Chapter 16

MICRO-COMPUTED TOMOGRAPHIC QUANTIFICATION OF TOOTH ROOT SIZE AND TISSUE PROPORTIONS IN THE SCLADINA I-4A JUVENILE, A SHORT-ROOTED NEANDERTAL

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1. Introduction

Scladina Cave (Belgium) has yielded the dentition of an eight-year-old juvenile Neandertal (Toussaint et al., 1998 & Chapter 1; Smith et al., 2007 & Chapter 8). A direct date of 127 +46/−32 ka BP was obtained on the mandible by gamma-ray spectrometry (Toussaint et al., 1998; Yokoyama & Falguères, Chapter 6), which points to a wide chronological range, between MIS 6 and 4. A recent reassessment of the stratigraphy of the site attributes the Neandertal remains to a secondary deposit (mainly in units 4A-CHE and 4A-POC, see Chapters 3 & 5 for description). The general chronostratigraphic framework of the sequence (Pirson et al., 2005, 2008; this volume, Chapter 4) however supports an attribution of the fossil to the second half of MIS 5 (Pirson et al., this volume, Chapter 5). On a regional scale, and because of excessively rigorous climatic conditions, it seems currently granted that the territory encompassing present-day Belgium and the surrounding areas of northwest Europe was deserted by human populations during the second half of MIS 4 (Cordy, 1984, 1988; Haesaerts, 1984; Toussaint et al., 2001; Van Peer, 2001; Pirson & Di Modica, 2011: 135). This is especially true for the calcareous areas where all the Neandertal remains of the Mosan Basin have been recovered. Except for the La Naulette mandible and for the mandible and the fragment of maxilla of Scladina which are more ancient, all the Mosan Neandertals are attributed to MIS 3, as for the eponymous site of Neandertal. This is well established for Spy (Semal et al., 2009), Couvin (Toussaint et al., 2010), Walou (Pirson et al., 2011; Toussaint, 2011) and Goyet (Rougier et al., 2009). So there is a clear distinction between fossils dated to MIS 5–MIS 4 (for this later time period, no Neandertal remains have ever been found in Belgium) and those attributed to MIS 3. This is the reason why, in this chapter, we chose to compare Scladina primarily with MIS 5 Neandertals.

Although the dental development of the Scladina specimen is well documented (Smith et al., 2007; Smith et al., 2010 & Chapter 8), its dental morphology has not yet been described in detail before the present monograph (Chapters 13 to 16 & 18). However, it has to be noted that Scladina has already been included in two large-scale studies focusing on the root morphology of Neandertals (see Kupczik & Hublin, 2010 for the molar root morphology; Le Cabec et al., 2013 for the incisors and canines).

Several studies using innovative techniques of investigation (e.g. tomographic imaging and synchrotron virtual histology) have emphasized that tooth roots can yield valuable information regarding taxonomy (Wood et al., 1988; Brunet et al., 2002; Bailey, 2005; Kupczik & Hublin, 2010; Emonet et al., 2012), life history (Smith et al., 2007; Smith et al., 2010), diet (Spencer, 2003; Kupczik & Dean, 2008; Kupczik & Hublin, 2010), tooth use (Le Cabec et al., 2013) and facial biomechanics (Smith, 1983). In this context, recent studies have shown that tooth root form can distinguish Neandertals from anatomically modern humans (Bailey, 2005; Kupczik & Hublin, 2010; Le Cabec et al., 2013).

Here we document and compare the permanent incisors, canines and first molars' root morphology of the Scladina Juvenile to European MIS 5 Neandertals from Krapina, Abri Bourgeois-Delaunay and Regourdou. MIS 5 Neandertals lie at the end of step 3 of the accretion model (Dean et al., 1998; Hublin, 1998). Although steps 1 and 2 of the accretion model show some of the facial features characterizing the Neandertal lineage, the derived Neandertal facial morphology is fully achieved in step 4 specimens (Dean et al., 1998; Harvati et al., 2010). The interpretation of the Neandertal crown and root morphology is very likely influenced by the geographic and chronologic distribution of the fossil record, in which the later stage of the evolution of the lineage, MIS 4–3 Neandertals, is better represented than earlier phases. Such a discontinuous fossil record often prevents an assessment of the intra- and interpopulational variability that is crucial for our understanding of the evolutionary history of the lineage.

The Krapina Neandertals are known for having very large crown dimensions compared to other European Neandertals, especially regarding their anterior teeth (Brose & Wolpoff, 1971; Smith, 1976[a]; Brace, 1979; Wolpoff, 1979; Mann & Vandermeersch, 1997; Wolpoff, 1999). The same observation was made for the Abri Bourgeois-Delaunay sample by Genet-Varcin (1975[a, b]) and Condemi (2001). Moreover, Krapina is also the most extensively studied MIS 5 Neandertal sample and because of its large dental sample size may bias characterizations of MIS 5 Neandertal dental morphology (Smith, 1976[a]; Smith, 1976[b]; Wolpoff, 1979; Fox & Frayer, 1997; Lee, 2006; Schwartz & Tattersall, 2006; Olejniczak et al., 2008). Regourdou 1 was shown to have rather small crowns in comparison to MIS 4-3 Neandertals (Maureille et al., 2001).

We used micro-computed tomography (micro-CT) to image and quantify internal tooth root tissues proportions of Scladina and the comparative MIS 5 Neandertal specimens. This technique has the particular advantage that it allows the virtual extraction of teeth still embedded in their jaws, and to access internal dental structures such as the pulp cavity. In addition to the focus on the Scladina Juvenile, this will allow us to question whether variation in Krapina can reliably represent MIS 5 Neandertal dental variability and whether the other three MIS 5 Neandertals samples can be accommodated within the variation represented by Krapina.

2. Material and methods

2.1. Sample

The external and the cross-sectional root morphology of the teeth of the Scladina Juvenile will be described for all the teeth present in the individual (for an extensive inventory of the teeth, see Chapter 1, Table 1 & Chapter 13). Further quantitative analyses will be restricted to the permanent incisors, canines and first molars, which have completed their roots.

In the metric study, the total sample includes 68 isolated and in situ permanent mandibular and maxillary central and lateral incisors, canines and first molars from Scladina and comparative MIS 5 Neandertals (Table 1). The selection of the teeth was based on preservation and formation of the roots. However, when a small portion of the root tip was missing for some anterior teeth, and given the small sample sizes available for study, these teeth were nonetheless included in the samples. The amount of root missing has been estimated following the protocol described in Le Cabec et al. (2013), which modeled the missing part as an elliptic cone and proved to be of good accuracy (Tables 1, 2a & 2b). The comparative Neandertal sample from the Croatian site of Krapina includes 43 teeth. These dental remains have been directly dated by ESR to ca. 130±10 ka BP (Rink et al., 1995). The second Neandertal sample includes a complete adult mandible (BD1) and nine non-associated isolated teeth (Condemi, 2001) discovered at the French site of La Chaise-Abri Bourgeois-Delaunay (Debénath, 1977), and which are attributed to the MIS 5e (Condemi, 2001). In addition, we analyzed four teeth preserved in situ in the adult mandible of Regourdou 1 (Montignac,

For Tables 1 to 6, abbreviations for permanent teeth are: **I_1** (mandibular central incisor), **I_2** (mandibular lateral incisor), **C,** (mandibular canine), **M_1** (mandibular first molar), **I^1** (maxillary central incisor), **I^2** (maxillary lateral incisor), **C'** (maxillary canine), **M^1** (maxillary first molar).

Tooth type	Krapina (Krp)	Abri Bourgeois-Delaunay (BD)	Scladina (Scla)	Regourdou 1 (Reg)
I_1	**55 (Mandible E), 58 (Mandible H), 59 (Mandible J)**	BD1, BD20, BD21	**Scla 4A-15**	Right I^1*
I_2	**53 (Mandible C), 54 (Mandible D), 55, 58, 59**	BD1	**Scla 4A-20***	Right I^2*
C,	**54, 55, 58, 59**	BD1, BD13	**Scla 4A-12**	Right C,
M_1	**53, 54, 55, 58, 57, 59, D80, D82**	BD1, BDJ4C9	**Scla 4A-9/M_1**	Left M_1
I^1	**49 (Maxilla E), 50 (Maxilla F), D123*, D126*, D157, D158**	BD12	**Scla 4A-11***	–
I^2	**49, 50, D122*, D125, D127, D156, D159, D160**	BD10	**Scla 4A-14**	–
C'	**D36, D37, D56, D76, 49, 50***	BD11, BD15, BD16	**Scla 4A-16***	–
M^1	**45 (Maxilla A), 48 (Maxilla D), D164**	–	**Scla 4A-4**	–

Table 1: Samples of permanent teeth of MIS 5 Neandertals. '*' denotes specimens in which a small part of the root tip is broken. Values used in the statistics of Tables 2a & 2b include an estimation of the missing part of the root following the protocol described in Le Cabec et al. (2013, S.I.1 and S.I.2).

