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Revisiting the Question of Neandertal Regional Variability: a View from the Rhône Valley Corridor

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A B S T R A C T

We compared the dental assemblage of the Rhône Valley corridor (RVC) with that of European Neandertals dating to MOIS 7–4 using two linear measurements and three indices. To test if the RVC population was significantly different from Western European Neandertals, we preformed a multi-tiered approached. First, we tested for the normality of the variables using a Shapiro-Wilks test. If the variables were normal, a stepwise Discriminant Function Analysis (DFA) (using Mahalanobis distances) was performed for the normally distributed variables. DFA uses correlation metrics to address weight combinations of variables and emphasizes between group variation while minimizing within group variation. Results show that there is no distinction between the RVC population and other Neandertals except for the Crown Module index of the upper canine. However, the presence of a single significant result does not provide evidence for a local RVC variant within the Neandertal population. These results are supported by evidence from archaeological analysis of this region. We propose that the high genetic control for dental size and shape may account for the reduced ability to distinguish between subpopulation groups based on dental dimensions in groups with small effective size such as the Neandertals.

Key words: *middle paleolithic, Payre, teeth measurements, mobility, isolation*

Introduction

The Rhône Valley corridor (RVC) has long been known as a rich center for Mousterian archaeological and paleoanthropological sites. The Rhône Valley, oriented north to south located in southern France, is composed of low plateaus and rivers. This area is a narrow corridor, and is located between the cities of Lyon in the north and Mediterranean Sea in the south. These plateaus are for the most part made up of calcareous formations. In the northern and western part of the district, the metamorphic and volcanic formations lie on the borders of the Massif Central Mountains and in the eastern part this area is bordered by the Alps. Most of the archaeological sites are located along the Ardèche canyon, in the same area as the Chauvet cave.

The Rhône valley has been associated with Neandertal populations during MOIS 9–3, as is the case in the rest of Europe. Archaeological sites in the region are dated between the MOIS 9–8 (Orgnac 3), MOIS 7–5 (Payre, Moula) and MOIS 4–3 (sites along the Ardèche river). Evidence attests that humans have occupied this area for at least 350,000 years[1–4]. The data suggest that contrary to the northern part of Europe, which was abandoned by hominins during the coldest periods[5,6], the Rhône Valley has been continuously inhabited by humans, perhaps due to its southern location and more ameliorate climate[1,7,8]. The mosaic landscape may explain this continuous occupation, since the raw material locations were probably available wherever there might have been surface vegetation. Its geographic location, ecology and topography has suggested that it may have been a refugium for Neandertals that resulted in identifiable behavioral and morphological characteristics of the population and thus it is unique in comparison to other regions in Europe[9].

Based on archaeological models developed in southwestern France by Bordes[10,11], Combier[9] suggested that

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the Rhône Valley supported a different kind of human settlement pattern. This was supported by the study of de Lumley[12,13] which suggested that the teeth from the Rhône Valley Corridor s*ensu lato*, Hortus (south of the RVC) and Genay (north of the RVC), were smaller than those of other contemporaneous French Neandertal. However, new excavations in the Rhône Valley dating from MOIS 9 to MOIS 4[14,15] did not support the idea that human groups with particular cultural traditions or subsistence strategies inhabited this region.

The question of Neandertal variability within a small geographic context has been discussed as early as the mid 1940's for the Saccopastore Neandertals[16]. Vandermeersch[17] has suggested that cranial features can distinguish the Neandertals of southwestern France from other Neandertal populations. In more recent studies of human fossils from this region (La Chaise Suard and Bourgeois-Delaunay), Condemi[18–20] has supported the hypothesis on the basis of the morphology of the temporal bones (notably in the mastoid area), which is not found among other Neandertals. This feature distinguishes the Neandertals of southwestern France from those originating in the Italian peninsula (Castel di Guido, Saccopastore and Circeo), and in northern Europe with sites like Biache-Saint-Vaast, Spy and Neanderthal. According to this author[18–20], the fossils found in Poitou-Charente (La Chaise Suard and Bourgeois-Delaunay) in southwestern France supports the idea of »a local variability« which can be interpreted as a stable local population subsisting with less gene flow from outside, and which is probably due to favorable climatic conditions in the region[21].

