statistically significant (p=0.237 and p=0.328 respectively). Therefore, no relationship could be shown between rotation of the lower P_3s and emergence of the lower third molars.

Only three of the specimens representing the Neandertal population show a P_3 rotation (Table 3). The three cases affect left premolars. Note that the La Naulette mandible which left P_3 socket looks rotated clockwise (Figure 8), does not appear rotated after our measurement method.

6.0% of the third premolars from the Neandertal population sample are rotated. This represents 8.8% of the individuals from this group. Left P_3s tend to be more frequently rotated than their right counterpart but they do not show a significantly different distribution (two-tailed Fisher exact test result is: p=0.236). The frequencies of rotated P_3s observed in the Neandertal population sample are comparable with those for Coxyde. This is also shown by a two-tailed Fisher exact test comparing the proportions of rotated premolars in the two groups (Table 4).

Figure 8. *The La Naulette mandible in upper view (not to scale).*

In the Krapina sample, four teeth are rotated. They are all from the left side (isolated P_3 #29 and mandibles #54, 55, 56 and 58). The other two left P_3s measured show a standard position (isolated tooth #27 and left P_3 from mandible #57). All the right third premolars appear well aligned with our measuring method (isolated P_3 #25 and 34 – associated with mandible 56 –, and mandibles #57 and 58). This represents 36.4% of the teeth and more than half of the Krapina individuals (57.1%). The difference in rotated teeth between the right and left sides is very close to significance (p=0.061).

When comparing the frequency of rotated premolars in the Krapina series and in the modern and Neandertal samples, critical differences appear. All the Fisher exact tests results are significant, both when the proportions of P_3 rotations are related to teeth and to numbers of individuals (Table 4). If we include the Krapina specimens to the Neandertal sample, and then compare its rotation frequencies with those from Coxyde, the statistical results are quite different from those obtained with the

TABLE 4

Results of two-tailed Fisher exact tests for P_3s rotation proportions between the Krapina, Neandertal lineage and Coxyde samples.

		Krapina		Neandertal population		Neand. population including Krapina	
		Teeth	Individuals	Teeth	Individuals	Teeth	Individuals
Neandertal lineage	Teeth	0.016	–	–	–	–	–
	Individuals	–	0.010	–	–	–	–
Modern sample	Teeth	0.006	–	1.000	–	0.172	–
	Individuals	–	0.008	–	0.764	–	0.419

Neandertal sample alone. The rotated teeth proportions do not become statistically different but the resultant Chi[2] probabilities decrease noticeably (Table 4).

These results have been complimented by a random resampling procedure with replacement. We repeatedly (1000 times) drew two samples, identical in size to the Krapina ones for teeth and individuals (n=7 and n=11), from the modern human and the Neandertal samples. We then determined the probability of observing 4 rotated P_3s by noting the frequency of this observation in 1000 randomly generated samples of Krapina size drawn from each comparative sample *(16)*. For each case, the probability of resampling the Krapina frequency was found to be less than p=0.05. The null hypothesis can be rejected (Table 5) and we have shown the likelihood of finding Krapina-like frequencies of rotation in these comparative samples is quite small.

TABLE 5

Probability to observe, after resampling (1000 times) with replacement, the frequency of rotated P_3s present in the Krapina tooth and individual samples size.

	Sample of 11 teeth	Sample of 7 individuals
Modern sample	0.003	0.004
Neandertals	0.002	0.001
Neandertals & Krapina	0.028	0.014

DISCUSSION AND CONCLUSIONS

The Krapina dental sample shows proportions of rotated lower third premolars that are unusual and very different from those encountered in our reference samples. This assessment is conservative because it is quite possible that the observed Krapina frequencies are underestimated. For example, the lower right third premolar Krapina #28 (KDP 18) appears to have been rotated *(see 5)*, Figure 3d, and our description in the Material section) but has not been measured since neither of our two methods could be applied to it (the reconstruction of the mesial side of KDP 18 dental arch is too uncertain given that there is no interproximal facet for the canine on Krapina #28). If this tooth was indeed measured rotated, it would be the only case of a rotated right P_3 within the Krapina sample. We also checked isolated lower P_4s and Cs from this series. The orientation of their interproximal wear facets gives indications of their position on the dental arch and the one of the adjacent teeth. Krapina #32 (KDP 20) is an isolated lower left P4 that shows an interproximal distal facet located at its distolingual angle and a mesial facet at the mesiolingual angle of its crown (Figure 3g). The position of the mesiolingual facet can only be explained by a clockwise rotated P_3 whose lingual face was in contact with the fourth premolar. The condition appears similar to the disposition observed on mandible #56 (Figure 1e), although even more pronounced. On the other hand, the lower right P_4 #35 (ex-KDP 34, now isolated, see note #1) has both its interproximal facets oriented quite parallel to each other (Figure 3h), thus not supporting an interpretation of rotation in the P_3.