From Le Cabec et al. (2013, S.I.1 and S.I.2).

Specimen	Tooth type	Side	Cause	rMD [mm]	rLL [mm]	rAv. [mm]	hMd [mm]	hLL [mm]	hAv. [mm]	RL meas. [mm]	Msg RL [mm]	%age Mis RL	Total estim. RL [mm]
Regourdou 1	I_1	R	t	*0.43*	*1.18*	0.81	0.26	1.11	*0.69*	15.72	0.69	**4.18**	16.41
Regourdou 1	I_2	R	t	*1.12*	*2.09*	1.6	0.78	1.05	*0.92*	16.88	0.92	**5.14**	17.80
Scla 4A-20	I_2	R	t	1.13	2.05	1.6	0.51	2.14	1.33	13.9	1.33	**8.70**	15.23
Scla 4A-11	I^1	R	t	1	1.07	1.0	1.24	1.45	1.35	13.97	1.35	**8.78**	15.32
Krp D123	I^1	L	t	*1.32*	*1.69*	1.5	1.36	2.64	*2.00*	17.57	2.00	**10.22**	19.57
Krp D126	I^1	R	t/d	*1.03*	*1.43*	1.2	1.31	1.39	*1.35*	15.24	1.35	**8.14**	16.59
Krp D122	I^2	L	d	*0.72*	*1.8*	1.3	0.69	1.42	*1.06*	16.36	1.06	**6.06**	17.42
Krp 50 [Max. F]	C′	R	t	*1.68*	*1.79*	1.7	1.81	2.29	*2.05*	20.99	2.05	**8.90**	23.04
Scla 4A-16	C′	R	d	0.5	0.83	0.7	0.37	0.7	0.54	17.15	0.54	**3.03**	17.69

Table 2a: Root length estimation for missing root apical portions in damaged or developmentally incomplete specimens (incisors and canines). We scored the reason why the root is incomplete as 't' for taphonomical break, 'd' for developmentally incomplete, 't/d' when the reason is uncertain between taphonomy and development. '**rMD**' stands for the mesiodistal radius of the elliptic cone, '**rLL**' for its labiolingual radius, '**rAv.**' for the average of both radii; '**hMD**' and '**hLL**' for the height of the cone measured in the mesiodistal and in the labiolingual plane respectively and '**hAv.**' for the average of both heights. '**hMd**', '**hLL**' and '**hAv.**' are italicized since they are used for further computations. '**RL meas.**' stands for the measured root length [incomplete], '**Total estim. RL**' is the reconstructed root length summing the average height and the measured root length, and '**%age Mis RL**' is the percentage of the total root length (bold in the table) represented by the portion of root that has been reconstructed. We notice that for Regourdou1 LI1, it is highly likely that the missing part of the root is actually some broken hypertrophic cementum.

France). This specimen is attributed to the second half of MIS 5 (Maureille & Tillier, 2008; Turq et al., 2008; Vandermeersch et al., 2008).

2.2. Micro-CT image acquisition and 3D model generation.

Isolated and in situ teeth were subjected to micro-CT at the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany) on a Skyscan 1172 micro-CT scanner or a BIR ARCTIS 225/300 industrial micro-CT scanner, with an isotropic voxel-size ranging from 25.5 to 34.8 µm. Data for BDJ4C9 were acquired at the European Synchrotron Radiation Facility (Beamline ID 17, Grenoble, France) and downloaded from the NESPOS website.

In order to facilitate the dental tissue segmentation in Avizo 6.1. (Mercury Systems), the reconstructed micro-CT slices were filtered using a median filter followed by a mean-of-least-variance filter (each with a kernel size of three). Dental tissues (enamel, dentine and pulp) were semi-automatically segmented using thresholding and manual editing, as well as the cracks in the enamel and dentine when they appeared clearly on the scans, to avoid any overestimation of root volume and surface area.

On several teeth from Krapina (Krp D36, D56 and D76) and Abri Bourgeois-Delaunay (BD11, BD15 and BD16), hypertrophic cementum has been successfully segmented as a separate material (see Figures 1, 3 & 5 in Le Cabec et al., 2013 for more details). As visible on the micro-CT

From Le Cabec et al. (2013, S.I.1 and S.I.2).

Specimen	Tooth type	RSA meas. [mm²]	Misg RSA [mm²]	%age Misg RSA	Total estim RSA [mm²]	RV meas. [mm³]	Misg RV [mm³]	%age Misg RV	Total estim. RV [mm³]
Regourdou 1	I_1	**257.47**	2.47	0.95	259.93	**251.96**	0.36	0.14	252.32
Regourdou 1	I_2	**319.84**	8.78	2.67	328.62	**355.33**	2.24	0.63	357.57
Scla 4A-20	I_2	**230.23**	9.98	4.16	240.21	**255.68**	3.21	1.24	258.89
Scla 4A-11	I^1	**239.46**	5.52	2.25	244.98	**327.83**	1.51	0.46	329.34
Krp D123	I^1	**357.72**	11.81	3.20	369.53	**576.45**	4.67	0.80	581.12
Krp D126	I^1	**281.84**	7.01	2.43	288.85	**387.65**	2.08	0.53	389.74
Krp D122	I^2	**360.61**	6.04	1.65	366.65	**510.62**	1.43	0.28	512.06
Krp 50 [Max. F]	C′	**430.75**	14.64	3.29	445.39	**617.58**	6.46	1.03	624.03
Scla 4A-16	C′	**309.50**	1.73	0.56	311.23	**406.63**	0.23	0.06	406.87

Table 2b: Root surface area and volume estimations for missing root apical portions in damaged or developmentally incomplete specimens (incisors and canines). '**RSA meas.**' stands for the measured root surface area (bolded), and '**RV meas.**' for the measured root volume (bolded). Further abbreviations follow the pattern used in Table 2a above.

scans, most of the Bourgeois-Delaunay teeth involved in this study, were affected by a taphonomic demineralization on an even thickness of the root involving both dentine and hypertrophic cementum when present. These demineralized tissues were attributed to their respective non-affected dental materials.

Following this segmentation process, 3D surface models of the teeth were generated using a constrained smoothing algorithm in Avizo. Each tooth was then virtually divided into crown and root(s), by cutting the 3D models at the cervical plane defined by a best–fit plane between landmarks set on the uppermost enamel margins on the labial/buccal and lingual sides of the cemento-enamel junction (Figure 1a).

2.3. Metric study of root and crown size.

2.3.1. Quantification of tooth crown size

Given the effects of both occlusal/incisal and interproximal wear on mesiodistal diameters, we used the dental crowns' breadths (bucco/labio-lingual) to account for crown size. Maximum buccolingual crown diameter (Cr) was measured following the definition of Martin (M81(1) in Bräuer, 1988) as the maximal distance between the buccal and the lingual aspect of the teeth, measured perpendicularly to the mesiodistal diameter of the tooth (Figure 1b). The Scladina and the Bourgeois-Delaunay crown data were directly measured on the specimens using a caliper. Data for the Krapina sample and for Regourdou 1 were collected from the literature (see Appendix 1 in Wolpoff, 1979; Maureille et al., 2001). Since no information was found in the literature on the dental dimensions of Krapina 59 (except for the permanent mandibular left central incisor), the buccolingual crown diameter was measured on the 3D models as described above.

2.3.2. Quantification of tooth root size

In all the four dental samples under study, root measurements were performed on the segmented roots on the 3D models in Avizo (mandibular first