Variability among Western French Neandertals has been also supported on the basis of the postcranial skeleton. On the basis of the morphology of the distal extremity of the humerus, Hambücken[22] advocates separating the European Neandertals into two groups: a Mediterranean group (including the European Neandertals of Hortus (France), Krapina (Croatia) and Lezetxiki (Spain), dated to MOIS 5 to 3, and a »classic« group including Western French Neandertals (notably La Chapelle-aux-Saints, Combe-Grenal, La Ferrassie, Régourdou, Saint-Césaire), Neanderthal (Germany) and Spy (Belgium), dated to MOIS 7 to 3, with most of them dated to MOIS 4.

It has been shown that dental remains are one of the best indicators of human population variability and are under tight genetic control[23]. Therefore, they are optimal for testing hypotheses regarding paleo-population isolation over time. Unfortunately, despite the many sites in the Rhône Valley, only few have published human remains in general and dental remains in particular and which have allowed to test these hypotheses. The site of Payre (Figure 1) located on the border of the valley[7–9] is one of the rare sites in this region to have revealed a relatively large and well preserved dental sample size (n=14) and which provides a unique opportunity to revisit the question of the confinement of the population of RVC. The recently published hominin dental assemblage from the site of Payre[24] allows us to re-examine the position of the Neandertals from eastern France in comparison to other European Neandertal dental assemblage as an example of a paleo-population.

In this paper, we test the hypothesis that the Neandertal population of the RVC (as represented primarily by the sample of Payre) is part of a variant population in relation to other Mousterian populations. Here we present evidence that the Neandertals from eastern France do not differ in dental measurements from Neandertal in both Central and Western Europe. Results of this study will shed light on Neandertal diversity and tooth variability across Europe.

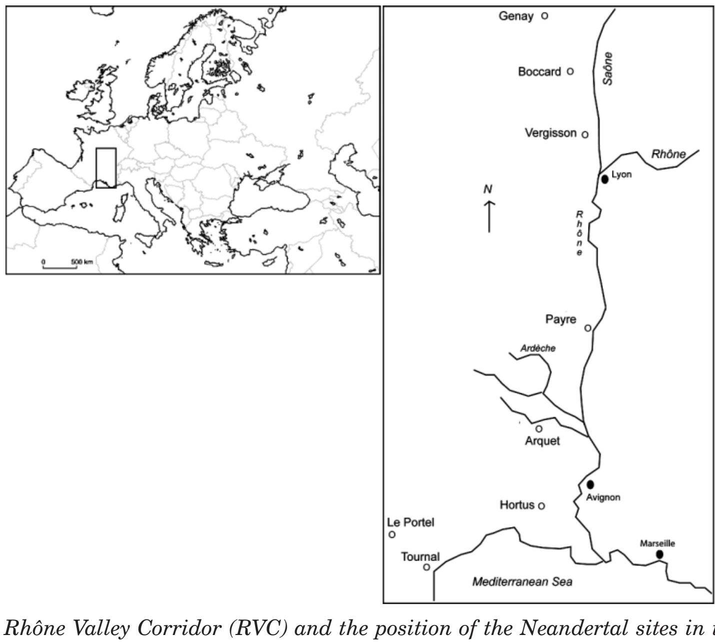

Fig. 1. The Rhône Valley Corridor (RVC) and the position of the Neandertal sites in this region.

Material and Methods

The site of Payre was discovered in the 1950's[9]. Human remains were discovered during excavations conducted between 1990 and 2002[8]. The human remains discovered in Payre are distributed among four layers G, F, E and D. The human remains are, for the most part, located in the oldest level G (MOIS 7)[25]. This level yielded 14 teeth and one parietal bone fragment, which are described elsewhere[24].

There are two approaches to test for dental variability. The first is dental metric variation and the second is the presence/absence of non-metric crown and root traits. The first has been used primarily for the study of diversity within regional populations, while the latter has been used for identification of major taxa/species and inter-regional populations[26]. The aim of this study is to test for the presence of variability within a regional population rather than identify in Neandertal non-metric unique trait combination and tooth form (e.g., the presence/absence of Carabelli's cusp, mid-trigonid crest, asymmetry and Y groove pattern). Analysis of these traits within the Neandertal population did not find a distinction between geographic Neandertal sub-groups[e.g. 27] and it has been shown that some of the non-metric traits are highly correlated with tooth size[28].