A few other Krapina teeth have not been measured for their angle since they were still erupting and the position of a tooth can be very variable until its formation reaches half its root length (Heuzé, pers. comm.). It is of some interest to mention them, because they support our contention that our observations are conservative.

The left premolars of mandible #52 (KDP 8) are still in their sockets but are directly observable since the buccal wall of the mandibular body is broken away. The P_4 is well aligned compared to the dental arch whereas the P_3 appears strongly rotated clockwise (Figure 1b). The observation of isolated left P_3 #33 (KDP 27) shows an interesting configuration as well. It was erupting against the mesial face of the left dm_2 #64 and both show corresponding interproximal facets (P_3's distal facet is high at the distolingual angle of the crown – Figure 3f; dm_2's mesial facet is on its mesial face under a large, pronounced facet for dm_1). P_3 #33 has no mesial interproximal facet yet, but from the position of the distal one, it is possible to conclude that it was erupting rotated clockwise, like the condition seen for individual KDP 18 (Figure 3d).

It is not possible to decide whether the left P_3s of KDP 8 and 27 would have been rotated once their dentition was established. We can only mention the study of McMullan and Richardson *(7)* who observed on a modern population that third premolars erupting rotated tend to recover a less rotated position when the dentition is fully erupted, »but to a lesser extent and less frequently than the second premolars« (*7*, p. 392).

Mandibular P_3 rotation is more frequently on the left side than the right one. This is a tendency observed with greater or lesser significance in all the samples considered. The modern and Neandertal samples show comparable P_3 rotation proportions that are statistically very different from those encountered in the Krapina sample. All the probabilities of drawing the number of rotated teeth or the number of individuals showing at least one rotated P_3 found at Krapina are extremely low in the comparative samples. The configuration found at Krapina could not have been drawn at random within a modern population like Coxyde nor within the other representatives of the Neandertal population with any reasonable likelihood. The Krapina dental sample therefore bears a particularity, and its origin, or causation, is of some interest.

First, a mechanical origin should be considered. We checked whether the observed rotations could be the consequence of the eruption sequence, in that the last of three adjacent teeth to erupt would have to erupt into the space left by the two others. If this space was not big enough, the tooth could merge in an unusual way. This possibility is not implicated in Krapina P_3 rotations. The isolated tooth Krapina #75 (lower right canine) shows a distal wear facet low on its crown indicating that the left P_3 of this individual (no number – the tooth has not been identified) was erupting after its canine. Mandibles #51 and 52 also provide relevant information. Radiographs of Mandible #51 *(12)* show that the eruption sequence of this individual was C – P_3 – P_4, following the most common order found within recent modern populations *(17)*. Mandible #52 does not preserve its left canine but shows the left P_3 as little more advanced in development than the adjacent P_4 (Figure 1b). Finally, no Krapina specimen shows mandibular P_3 eruption later than the adjacent C and P_4.

The radiographs of the Krapina sample *(12)* have also been observed for root configuration in the area of the third premolars, because their rotation could potentially be explained by crowding of the roots of the adjacent teeth in the bone. This again does not appear to be the case at Krapina. Moreover, no link was found between presence of M_3s – and the eventual crowding of the dental arch – and the appearance of P_3 rotation in our modern sample. This is in agreement with Iizuka's *(9)* results and we have no reason to assume a different situation in the Krapina sample. We must also consider the high frequency of rotated P_3s on the *left side*. If local factors were to be involved, processes influencing preferentially the left side would have to be evoked, and there is no basis for this at Krapina. Given all the previous observations, a mechanical hypothesis for P_3 rotation at Krapina is not supported.

We suggest an alternative explanation; a biological origin, an inherited condition common in the Krapina people. This possibility could be a significant factor in interpreting the Krapina assemblage. The stratigraphic provenance is known for only some of the specimens included in this study. Mandibles #58, 54 and 55 come respectively from levels 3, 4 and 5 whereas mandible #57 comes from level 6. The three first specimens have their left P_3 rotated; this is not the case for mandible #57. The sample is too small for the observation to have significance, but we believe a hypothesis of biological relationship among the individuals found in Krapina levels 3 to 5 can be proposed to explain our results. Such a hypothesis is supported by the unusual superior deflection of the internasal suture in the only three Krapina specimens to preserve the suture *(18)*.

The continued or periodic use of the Krapina cave by groups of related individuals over the long periods of time represented by these layers has significant implications for interpreting the ability of these people to communicate across the generations. Especially because few older individuals are known among the Krapina Neandertals, indeed among all Neandertals *(19)*, there was little overlap of second generations, grandparents with grandchildren. Culture, habit, and tradition in the systematic, probably seasonal, occupation of the Krapina cave implies the possibility of a sophisticated formalized communication system that transmits knowledge through story, song, and myth. These are hardly proven facts, but they are compatible with the interpretation of Neandertal burials at Krapina *(20)*, and indeed with the more general contention that the Neandertal folk were human beings.

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