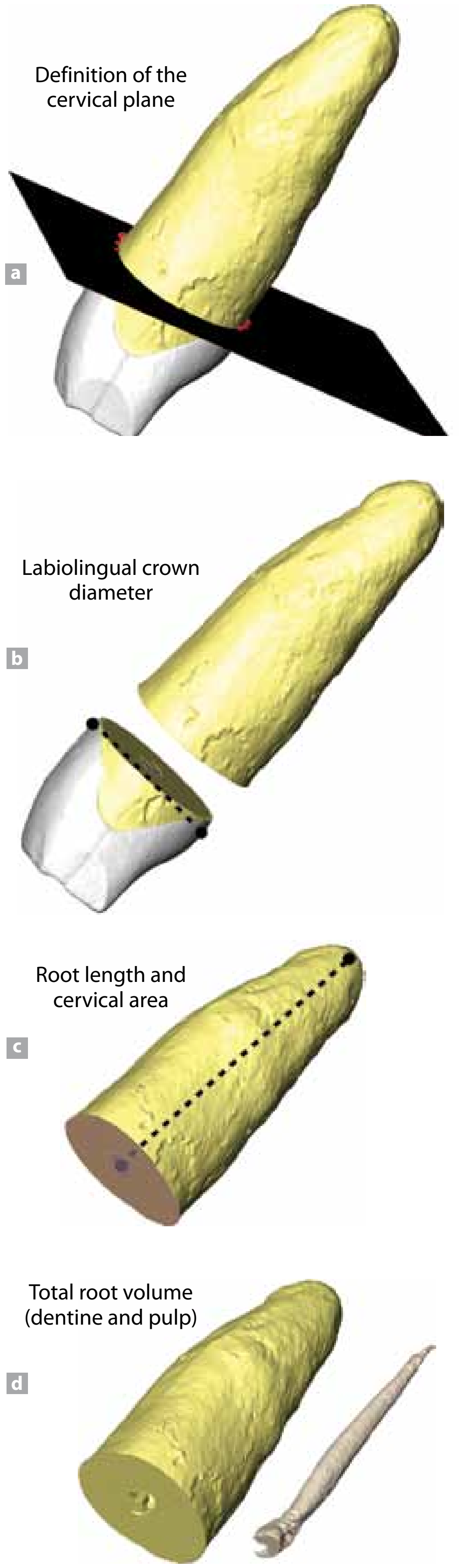


Figure 1: Crown and root measurements used in this study (modified after Figure 2 in Le Cabec et al., 2013). After defining the cervical plane based on a best fit plane (a), the tooth is virtually cut into a root and a crown (b), which allows measurement of the maximum labiolingual crown diameter (b), the cervical area (in light purple) and the root length from the center of the cervical plane to the root apex (c). The total root volume includes dentine and pulp (d).

molar root data from Kupczik & Hublin, 2010; incisor and canine data from Le Cabec et al., 2013; regarding the specimens with incompletely preserved root tips, see Tables 2a & 2b for the estimation of the missing root part). Root length (RL) was measured from the center of the pulp cavity at the cervical plane to the root apex for single rooted-teeth (Figure 1c), on the lingual root of the maxillary molars and on the distal root of the mandibular molars. In addition, within the most complete mandibular dentitions, we computed the relative differences in root length of the incisors and canine compared to the root length of M_1 as follows: $p(x) = -100+([RL(x)*100]/RL(M_1))$, with p(x) for this relative difference for each tooth type, RL for root length, and x for I_1, I_2 and C,. The cervical surface area (CA) has been computed as the area of the section of the tooth at the cervical plane previously defined (Figure 1c). The root surface area (RSA) as the surface area of the radicular dentine, the total root volume (RV), and the volume of radicular pulp (RPV) were measured as well (Figure 1d). The hypertrophic cementum was included in the total root volume.

2.3.3. Relationship between crown size and root size

For each tooth type within each of our four subsamples, we estimated the proportion of crown size to root length by the ratio: (Cr* 100)/RL. This will allow us to discuss the relationship between crown size and root size in our samples.

2.4. Statistical analyses

Descriptive statistics (sample size, mean, standard deviation, range and coefficient of variation) were computed for the crown and root variables. For all measurements and for each tooth type, adjusted z-scores (Maureille et al., 2001) were performed (abbreviated as '*Azs*', $\alpha = 0.05$) to test whether Scladina can be statistically accommodated within the variability of the Krapina sample. $Azs<-1$ and $Azs>1$ mean that the specimen studied (here, Scladina) is excluded from the range of variation of the comparative sample (Krapina, in this study) while $-1<Azs<0$ and $0<Azs<1$ place the specimen in the lower or upper half of the variation of the comparative sample, respectively. *Azs* close to 0 corresponds to a specimen whose dimensions are very similar to the mean of the comparative sample. Statistical analyses and graphs were performed using R 2.15.0 (R Development Core Team, 2012).

3. Results

3.1. Description of the external and cross-sectional root morphology in the Scladina I-4A mixed dentition

Overall, the roots of Scladina are well preserved. Table 3 lists the cross-sections and a general description of the external root morphology of all the Scladina teeth that have been scanned. The permanent anterior tooth roots show a labial convexity, typical in Neandertals. This is illustrated in Figure 2 (from Le Cabec et al., 2013), showing that the root shape of the Scladina I^2 falls in the middle of Neandertal variability. The fully formed molar roots are divergent and do not show the typical Neandertal taurodontic morphology.

3.2. Crown and root size metrics

3.2.1. Overall variability in crown and root size

The surface models of a selection of teeth illustrating the variation in tooth morphology in the samples are presented in Figure 3. For the Krapina and Bourgeois-Delaunay subsamples, the coefficient of variation of the buccolingual crown diameter (ranging from 3.84% to 7.39% for Krapina, and from 0.63% to 3.78% for Bourgeois-Delaunay, Table 4) is much lower than that of the root measurements (RL, RSA, CA and RV) for all tooth types (varying from 4.23% to 22.31% for Krapina, and from 0.38% to 12.42% for Bourgeois-Delaunay, Tables 5-8). The root pulp volume is the most variable dental parameter for all tooth types (CV ranging from 19.01% to 78.55% for Krapina, and from 22.61% to 33.06% in Bourgeois-Delaunay, Table 9).

3.2.2. Tooth crown size

The tooth crown size descriptive statistics are presented in Table 4. The adjusted z-scores show that the buccolingual crown diameters of the Scladina teeth consistently fall within the lower half of the Krapina variation, the M^1 being very close to the Krapina mean (Figure 4). The incisors of Scladina have crowns strictly smaller than the incisors from Bourgeois-Delaunay, and from

Maxillary dentition

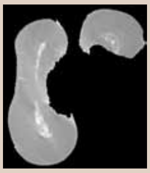
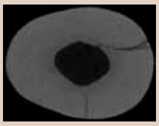
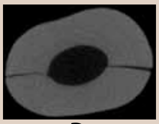
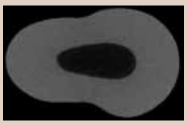
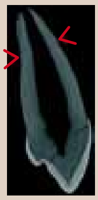
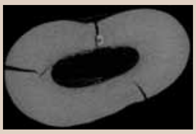
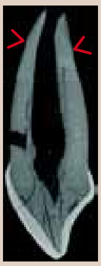
Tooth	Specimen ID	Root complete?	#R	External root morphology
dm^1 (R)	Scla 4A-7		3 (supposedly)	More than the cervical third of the roots is preserved. For all roots: root resorption. Eight-shaped L root and circular MB root. Picture taken at the 2/3 of what is left of the roots.
dm^2 (R)	Scla 4A-5		3	3 divergent roots. The furcation occurs at the cervical quarter of the divergent roots. One C-shaped L root, one DB and one MB eight-shaped roots. Slightly more apical location of the root furcation between the L and the DB roots. MB root complete, L and DB root tips broken. Picture taken below at half root.
I^1 (R)	Scla 4A-11		1	The root tip is broken (estimation at 8.78% of the total root length). Circular root cross-section.
I^2 (R)	Scla 4A-14		1	The root is complete. More elliptical in root cross-section. The root tip bends distally.
I^2 (L)	Scla 4A-17		1	The root is complete. More elliptical in root cross-section. The root tip bends distally.
C′ (R)	Scla 4A-16	 	1	The root is not fully formed, a small portion of the root tip remains to develop. Irregular circular root cross-section (broader labially). Conspicuous thickening with a rough aspect of the apical third of the root surface (red lines). This is possibly related with deposition of secondary cementum around the apex, suggesting a case of hypercementosis. This is however very surprising considering the young age of the Scladina Juvenile, and the fact that the canine apex is not fully closed yet.
C′ (L)	Scla 4A-18	 	1	The root is not fully formed, a small portion of the root tip remains to develop. Irregular circular root cross-section. Conspicuous thickening with a rough aspect of the apical third of the root surface (red lines). This is possibly related with deposition of secondary cementum around the apex, suggesting a case of hypercementosis. This is however very surprising considering the young age of the Scladina Juvenile, and the fact that the canine apex is not fully closed yet.
P^4 (R)	Scla 4A-2/P^4		1	About half of the root is formed. C-shaped cross-section, strong invagination on the distal side.

Table 3 (continues on the next pages): Description of the external root morphology in the Scladina mixed dentition. **Specimen ID**: identity of the specimen described; **#R**: number of roots; (R) stands for right and (L) for left, dm_x and dm^x stand for mandibular and maxillary deciduous molars. P_3, P_4 and P^3, P^4 stand for the mandibular and maxillary first and second premolars; M for mesial, L for lingual, B for buccal/labial; D for distal; MB for mesiobuccal; MD for mesiodistal. It has to be noted that Scla 4A-19 (left I_2) has not been scanned.