Thus, two linear measurements and three indices were used for comparison. The two linear measurements were the mesiodistal (MD) and buccolingual (BL) diameters and were taken with the method recommended by Brauer[29]. Measurements were taken with digital calipers on both modern and fossil specimens to an accuracy of two decimal places. Three indices were calculated based on the two measurements and included the crown module (CM) (calculated as MD diameter+BL diameter)/2; Crown Index (CI) (calculated as (100 × BL diameter/MD diameter and Robustness Index (RI) or crown area, calculated as MD diameter × BL diameter)[23].

The RVC sample included teeth from three sites north of Lyon (Genay, Boccard and Vergisson), the sample from Payre and unpublished teeth from the site of Arquet and three in the south (Hortus, Le Portel and Tournal) near the Mediterranean Sea (Table 1, Figure 1). This group was compared to Neandertal teeth dating from MOIS 7 to MOIS 4 from Western and Central Europe. The measurements for the comparative sample were obtained directly from fossils and augmented by data retrieved from the literature (Table 2). For all samples, we used adult teeth and have excluded specimens, which exhibit extensive occlusal wear.

In comprising our comparative sample, we also excluded specimens derived from the Levant as well as the Far East Neandertal because there has been a discussion about the taxonomic position of the fossils[30,31]. We also excluded Archaic populations which pre date MOIS 7 as their morphology differed to a greater extent from those of last glacial Neandertal[32] and excluded the so-called transitional Neandertals dated to MOIS 3, since during the same time there is evidence in Europe for the presence of *H. sapiens* with claims for interbreeding between the two populations[33–38]. Furthermore, in order to avoid pseudo-replication, only one tooth (i.e. either right or left, depending on state of preservation) from each specimen was included in the analysis.

TABLE 1
RHÔNE VALLEY CORRIDOR (RVC) DENTAL REMAINS ASSOCIATED TO MOIS AND BIBLIOGRAPHICAL REFERENCES. MOST OF THE ANCIENT SITES HAVE GLACIAL STRATIGRAPHY AND NO MOIS ARE AVAILABLE. ALL WÜRM AGES WOULD BE ASSOCIATED WITH MOIS 4

MOIS	Site	Type (number)	Authors
4	Arquet	I_1 (1), I_2 (1), I^1 (1), Pm^3 (1), Pm^4 (1), M_2 (1)	86
4	Boccard	Pm^4 (1)	70
4	Hortus	I^2 (1), M_2 (2	13, 71
4	Le Portel	I_1 (2), I_2 (3), Pm_3 (2), M_2 (2)	72
4	Tournal	I_1 (1), M_2 (1)	72
4	Vergisson	Pm_4 (1)	71, 86
5	Genay	M_2 (1), I_1 (1)	73
7 and 5	Payre	I_1 (1), I_2 (1), Pm_3 (2), M_1 (3), M_2 (1), C^1 (1), Pm^3 (1), M^2 (1)	24

To test if the RVC population was significantly different from Western European Neandertals, we performed a multi-tiered approached. First, we tested for the normality of the variables using a Shapiro-Wilks test. If the variables were normal, a stepwise Discriminant Function Analysis (DFA) (using Mahalanobis distances) was performed for the normally distributed variables. DFA uses correlation metrics to address weight combinations of variables and emphasizes between group variation while minimizing within group variation[39].

If the variables were normally distributed, but the RVC Group was comprised of only one specimen, the comparison between the RVC specimen and the other population means was performed using the single observation means t-test[39]. If a single variable or more was not normally distributed, the Mann-Whitney test was used for these variables.

Multiple comparisons, such as the one performed here, which compared 16 teeth type and at times several measurements per tooth, require adjusting the probability values for the number of simultaneous tests to avoid Type I errors. To increase the power of the test, the Bonferroni method was applied and a p-value of 0.0015 was set as the test criterion of the p-value for an experiment-wise p value of 0.05[39].

All analyses were performed using SPSS (version 16.0) statistical software.

TABLE 2
NEANDERTAL DENTAL REMAINS WHICH NOT BELONG TO THE RVC ASSOCIATED TO MOIS AND BIBLIOGRAPHICAL REFERENCES. MOST OF THE ANCIENT SITES HAVE GLACIAL STRATIGRAPHY AND NO MOIS ARE AVAILABLE. ALL WÜRM AGES WOULD BE ASSOCIATED WITH MOIS 4

MIS	Site	Type (number)	Authors
4	Saint Brais	I_1 (1)	74
4	Spy 1-2	I_1 (1), I_2 (1), Pm_3 (2), M_1 (1), M_2 (2), M_3 (2), C^1 (2), Pm^3 (2), Pm^4 (2), M^1 (2), M^2 (2), M^3 (2)	74
4	La Ferrassie 1-2	M_3 (1), C^1 (1), Pm^4 (1), M^1 (1), M^2 (1)	75
4	La Quina 9	Pm_3 (1), M_1 (1), M_2 (1), M_3 (1)	76
4	La Quina 4-5-18-20-21-22-31-35	I_1 (1), Pm_3 (1), M_2 (2), M_3 (1), C^1 (1), Pm^3 (1), Pm^4 (1), M^1 (2), M^2 (2), M^3 (2)	77
4	Monte Circeo	Pm_3 (1), M_1 (1), M_2 (1), M_3 (1)	74
4	Neanderthal	I^1 (1), I^2 (1), Pm^4 (1), M^2 (2), M^3 (1)	78
4	Regourdou	I_1 (1), M_2 (1)	79, 80
4	Monsempron	Pm_3 (1), I^1 (1), I^2 (2), C^1 (1), Pm^3 (1), Pm^4 (1), M^1 (1), M^2 (2)	83
4	Pech-de-l-Aze	M^1 (1)	74
4	Le Moustier	I_1 (1), I_2 (2), Pm_3 (1), M_2 (1), I^1 (1)	74
4	Le Placard	M_3 (1)	74
4	Montgaudier	I_2 (1), M_1 (1)	71
4	La-Croze-de-Dua	C^1 (1), M^1 (1), M^3 (2)	71
4	Sipka	I_1 (1), I_2 (1), Pm_3 (1)	74
4	Subaluk	I_1 (1), I_2 (1), Pm_3 (1), M_3 (2)	74
4	Shovakh-1	M_3 (1)	81
5	Bourgeois-Delaunay	I_1 (2), I_2 (2), Pm_3 (2), M_1 (1), M_2 (1), M_3 (1), I^1(1), I^2 (1), C (3), Pm^4 (1), M^1 (1), M^2(1), M^3 (1)	19
5	Krapina	I_1 (4), I_2 (4), Pm^3 (6), M_1 (8), M_2 (6), M_3 (9), I^1 (4), I^2 (2), C^1 (7), Pm^3 (8), Pm^4 (9), M^1 (1), M^2 (1), M^3 (2)	31
5	Saccopastore	C^1 (1), Pm^3 (1), Pm^4 (1), M^1 (2), M^2 (1), M^3 (2)	82
5	Ochoz	I_2 (1), M_1 (1), M_2 (1), M_3 (1)	74
5 to 3	Jersey	I_2 (1), Pm_3 (1), M_2 (1), M_3 (1), Pm^4 (1), M^2 (1), M^3 (1)	74
5 or 4	Gibraltar	Pm^3 (1), Pm^4 (1) M^1 (1), M^2 (1)	74
7	Biache Saint Vaast	I^2 (1), Pm^3 (1), Pm^4 (1), M^1 (1), M^2 (1), M^3 (1)	84
7 to 5	Ehringsdorf	I_1 (1), I_2 (1), Pm_3 (1), M_1 (1), M_2 (1), M_3 (1), I^1 (1), I^2 (1)	85

Results

Table 3 presents the metric data for the RVC and comparative Neandertal samples for the five variables (mesiodistal diameter, buccolingual diameter, Crown Index, Crown Module, Robustness Index) for each tooth.

Table 4 presented the results for the statistical comparison between the RVC and European Neandertal. Results suggest that overall we could not distinguish between RVC Neandertals and European Neandertal based on dental measurements.

Only two measurements produced significant results at the 0.01 significance level: the Crown Index of the upper 1st incisor and the crown module of the upper canine. Of these, the first was no longer significant after we corrected for multiple comparisons and accepted an experiment wise p value of 0.0015. However, after the extremely conservative estimation presented here, the p value obtained for the single sample t-test that compared the Crown Module for the upper canine between the specimen Payre-482-d and the Neandertal comparative sample was highly significant with a p value of 0.0009. Specifically, the Payre specimen 482d had a higher Crown Module Index (10.3 mm) that the comparative sample (8.86±0.359 mm). Interestingly despite being only marginally significant (p value=0.006), a similar pattern was obtained for the Crown index of the upper 1st incisor, which is also larger (1.858) mm compared to other Neandertals (1.2±0.176 mm).