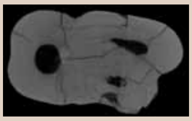
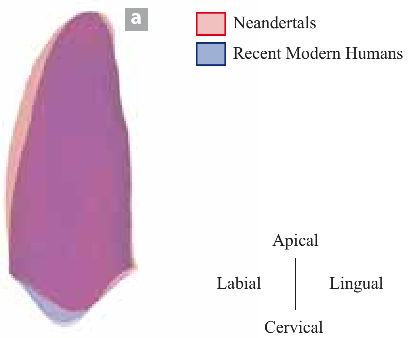
	Tooth	Specimen ID	Root complete?	#R	External root morphology
Maxillary dentition	M¹ (R)	Scla 4A-4	M L  B D	3	Only the L root is preserved, while the MB and DB roots are broken at the level of the bifurcation, at the cervical third of the roots. From the L, one can suppose that the roots were fully formed with closed apices. The mesiobuccal root appears to be wider buccolingually than the distobuccal root. Picture taken just above the point of root furcation.
	M² (R)	Scla 4A-3	M L  B D	3?	About half of the roots is formed; the furcation point would be at the cervical third of the fully formed root. The DB and MB roots are not separated yet, and the DB root seems to be larger and more flattened mesiodistally than the MB root.
	M³ (R)	Scla 4A-8		—	No root formed yet (crown almost complete).

Table 3 (continued): Description of the external root morphology in the Scladina mixed dentition.



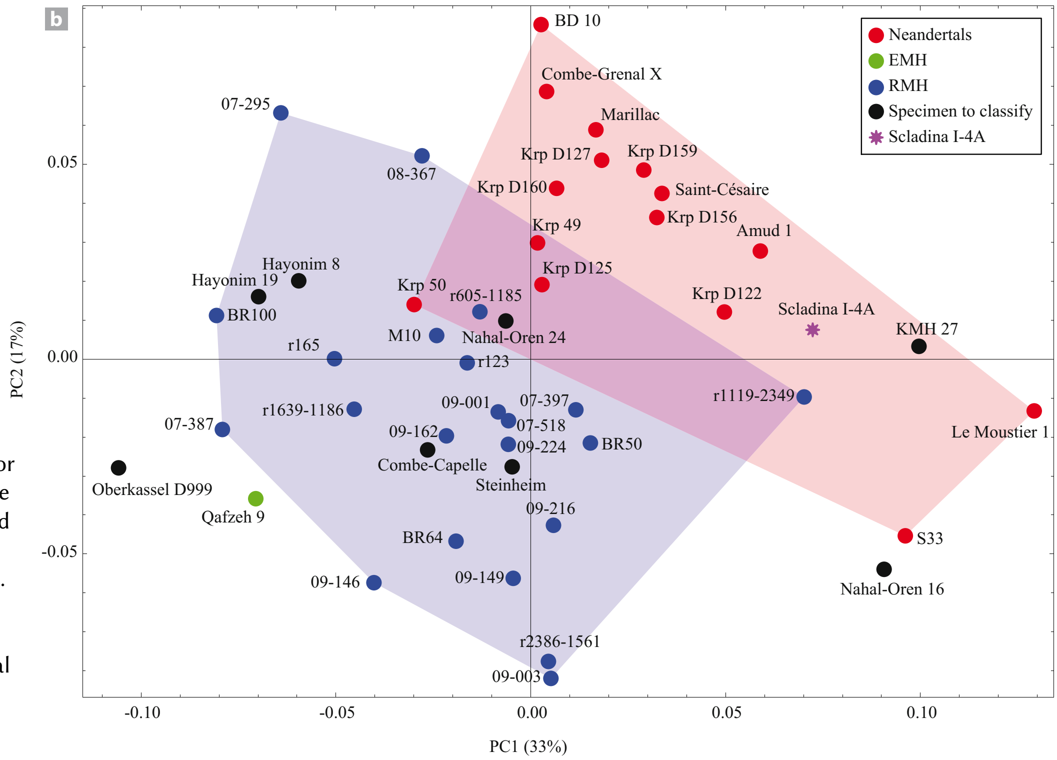


Figure 2: Maxillary lateral incisor root shape in a large comparative context of Neandertals, Early and Recent Modern Humans (after Figure 7 in Le Cabec et al., 2013). Scladina falls right within the Neandertal variation, showing a pronounced supero-inferior labial convexity of its root surface.

the mandibular canine and incisors of Regourdou 1. The Scladina mandibular canine crown size falls in between the values of the two Bourgeois-Delaunay canines. In contrast, regarding the maxillary canine and M_1, Scladina has clearly larger crowns than the Bourgeois-Delaunay teeth, and the same applies for the M_1 compared to Regourdou 1 (Table 4).

The crown size of the I^1 and I_2 of Bourgeois-Delaunay are very close to the Krapina mean, while the I^2 falls within the lower end of the Krapina variation (Table 4). The variability of the I_1 from Bourgeois-Delaunay is equivalent to the one described in Krapina. In contrast, the M_1 and both the maxillary and mandibular canine crowns are strictly smaller than the ones of Krapina.

Regarding the Regourdou 1 mandible, its central incisor and first molar have a labiolingual crown diameter falling below the lower half of the Krapina range of variation (Table 4). The lateral incisor is included in the lower half of the Krapina variability. In contrast, the mandibular canine crown is larger than any value reported for the Krapina sample.

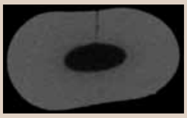
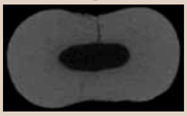
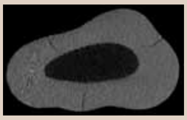
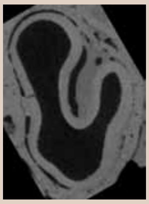
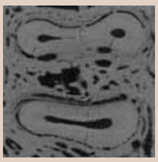
	Tooth	Specimen ID	Root complete?	#R	External root morphology
Mandibular dentition	dm_2 (R)	Scla 4A-13	M L  B D	2	Supposedly 2 roots, one M and one D. The roots are broken very close to the cervix. Only the very cervical part of the distal root is preserved.
	I_1 (R)	Scla 4A-15	D L  B M	1	Root apex is fully closed. Root mesiodistally compressed resulting in an elliptical root cross-section. Supero-inferior labial convexity of the root surface. Picture taken at mid-root.
	I_2 (R)	Scla 4A-20	D L  B M	1	Root tip is broken (estimation at 8.70% of the total root length). Root mesiodistally compressed resulting in an elliptical root cross-section. Supero-inferior labial convexity of the root surface. Sagittal groove on the distal aspect of the root. Picture taken at mid-root.
	C_1 (R)	Scla 4A-12	M L  B D	1	The root is complete. A slight thickening is observed at the apical root third, and the same hypothesis can be made as for the maxillary canines. Elliptical root cross-section. Midline groove on the mesial aspect and to a lesser extent on the distal aspect of the root.
	P_3 (R)	Scla 4A-6	D L  B M	1	About two thirds of the root are formed. The mesiodistally compressed root is bent distally and exhibits a single central groove on its distal aspect and two grooves on the mesial aspect. The cervix is elliptical in cross-section. Picture taken at mid-root.
	P_4 (R)	Scla 4A-1/P_4	M B  L D	1	About two thirds of the root are formed. Strong mesiolingual invagination (Tomes' root morphology described in Hillson, 1996). The lingual component of the root is the largest. Since the root formation is not complete, it cannot be ascertained whether the root would have been completely bifurcated more apically. Picture taken towards the end of the formed root.
	P_4 (L)	Scla 4A-9/P_4	B M  D L	1	About two thirds of the root are formed. Strong mesiolingual invagination (Tomes' root morphology described in Hillson, 1996). The lingual component of the root is the largest. Since the root formation is not complete, it cannot be ascertained whether the root would have been completely bifurcated more apically. Picture taken towards the end of the formed root.
	M_1 (R)	Scla 4A-1/M_1	M L  B D	2	Fully formed roots with closed apices. In cross-section, the mesial root is 8-shaped while the distal root is C-shaped. The mesial root is bifurcated apically. Picture taken towards the end of the roots.
	M_1 (L)	Scla 4A-9/M_1	D L  B M	2	Fully formed roots with closed apices. In cross-section, the mesial root is 8-shaped while the distal root is C-shaped. The mesial root is bifurcated apically. Picture taken towards the apical third of the roots.

Table 3 (continued): Description of the external root morphology in the Scladina mixed dentition.

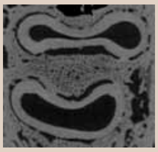
	Tooth	Specimen ID	Root complete?	#R	External root morphology
Mandibular dentition	M_2 (R)	Scla 4A-1/M_2	M L  B D	2	About two thirds of the roots are formed. The point of root furcation is below the cervical third of the total root size. In cross-section, the mesial root is 8-shaped while the distal root is C-shaped Picture taken towards the end of the formed root.
	M_2 (L)	Scla 4A-9/M_2	D L  B M	2	About two thirds of the roots are formed. The point of root furcation is below the cervical third of the total root size. In cross-section, the mesial root is 8-shaped while the distal root is C-shaped Picture taken towards the end of the formed root.
	M_3 (R)	Scla 4A-1/M_3	—	—	No root formed yet (crown about complete).