Discussion

The new large and well-preserved dental assemblage of Payre with other fossil teeth from the RVC allows us to revisit the question of the unique morphological position of the RVC Neandertals *vis a vis* contemporaneous and later classical MOIS 4 Neandertals. Contrary to cranial and post-cranial evidence, which point to regional variation in Southwestern France[17,18,20,22], results from this

TABLE 3
METRIC RESULTS COMPARISON RHÔNE VALLEY SAMPLE VERSUS NEANDERTHAL FOR THE 5 VARIABLES AND ALL TEETH
(N, X±SD)

Tooth		MD	BL	CI	CM	RI
I_1	Rhône Valley	(5) 5.42±0.94	(5) 6.80±0.56	(5) 2.84±0.85	(5) 6.11±0.70	(5) 37.16±8.30
	Neanderthal	(13) 5.80±0.39	(13) 7.43±0.48	(13) 2.34±0.22	(13) 6.62±0.33	(13) 43.14±4.42
I_2	Rhône Valley	(5) 6.34±0.99	(5) 7.64±1.56	(5) 2.23±0.84	(5) 6.99±1.21	(5) 49.4±16.28
	Neanderthal	(15) 6.61±0.84	(15) 7.75±0.54	(15) 2.01±0.41	(15) 7.18±0.57	(15) 51.32±8.05
Pm_3	Rhône Valley	(4) 8.35±0.93	(4) 8.46±0.45	(4) 1.43±0.08	(4) 8.41±0.24	(4) 70.35±4.12
	Neanderthal	(20) 8.01±0.69	(20) 9.15±0.77	(20) 1.39±0.22	(20) 8.58±0.61	(20) 73.49±10.29
M_1	Rhône Valley	(3) 10.6±0.56	(3) 9.82±0.88	(3) 0.97±0.14	(3) 10.21±0.71	(3) 104.37±14.70
	Neanderthal	(15) 11.92±1.01	(15) 11.17±0.89	(15) 0.76±0.12	(15) 11.55±0.91	(15) 113.90±21.48
M_2	Rhône Valley	(8) 11.57±0.65	(8) 10.71±0.73	(8) 0.81±0.1	(8) 11.14±0.63	(8) 124.16±14.06
	Neanderthal	(18) 12.12±0.89	(18) 11.37±0.67	(18) 0.73±0.09	(18) 11.75±0.68	(18) 138.09±15.88
M_3	Rhône Valley	No tooth	No tooth	No tooth	No tooth	No tooth
	Neanderthal	(21) 11.91±0.81	(21) 11.02±0.73	(21) 0.77±0.08	(21) 11.48±0.60	(21) 131.76±13.75
I^1	Rhône Valley	(1) 6.9	(1) 7.8	(1) 1.86	(1) 7.35	(1) 53.82
	Neanderthal	(10) 9.87±1.27	(10) 8.57±0.42	(10) 1.20±0.18	(10) 9.23±0.68	(10) 84.73±11.92
I^2	Rhône Valley	(1) 7.34	(1) 10.68	(1) 1.28	(1) 9.01	(1) 78.39
	Neanderthal	(7) 7.76±1.14	(7) 8.04±0.99	(7) 1.67±0.40	(7) 7.9±0.77	(7) 62.49±12.32
C^1	Rhône Valley	(1) 9.6	(1) 11.1	(1) 0.94	(1) 10.35	(1) 106.56
	Neanderthal	(17) 8.60±0.83	(17) 9.78±0.86	(17) 1.22±0.21	(17) 9.19±0.79	(17) 84.66±14.63
Pm^3	Rhône Valley	(2) 7.80±0.57	(2) 10.5±0.00	(2) 1.22±0.09	(2) 9.15±0.28	(2) 81.90±5.94
	Neanderthal	(15) 8.05±0.79	(15) 11.03±0.57	(15) 1.14±0.17	(15) 9.54±0.65	(15) 89.18±12.79
Pm^4	Rhône Valley	(2) 7.70±0.14	(2) 9.44±1.78	(2) 1.40±0.29	(2) 8.57±0.96	(2) 72.81±15.06
	Neanderthal	(18) 7.48±0.81	(18) 10.52±0.78	(18) 1.30±0.23	(18) 9.00±0.74	(18) 79.12±13.42
M^1	Rhône Valley	(2) 10.69±0.83	(2) 11.95±0.07	(2) 0.79±0.07	(2) 11.32±0.45	(2) 127.72±10.64
	Neanderthal	(15) 11.07±0.76	(15) 11.71±0.85	(15) 0.78±0.09	(15) 11.39±0.61	(15) 129.68±13.64
M^2	Rhône Valley	(1) 10.4	(1) 12.9	(1) 0.75	(1) 11.65	(1) 134.16
	Neanderthal	(18) 10.61±0.62	(18) 12.54±1.11	(18) 0.76±0.10	(18) 11.57±0.76	(18) 133.32±16.97
M^3	Rhône Valley	No tooth	No tooth	No tooth	No tooth	No tooth
	Neanderthal	9.52±0.88	11.89±0.94	0.90±0.16	10.71±0.82	113.73±16.85

study do not point to a morphological variability between RVC specimens and other European Neandertals.

This study suggests that the RVC Neandertals did not differ from European Neandertal in tooth dimensions. The single significant result obtained for the crown module of the upper canine indicates that the RVC Neandertals had larger teeth than European Neandertal. This trend is also supported by the Crown Index of the upper 1st incisor. These results are surprising given the fact that the comparative canine sample includes a large quantity of Krapina canines that are much larger than other Neandertals[31]. It has been suggested that modern human canines exhibit high sexual dimorphism[40]. Therefore, it may be argued, that these results may be attributed to sexual dimorphism and that Payre 482 is a male individual. However, we contend that this is not possible, since it would require us to suppose that all the other canines in the comparative study (N=16) are female including a large sample from Krapina with relatively large tooth size[31,41].

It has been suggested that based on the Hortus and Genay sample, the Neandertals from the RVC exhibits a smaller tooth size dimension[12,13]. Our study rejects this hypothesis. Teeth from the different populations, overall could not be distinguished based on size and when they could, they RVC teeth were larger. While we do not suggest that the pattern observed by previous researchers does not reflect local tooth variability, since the original study did not include the analysis of either upper canines or upper 1st incisors (that were not present in either site) and our study is based on a sample different in scope, we contend that this current analysis may reflect broader variability patterns (or lack thereof) among Neandertal populations.

Despite having a significant specimen which has provided contrary results, we feel that the over arching result suggesting that there is no difference between the two population, is indeed robust. Not only were we extremely conservative in preventing type I errors (see above) but our study was also very cautious in the composition of the comparative sample which encompassed a broad sample, both chronological and geographically within the RVC and the comparative sample excluding debatable specimens such as the Levantine Neandertals and the fossils from MOIS 3. Additional discoveries which may increase sample size, will allow us to future explain the position of Payre 482d.

The morphological results from Neandertals from Eastern France, which indicate lack of population isolation, appear to contradict evidence from Western France. In western France, there is evidence for a local population, which is distinguished from other Neandertal population in Europe both in morphology i.e. cranial and temporal bones, and in behavior. Specifically, the presence in southwestern France of a particular Mousterian industry (the MTA = Mousterian of Tradition Acheuliean) and a Châtelperronian industry, both of which are absent in the RVC[14,15,42]. How can this apparent discrepancy be explained?

In Northern Europe, where climate fluctuations were extreme, we have evidence of »desertification« of the region during the cold glacial period and reoccupation during the interglacial ones. This phenomenon of recurring occupation and desertification[43] perverted the formation of local human variants and created isolated populations. However, in contrast to Northern Europe, in Western Europe and most notably in Southwestern France, ecological condition[44] have remains relatively stable from MOIS 7 to MOIS 4 and the climatic fluctuations that plagued Europe did not effect this area so severely[45], as is known for other mid latitudes regions at the same time period[46,47]. The ameliorate and stable climate may explain local continuity of the population and which may have lead to a local morphological and behavioral variant that seems evident in the southwestern France[17,19] and in central Italy[18,20].

The RVC, also situated in mid latitudes, exhibits ameliorate climate and lack of extreme climate fluctuations. Comparison with the geography and topography with Western France would have led us to expect the formation of a local variant population similar to that region. The lack of evidence presented in this study of such an isolate population, raises the question of the mobility of the Neandertal population within the RVC and specifically in comparison Central Europe.