Table 3 (continued): Description of the external root morphology in the Scladina mixed dentition.

3.2.3. Tooth root size

The root length (RL), surface area (RSA) and total volume (RV) of the Scladina teeth are included in the lower half of the Krapina variation (I_2 and M_1) or strictly smaller (I_1, I^2 and C') than in the Krapina teeth (Figures 3 & 5 and see adjusted z-scores in Figure 4). However, the root length of the M^1 is very close to the Krapina mean. The cervical area (CA) of all the Scladina teeth falls within the lower half of the Krapina variability. Regourdou 1 and Bourgeois-Delaunay have strictly larger roots (for RL, CA, RSA and RV) than Scladina (Figure 5 & Tables 5–8).

Among the 28 root measurements of Bourgeois-Delaunay (RL, RSA, CA, RV, excluding RPV), 24 fall in the lower half of the Krapina range of variation, whereas only the I^1 root length is superior to the Krapina upper end. The root length of the I_1 and the cervical area of the I^1 and C' are above the Krapina range (Tables 5 & 7).

For Regourdou 1, all the root measurements of the I_1, except the root pulp volume, are strictly inferior to the Krapina range. Overall, the I_2, C, and M_1 of Regourdou 1 are included within the lower half of the Krapina variability. It has to be noted that the root length of its M_1 falls in the upper half of the Krapina range of variation (Tables 5–8).

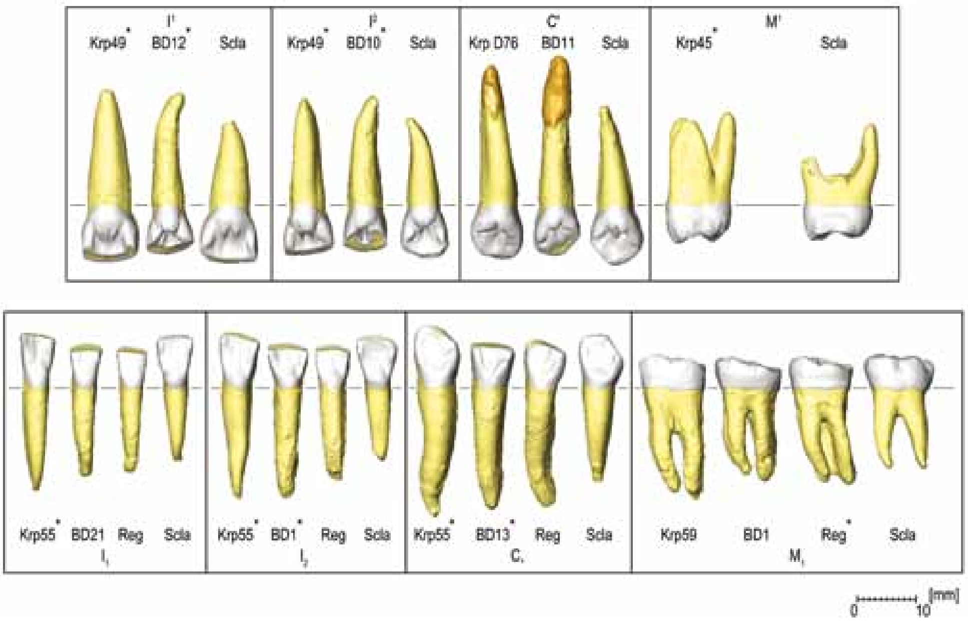


Figure 3: 3D surface models of selected right teeth for each tooth type from Scladina (Scla), Krapina (Krp), Abri Bourgeois-Delaunay (BD) and Regourdou (Reg). Note the presence of hypercementosis on the permanent maxillary canines root apex (shown in light brown). Several specimens were mirrored for illustrative purposes (indicated by an asterisk).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C'	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 8.90 ± 0.66 [8.10–9.50] (7.39)	N=8 8.99 ± 0.35 [8.40–9.50] (3.84)	N=6 10.20 ± 0.68 [9.50–11.10] (6.66)	N=3 11.90 ± 0.53 [11.30–12.30] (4.45)	N=3 7.57 ± 0.38 [7.30–8.00] (5.00)	N=5 7.94 ± 0.57 [7.30–8.75] (7.22)	N=4 9.11 ± 0.37 [8.75–9.50] (4.02)	N=8 11.42 ± 0.62 [10.70–12.15] (5.40)
Abri Bourgeois-Delaunay	N=1 8.40	N=1 8.50	N=3 9.23 ± 0.06 [9.20–9.30] (0.63)	—	N=3 7.63 ± 0.29 [7.30–7.80] (3.78)	N=1 7.90	N=2 7.90; 9.10	N=2 10.50; 10.66
Regourdou 1	—	—	—	—	N=1 7.00	N=1 7.90	N=1 9.60	N=1 10.40
Scladina I-4A	**N=1 7.98**	**N=1 8.27**	**N=1 9.65**	**N=1 11.92**	**N=1 6.79**	**N=1 7.28**	**N=1 8.75**	**N=1 10.68**

Table 4: Descriptive statistics for the labiolingual crown diameter (in mm).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C'	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 18.75 ± 1.28 [16.59–19.58] (6.85)	N=8 19.11 ± 0.83 [17.42–19.97] (4.33)	N=6 23.01 ± 1.07 [20.94–23.81] (4.63)	N=3 13.58 ± 1.32 [12.07–14.51] (9.72)	N=3 19.89 ± 0.84 [19.36–20.86] (4.23)	N=5 19.72 ± 1.78 [17.70–21.63] (9.05)	N=4 23.93 ± 2.16 [21.04–25.64] (9.04)	N=8 16.43 ± 1.48 [14.47–18.45] (9.00)
Abri Bourgeois-Delaunay	N=1 19.79	N=1 18.72	N=3 25.05 ±0.10 [24.98–25.16] (0.38)	—	N=3 17.56 ± 1.58 [16.46–19.37] (9.00)	N=1 19.44	N=2 21.78; 22.22	N=2 13.33; 15.67
Regourdou 1	—	—	—	—	N=1 16.41	N=1 17.80	N=1 22.95	N=1 17.00
Scladina I-4A	**N=1 15.32**	**N=1 15.15**	**N=1 17.69**	**N=1 13.65**	**N=1 13.80**	**N=1 15.23**	**N=1 16.51**	**N=1 13.41**

Table 5: Descriptive statistics for the root length (in mm).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C'	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 355.95 ± 47.04 [288.85–409.32] (13.22)	N=8 376.03 ± 25.06 [337.81–409.22] (6.66)	N=6 473.00 ± 43.06 [414.18–539.41] (9.10)	N=3 —	N=3 337.36 ± 19.60 [320.50–358.86] (5.81)	N=5 360.49 ± 48.09 [279.72–403.59] (13.34)	N=4 508.51 ± 93.07 [393.47–619.68] (18.30)	N=8 615.61 ± 76.35 [491.46–691.67] (12.40)
Abri Bourgeois-Delaunay	N=1 356.45	N=1 371.10	N=3 492.02 ± 14.02 [481.21–507.86] (2.85)	—	N=3 331.55 ± 26.65 [305.10–358.40] (8.04)	N=1 383.05	N=2 427.08; 462.15	N=2 457.84; 555.37
Regourdou 1	—	—	—	—	N=1 259.93	N=1 328.62	N=1 468.91	N=1 569.38
Scladina I-4A	**N=1 244.98**	**N=1 252.79**	**N=1 311.23**	**N=1 —**	**N=1 195.57**	**N=1 240.21**	**N=1 302.09**	**N=1 446.07**

Table 6: Descriptive statistics for the root surface area (in mm²).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C'	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 47.74 ± 9.42 [36.53–59.07] (19.74)	N=8 41.89 ± 4.98 [35.13–49.56] (11.89)	N=6 49.15 ± 5.29 [44.64–55.84] (10.76)	N=3 —	N=3 25.91 ± 1.48 [24.87–27.61] (5.72)	N=5 30.14 ± 3.91 [25.13–35.72] (13.00)	N=4 45.55 ± 3.16 [41.54–48.54] (6.94)	N=8 95.01 ± 11.95 [77.99–111.53] (12.58)
Abri Bourgeois-Delaunay	N=1 33.15	N=1 36.06	N=3 41.59 ± 2.59 [40.00–44.57] (6.22)	—	N=3 27.00 ± 2.70 [25.30–30.12] (10.01)	N=1 26.99	N=2 35.20; 43.77	N=2 77.70; 78.79
Regourdou 1	—	—	—	—	N=1 23.03	N=1 28.60	N=1 44.03	N=1 85.70
Scladina I-4A	**N=1 37.19**	**N=1 33.35**	**N=1 43.34**	**N=1 —**	**N=1 20.99**	**N=1 24.83**	**N=1 40.07**	**N=1 76.08**