We suggest that the difference in Neandertal isolation between the two regions is due to the absence of real geographical barriers with other European areas in the RVC compared to the geographic isolation between Southwestern France and Central Europe. The RVC is a natural passage joining northern and southern Europe. It was already a migrational route[42,48] as patterns of animal mi-

TABLE 4

TEST OF NORMALITY FOR EACH OF THE VARIABLES: MD, BL, CI, CM AND RI. VARIABLES DENOTE A VARIABLE WHICH IS NOT NORMALLY DISTRIBUTED FOR AT LEAST ONE OF THE GROUPS. SIGNIFICANT LEVEL FOR NORMALITY WAS SET AT 0.01 TO CORRECT FOR MULTIPLE COMPARISON. GIVEN 32 INDIVIDUAL COMPARISON, A P-VALUE WAS SET AS SIGNIFICANT AT 0.0015

Tooth	Europe	Rhone Valley	Shapiro Wilks	Test used:	Results
Lower I1	13	6		Stepwise DFA	NS
Lower I2	15	5	CI	Stepwise DFA Except for CI	NS
				Mann-Whitney for CI.	NS
Lower P3	19	4		Stepwise DFA	NS
Lower P4	18	3	BL	Stepwise DFA expect for BL	NS
				Mann-Whitney for BL	NS
Lower M1	15	3		Stepwise DFA	NS
Lower M2	19	7	CI	Stepwise DFA for all variable but CI	NS
				Mann-Whitney for CI	NS
Lower M3	21	0		NONE	–
Upper I1	10	1		Single sample t test	CI is 0.006
Upper I2	7	1	MD	Single sample t test	NS
				Mann-Whitney for MD	NS
Upper canine	16	1		Single sample t test	CM 0.0009
Upper P3	15	2	All	Mann-Whitney	NS
Upper P4	18	2	All	Mann-Whitney	NS
Upper M1	15	2		Mann-Whitney	NS
Upper M2	18	1		Mann-Whitney	NS
Upper M3	13	0	None	–	

gration illustrate[49] and as indicated by the faunal analyses which suggest that the Rhône Valley was a corridor facilitating the mobility of animals[49].

Furthermore, studies concerning the gathering of flint indicate that humans moved along plateaus bordering the Rhône Valley far away in the south[42]. This rhodanian corridor could have provided easy human exchange in the area between Southeast France and Central Europe. This would have been facilitated by the expansion of human populations during the »glacial periods«. This has undoubtedly contributed to preserve the genetic unity of the Neandertal populations (the regions that were highly affected by the incoming populations increased their gene pool and increased their variability).

Human dispersal often follows along rivers, corridors and natural topographic land-marks[50]. The dispersal route from Northern Europe to the Rhône Valley would have been along the major rivers and therefore would have resulted in a high proportion of hominins in the rhodanian corridor arriving from Northern Latitudes. In contrast, Western France was covered with dense forest and surrounded by geographical barriers connected with the rest of Western Europe by narrow and limited passages. This may have impeded the mobility of populations into the region and thus reduced the possibilities for genetic exchange between the two groups. This comparison between the regions highlights the variability across Europe. For example, the situation in the Swabia region and the Danubian Corridor suggests that during extreme climatic conditions such as the H4 event, Neandertals depopulated the region, which allowed subsequent rapid colonization by incoming modern humans and allow them to establish demographic dominance is cca. 40 kya[51]. Thus, the relationship between the presence of geographic corridor, topography and varying amplitudes of climate change can serve as a basis to model the development of human local populations, interaction spheres and population replacements.

This research may also shed light on the interesting question of the variability within Neandertals population in general. The hypothesis of Neandertal variability has recently been lent additional support from mtDNA analysis[52–54], which fit in well with the hypothesis of a group of northern Neandertals (Sclayn) and a Mediterranean group (Monte Lessini and El Sidron). A Mediterranean variation has also been shown by a recent study modeling the evolution of genetic variation on Neandertals[55]. However, morphological studies that attempted to define two or three groups, which mirrored the genetic grouping i.e., Western Europe, Mediterranean group and Eastern Europe, were not successful. Based on dental measurement of a Mediterranean group and a continental group (both Central and Eastern Europe) sub populations of Neandertals[56,57] could not be distinguished. These conclusions are in agreement with the results that we present here and moreover so, since the definition of the sub groups used by Maureille and Houet[56] are extremely broad and encompassed a wide range of population mobility with the regions preventing the evolution of local variants. Maureille and Houet[56] attribute their lack of ability to distinguish between Neandertal sub groups resulting from the sample size, methodological considerations and group membership. However, based on the results presented in this study, we suggest that the tight genetic control of teeth size may render them as useless morphological elements when attempting to identify subpopulation at the microevolutionary level within groups with small effective population size[58–61] such as the Neandertals. In modern humans tooth size has been shown to differ among living populations[62] where some studies have claimed the level of genetic control of dental size to be as high as 90%[63,64].