Table 7: Descriptive statistics for the cervical surface area (in mm²).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C^1	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 549.58 ± 122.61 [389.74–693.61] (22.31)	N=8 528.47± 72.18 [431.09–633.22] (13.66)	N=6 690.61 ± 74.58 [617.91–817.26] (10.80)	N=3 —	N=3 371.65 ± 26.36 [341.36–389.32] (7.09)	N=5 430.65 ± 70.13 [313.68–491.84] (16.29)	N=4 740.28 ± 157.65 [524.13–902.34] (21.30)	N=8 832.07 ± 148.43 [582.45–999.90] (17.84)
Abri Bourgeois-Delaunay	N=1 473.62	N=1 504.64	N=3 680.57 ± 46.81 [650.64–734.51] (6.88)	—	N=3 371.12 ± 46.10 [331.53–421.73] (12.42)	N=1 455.70	N=2 568.60; 656.03	N=2 561.68; 691.22
Regourdou 1	—	—	—	—	N=1 252.32	N=1 357.57	N=1 619.29	N=1 774.13
Scladina I-4A	**N=1 329.34**	**N=1 310.68**	**N=1 406.87**	**N=1 —**	**N=1 200.08**	**N=1 258.89**	**N=1 387.93**	**N=1 513.92**

Table 8: Descriptive statistics for the root volume (in mm³).

	Maxillary Dentition				Mandibular Dentition			
	I^1	I^2	C^1	M^1	I_1	I_2	C_1	M_1
Krapina	N=6 48.86 ± 24.17 [18.88–85.97] (49.48)	N=8 31.81± 21.82 [12.41–81.67] (68.60)	N=6 42.67 ± 8.11 [27.27–49.49] (19.01)	N=3 —	N=3 13.86 ± 8.69 [7.47–23.75] (62.70)	N=5 27.07 ± 21.27 [8.02–63.03] (78.55)	N=4 41.77 ± 22.10 [17.19–70.75] (52.91)	N=8 75.19 ± 42.75 [44.51–167.45] (56.86)
Abri Bourgeois-Delaunay	N=1 19.40	N=1 11.36	N=3 24.66 ± 5.58 [18.26–28.49] (22.61)	—	N=3 8.40 ± 2.78 [6.42–11.57] (33.06)	N=1 16.62	N=2 13.77; 19.37	N=2 38.09; 102.17
Regourdou 1	—	—	—	—	N=1 12.53	N=1 16.41	N=1 34.30	N=1 67.88
Scladina I-4A	**N=1 44.32**	**N=1 43.33**	**N=1 66.34**	**N=1 —**	**N=1 20.32**	**N=1 29.60**	**N=1 55.85**	**N=1 64.83**

Table 9: Descriptive statistics for the root pulp volume (in mm³).

By contrast, for most of the tooth types (except M_1 and I^1), the radicular pulp volumes (RPV) of the Scladina teeth are systematically higher than the Krapina means (Figure 4 & Table 9). The maxillary canine even has a RPV strictly superior to Krapina. Volumetric proportions of root dentine and pulp reveal a consistent pattern for all tooth types. Scladina has a larger proportion of pulp despite its short roots (Figure 6; Tables 8 & 9). However, the I_2 and M_1 of Krp 53 and the I^2 of Krp D122 have extremely large pulp cavities, exceeding the corresponding Scladina teeth by 1.4%, 4.1% and 2.0% respectively (Figure 6). Regourdou 1 has radicular dentine to pulp proportions similar to Bourgeois-Delaunay for the incisors, and to Krapina for the canine and first molar (Figure 6).

The intra-individual comparison in relative differences in root lengths has yielded an interesting and consistent pattern (Figure 7 & Table 5). Compared to the M_1 root length, one observes relatively longer mandibular anterior tooth roots in our Krapina individuals (Krp 54, 55, 58 and 59; 27.89% on average), Bourgeois-Delaunay (BD1; 28.89%) and Scladina (13.19%). The root length increases gradually from I_1 to mandibular canine although both incisors have a similar root length. Regourdou 1 follows the same pattern, except that its I_1 root is shorter than its M_1 roots.

3.2.4. Relationship between crown size and root size

Figure 8 presents the ratio between the bucco-lingual crown diameter and the root length for each tooth type in our four subsamples. Scladina shows consistently the highest value for each tooth type, meaning that these teeth display large crowns in proportion to their short roots. Crown size and root size proportionally contribute with the same amount to the tooth size (percentages around 50% in Figure 8) in the Scladina incisors and canines. However, the first molars have markedly short roots for the size of their crown (percentages about 80–90% in Figure 8). Overall, Bourgeois-Delaunay shows relatively small crowns for large roots, although it has to be noted that the M_1 has a proportionally shorter palatal root. Regourdou 1 follows the same pattern as Bourgeois-Delaunay, although its roots are shorter. Finally, Krapina shows for all tooth types a very large variability that encompasses all the previously described

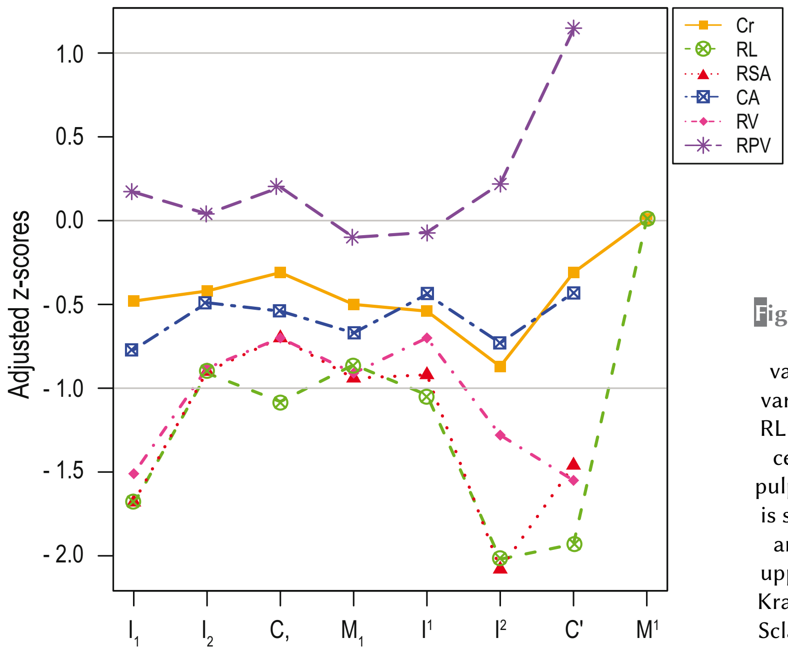


Figure 4: Adjusted z-scores (Azs) comparing how Scladina fits into the Krapina variability using six tooth crown and root variables (Cr: labiolingual crown diameter; RL: root length; RSA: root surface area; CA: cervical area; RV: root volume; RPV: root pulp volume). For *Azs* close to zero, Scladina is similar to the Krapina mean; for *0<Azs<1* and *–1<Azs<0*, Scladina falls whithin the upper and the lower half of the variation of Krapina, respectively; for *–1<Azs* and *Azs>1*, Scladina is outside of the Krapina variation.

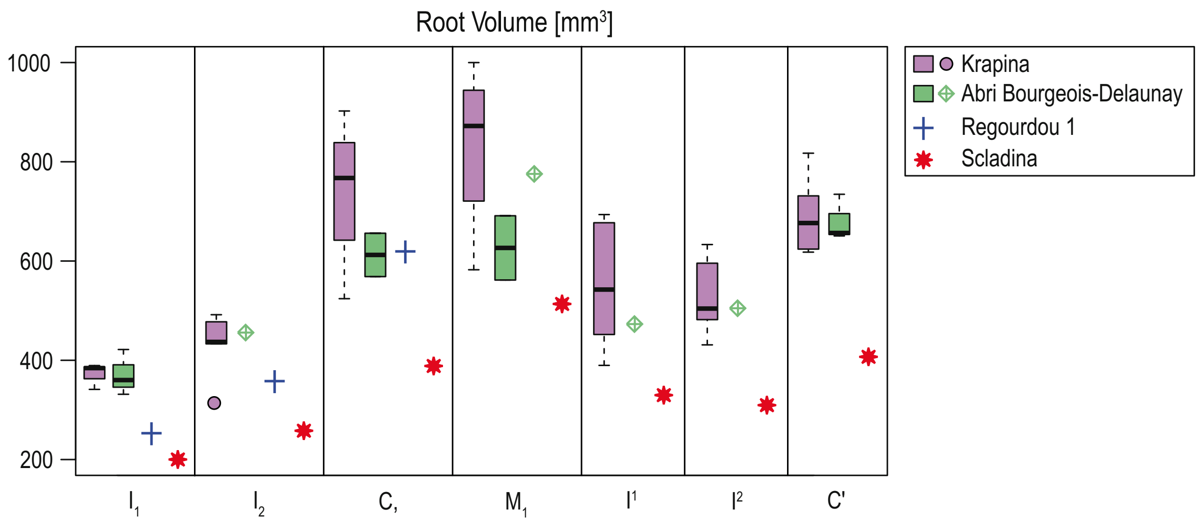


Figure 5: Total root volume [mm³] of the mandibular and maxillary permanent incisors, canines and first molars of Bourgeois-Delaunay, Krapina, Regourdou 1 and Scladina (minimum, first quartile, median, third quartile, and maximum; outliers are denoted by circles).