Contrary to morphological elements such as teeth, genetic elements which are not under tight genetic control such as the hyper variable region of the mtDNA, allow to distinguish three sub-groups within these populations of Neandertals, even using only a relatively small sample size[55]. The heritability of adult tooth dimensions (BL and MD) is high and is based on autosomal DNA[65,66]. The difference between the mtDNA and autosomal DNA may partially explain the differences between the two results. mtDNA is known as a single copy circular double stranded molecule with a very high copy rate, a high mutation rate, but with no recombination. Thus, it is used to study relatively recent migration events using the lineage-based approach and haplogroups[67]. In contrast, the coalescence time for autosomal DNA (and therefore for the metric data in this study) is much longer, given the presence of recombination and may not track migratory events in the same fossil population during the same time period[68]. Studies from modern human population suggest that the variability in mtDNA loci is much higher as that of autosomal loci. In essence, the results from the genetic studies and the metric study in this paper represent different data and thus are not directly comparable but are complementary, and they mirror results from modern human population. The intra-geographic variability in modern human dental metrics represented among European populations is less than 1%[26], while the variability in mtDNA is cca. 6% and 2% for autosomal DNA[69]. Obviously, other morphological elements such as those on the cranium or postcranium may be under less selection and therefore can be used to indentify local variants, as has been suggested for Neandertals in Western France[17,19,20] and Italy[18,20]. Thus, this study supports previous studies that have suggested that odontometric variation data are of little value in distinguishing between intra-population variation on a microevolutionary scale[69] and references therein. However, studies in modern human dental metric have suggested that odontometric variation can track inter-population variability[69]. Thus, comparison of Neanderthal dental metric variability across regions (Europe, Near East, Central Asia), rather than within a single region, may prove efficacious for the assessment of the presence sub populations in addition to other craniometric, post cranium and genetic studies.

Conclusion

We compared the dental assemblage of the Rhône Valley corridor with that of European Neandertals dating to MOIS 7–4 using two linear measurements and three indices. Results show that the there is no distinction between the RVC populations and that of other Neandertals except for the Crown Module of the upper canine. However, the present of a single significant result does not provide evidence for a local RVC variant within the Neandertal population. These results support evidence from archaeological analysis of this region.

The absence of the local East France Neandertal (on the Rhodanian Corridor) variant is in contrast to evidence for a Western France local Neandertal one. However, evidence for the latter is based on cranial and post-cranial data while our study focuses on dental metrics. We propose that the high genetic control for dental size and shape may account for the low ability to distinguish between sub population groups based on dental dimensions in groups with small effective size.

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PONOVNO POSTAVLJANJE PITANJA O REGIONALNOJ RAZNOLIKOSTI NEANDERTALACA: POGLED IZ DOLINE RIJEKE RONE

S A Ž E T A K

Usporedili smo ostatke zubi neandertalaca iz doline rijeke Rone s onima europskih neandertalaca datiranih iz stadija izotopa kisika 7-4, koristeći dvije linearne mjere i tri indeksa. Za testiranje značajne razlike između populacije doline rijeke Rone i zapadnoeuropskih neandertalaca koristili smo višeredni pristup. Prvo, koristili smo Shapiro-Wilksov test, da bi se testirala normalnost varijabli. Ukoliko su varijable bile normalne, radila bi se analiza diskriminantne funkcije (DFA) (koristeći Mahalanobisove udaljenosti). DFA koristi korelacijske matrice kako bi se testirale težine varijabli i naglasile međupopulacijske različitosti, a smanjile unutargrupne različitosti. Rezultati pokazuju da nema razlike između neandertalaca doline rijeke Rone i ostalih neandertalaca, osim u slučaju indeksa modula krunice gornjih očnjaka. Međutim, prisutnost jednog značajnog rezultata ne daje dovoljne dokaze za postojanje lokalne karakteristike neandertalaca doline rijeke Rone. Rezultati su poduprijeti dokazima arheoloških analiza ove regije. Pretpostavljamo da visoka genetička kontrola veličine i oblika zubi može umanjiti razlikovanje temeljeno na dentalnim dimenzijama među podgrupama populacije s malom efektivnom veličinom, kao što su neandertalci.