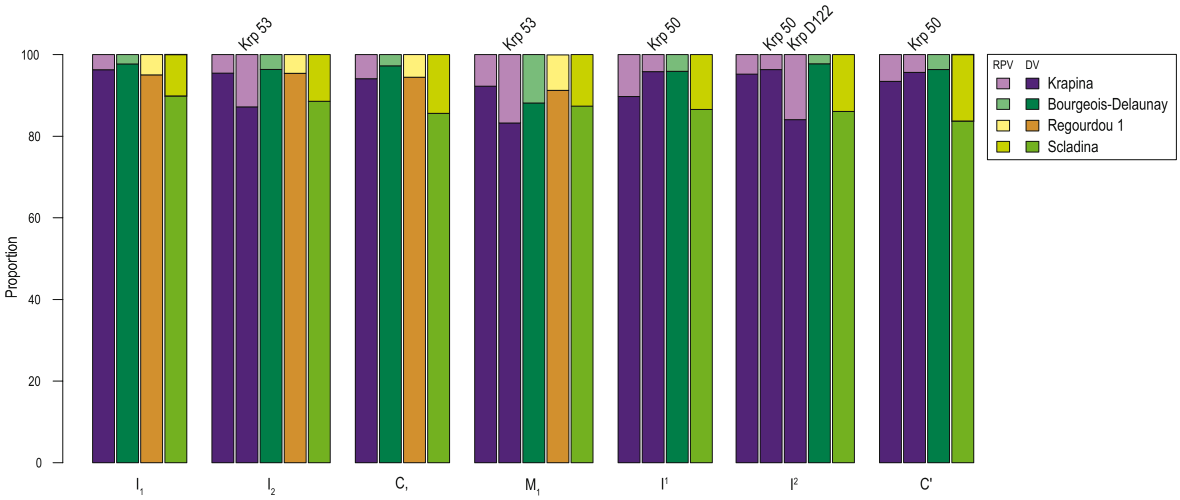


Figure 6: Proportions of tooth root dentine (DV) and pulp (RPV) volumes. The proportions of individuals of similar age as Scladina are represented separately.

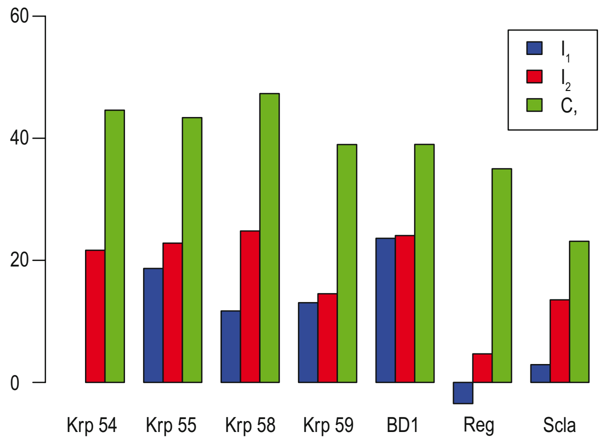


Figure 7: Intra-individual proportions in root length of I_1, I_2 and C, compared to M_1 for individuals with most complete mandibular dentitions. This percentage is calculated as follows: p(x) = – 100 + ([RL(x)*100]/ RL(M_1)), with RL for root length, and x for I_1, I_2 and C,.

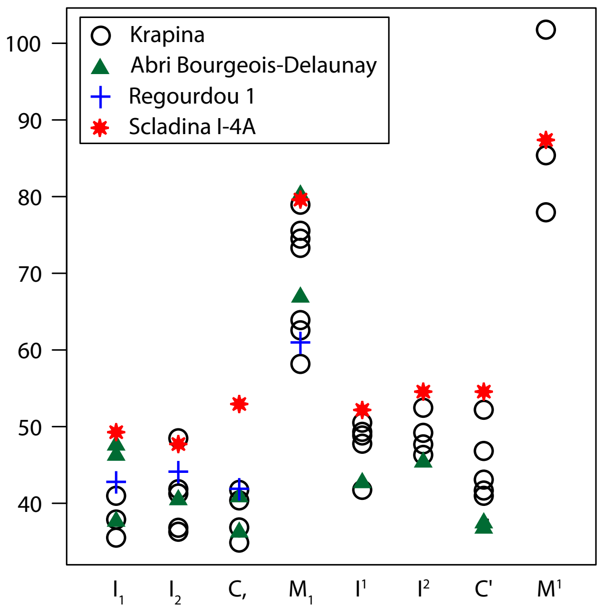


Figure 8: Proportion of the maximum buccolingual crown diameter (Cr, in mm) to the root length (RL, in mm) computed as: (Cr* 100)/ RL.

patterns. About half of the Krapina sample has relatively shorter roots for the size of its crowns, while the other half has relatively longer roots for its crown size.

To summarize, our results show that overall root size is much more variable than crown size. The measurements of the Scladina maxillary and mandibular teeth fall within the lower half of the Krapina range of variation or are excluded from their variation. Only the Scladina pulp volumes are among the largest measured in our sample. The Krapina sample has the largest crown and root dimensions of the four samples (Tables 4–9). The Bourgeois-Delaunay and Regourdou 1 teeth are smaller than those from Krapina but the Bourgeois-Delaunay remains are always included in the lower half of the Krapina range of variation.

4. Discussion

This study aimed to document the tooth root morphology of the permanent mandibular and maxillary incisors, canines and first molars of the Scladina Juvenile. After a description of the external morphology of all the roots of the Scladina mixed dentition, the root morphology of its permanent teeth was further investigated using micro-computed tomography and in the comparative context of other MIS 5 Neandertals from Krapina, Abri Bourgeois-Delaunay and Regourdou. Our results show that Scladina has comparatively very short tooth roots while the size of its crowns is similar to those of the other Neandertals. Scladina also displays the largest pulp cavities among all samples studied.

4.1. Taxonomical interest of root dimensions: the case of Scladina I-4A, a short-rooted MIS 5 Neandertal

The root length of I^1, I_1, C' and P^4 has been proposed to taxonomically discriminate Neandertals from anatomically modern humans (Bailey, 2005; Bailey & Hublin, 2006). However, in view of our results, we recommend a cautious taxonomical diagnosis of Neandertal fossil teeth, based solely on tooth root metrics (see Le Cabec et al., 2013 for examples on taxonomically debated specimens). Indeed, the root lengths of all the corresponding Scladina teeth (except for the premolars which were not studied here due to incompleteness of their roots) are outside the Neandertal range of variation provided in Bailey (2005), but fall within the Upper Palaeolithic range of variation sampled in her study. The Scladina dental dimensions are very small compared to other MIS 5 Neandertals sampled in this study. Such interpopulational or interindividual differences also exist for MIS 3 Neandertals specimens. The Spanish Sima de Las Palomas Neandertals (Walker et al., 2008) have shorter anterior tooth roots than more northern Neandertals, but they are still longer than those of Scladina, except for an I^2 (SP48) and a C' (SP26).

The first molars of Scladina also have short and overall small roots compared to our MIS 5 Neandertals. They do not display any degree of taurodontism, typical root morphology very frequently seen in Neandertals.

The case of Scladina thus extends the range of variability in tooth root dimensions in Neandertals, and requires a careful assessment of taxonomical identity using root length including both Early and Late Neandertals from different geographic origins.

4.2. In light of this study, is Krapina representative of the MIS 5 Neandertal dental variation?

Both Krapina and Bourgeois-Delaunay are known to have large-crowned teeth (Wolpoff, 1979; Condemi, 2001). Our results extend these previous studies by including the external (root length, surface area, and volume) and internal (root pulp volume) tooth root measurements.

On the one hand, crown size seems to be stable overall in MIS 5 Neandertals (CV<7.5%, Table 4), with Scladina, Regourdou 1 and Bourgeois-Delaunay falling in the majority of cases within the lower half of the Krapina variation. On the other hand, root dimensions are much more variable (on average 11.15% for Bourgeois-Delaunay and 19.83% for Krapina), especially root pulp volumes. This could be explained by the fact that crown development is said to be under strong genetic control, whereas root development is more influenced by environmental factors (Kovacs, 1967). Krapina was found to have the largest crown and root dimensions of our Neandertal samples, while the Bourgeois-Delaunay teeth are slightly smaller. The latter, however, consistently fall within the lower half of the Krapina range of variation. These two samples thus represent populations with both robust crown and root dimensions.

Overall, Regourdou 1 is smaller than Bourgeois-Delaunay and Krapina, for both crown and root dimensions. While Scladina has crowns of comparable size with the other MIS 5 Neandertals, its roots are markedly short. Moreover, one can notice that variation in relative incisors root dimensions (Figure 7) does not appear to be related to geography as suggested by the large-rooted Krapina and Bourgeois-Delaunay (central Europe and southwestern Europe) in contrast to the relatively smaller Scladina and Regourdou 1 (northern Europe and southwestern Europe).

In addition, a comparison of the crown dimensions of the four MIS 5 samples with published values for the MIS 5e skulls of Saccopastore 1 and 2 (Italy) indicates a marked variability among Early Neandertals. For example, the buccolingual crown diameters of the maxillary canine and first molars of Saccopastore 1 and 2 reported in Condemi (1992) are smaller and consistently excluded from the variation we observed in the Neandertals from Krapina, Bourgeois-Delaunay and Scladina (see also Stringer, 1982 for a comparison between Saccopastore and Krapina). However, no information is currently available in the literature regarding the dimensions of the maxillary tooth roots of those Italian specimens. Future studies involving micro-CT data are needed to document the root morphology in the Saccopastore specimens.

Although Krapina is often used because of its large sample size, it is not representative of the MIS 5 Neandertal variability, this population being exceptionally robust. Scladina and Regourdou 1 are good examples of small-rooted contemporaneous Neandertals.

4.3. What about crown to root size proportions?

The analysis of the proportion of crown size to root size reveals that Krapina has relatively large roots for the size of its crowns and the same applies to Bourgeois-Delaunay and Regourdou 1, although to a lesser extent. Conversely, Scladina has relatively short roots for his/her crowns (Figure 8). This raises the question whether one can estimate tooth root size from its crown size. In other words does a tooth with a large crown have associated big root(s)? The case of Scladina suggests that there would be no predictive relationship between crown size and root size. Interestingly, Smith and Paquette (Paquette, 1985; Smith & Paquette, 1989) concluded that there was a positive correlation between crown and root size in the Krapina anterior teeth, that is, large-crowned teeth have large roots. Conversely, Le Cabec et al. (2013) cannot find any significant correlation in a geographically and chronologically broad sample of Neandertal anterior teeth. Smith and Paquette (Paquette, 1985; Smith & Paquette, 1989) have also shown that the ratio of the crown labiolingual diameter to the root length still distinguish Neandertals from extant humans. This discordance may stem from the fact that these authors took into account the crown diameters and the corresponding root diameters, whereas Le Cabec et al. (2013) tested the correlation between the root length and the labiolingual crown diameter. Kupczik & Hublin (2010) have reported that mandibular molar root surface area correlates significantly with cervical plane area and enamel-dentine junction area in both Neandertals and modern humans. There are indications of a low correlation between crown and root size in Recent Modern Humans (Garn et al., 1978[a]; Garn et al., 1978[b]; Smith et al., 1986; Ozaki et al., 1988; Smith et al., 1989; Kupczik, 2003; Kupczik et al., 2009). As pointed out by Spencer (2003) on platyrrhine seed-eaters, crown and root size may not covary the same way in all taxa. Moreover, as shown by the divergence between Smith and Paquette's findings and the Le Cabec et al. (2013) study, results may depend on the measurements selected (e.g. root length vs. crown diameters, root diameters vs. crown diameters, root surface area vs. enamel-dentine junction area). However, the case of Scladina with its short roots for its relatively large crowns questions the relation of crown size to root size in Neandertals.

4.4. What can be discussed about sexual dimorphism?

Clinical studies on Recent Modern Humans have shown that sexual dimorphism is greater in root length than in crown diameters (Garn et al., 1978[c]; Garn et al., 1979), males having longer roots than females (Jakobsson & Lind, 1973). Furthermore, studies of genetic disorders support the role of sex chromosomes in root length (Alvesalo et al., 1991; Lähdesmäki, 2006; Lähdesmäki & Alvesalo, 2007). In the light of these clinical studies, the short roots of Scladina would suggest that this individual may have been female. Toussaint (Chapter 9) highlights the small mandibular corpus dimensions of Scladina, in comparison with other Neandertals of the same age group, and he further suggests that Scladina could have been female. The pulp cavity volumes of all the investigated Scladina teeth are among the largest of the teeth measured in this study. It has been proposed that secondary dentine deposition would be related to sexual dimorphism, with males having thicker radicular dentine than females (Schwartz & Dean, 2005). In addition to the short roots, this would be a second argument to suggest that this individual may have been female.

4.5. How influential can the young age of Scladina be on its roots dimensions?

Zilberman & Smith (2001) further suggested that sexual dimorphism combined with ageing would affect the progressive closing of the pulp cavity throughout life. Having significantly smaller total root volumes than the three other samples, the Scladina teeth therefore display thinner dentine walls of their large pulp cavities. A possible explanation for this may be the young age of the Scladina individual, estimated at eight years old (Smith et al., 2007). It has to be reminded that contrary to bone which is subject to remodeling throughout life, the teeth initiate and complete their mineralization while they erupt, to reach functional emergence, and they do not remodel afterwards. They can be subject to various pathologies or traumatic events, the roots can resorb, and the only way of healing or changing the shape of a tooth is to secrete hypertrophic cementum (see Le Cabec et al., 2013 for a discussion in the functional context of the Neandertal dentition). Among our Krapina sample, Krp53 (Mandible C), whose age at death is estimated at 11 years old (Wolpoff, 1979), also shows outlier values for the pulp volume of its lateral incisor and first molar. The permanent maxillary lateral incisor Krp D122 estimated to belong to a 13 years old individual also shows a large pulp volume (Figure 6). Several studies have shown that apposition of secondary dentine on the walls of the pulp chamber increases with age (Gustafson, 1950; Philippas, 1961; Philippas & Applebaum, 1967; Woods et al., 1990; Paewinsky et al., 2005). Furthermore, secondary dentine is commonly thought to be deposited throughout life to compensate for occlusal wear (also referred to as tertiary dentine or irregular dentine, e.g. Kuttler, 1959), leading to a progressive retraction of the pulp (e.g. Broeste et al., 1944; Pedersen, 1949; Sicher & DuBrul, 1970; Barrett, 1977). The filling of the pulp cavity occurs then from the cervix to the apex whereas wear erodes the coronal dentine core (Berry & Poole, 1976; Barrett, 1977). No systematic clear-cut identification of secondary dentine apposition in the pulp cavity could be made from our micro-CT data, as the two types of dentine have a very similar density. Yet, in some cases, a slight difference in gray-values delineates the secondary dentine evenly deposited on the walls of the pulp cavity, in some of the older specimens from Krapina (e.g. permanent mandibular right canine in Krp59, estimated age at death of 20 years following Wolpoff, 1979) and Bourgeois-Delaunay (e.g. BD15, see Figure 1E in Le Cabec et al., 2013). Then, only the use of appropriate filters (as described in the Materials and Methods section and Figure 1E in Le Cabec et al., 2013) could reveal the border between these two materials. Combined observations of photographs and of our micro-CT data reveal that the reparative secondary dentine was sometimes exposed by severe attrition, e.g. on the permanent mandibular left central incisors of Krp58 and Krp59. Therefore, differences in individual age could account for the difference in pulp volume observed between Scladina and Krapina.

4.6. How reliable is it to discuss about sexual dimorphism and age in fossils?

Although it is impossible to discern the relative importance of age and sex in the conformation of the Scladina roots, its large pulp cavities are likely accounted for by its young age whereas its short roots and thin root dentine walls of the pulp cavities point that it could be a female individual. However, sexual dimorphism in root length and root pulp volume cannot account alone for the difference between Scladina on one hand, and Regourdou 1, Krapina and Bourgeois-Delaunay on the other hand. As the two last samples contain isolated, non-associated teeth, especially for the larger Krapina sample, it is likely that males and females are sampled in this archeological population. Wolpoff (1979) and Bermúdez de Castro et al. (1993) highlight a low sexual dimorphism in the dental remains from Krapina. Only mandibular corpus variation accurately estimates the sex of the extremes, such as Krp 58 and Krp 59 being likely males. This means that, although the level of sexual dimorphism in Krapina is low, this population likely includes females and is overall larger in dental dimensions than Scladina, Regourdou 1 and Bourgeois-Delaunay. The sex-ratio being unknown in our samples, any more developed discussion regarding sexual dimorphism would be speculative.

4.7. Dental development

The short roots of Scladina could be attributable to variation in particular dental developmental parameters.

Most of the developmental studies have focused on enamel growth involving enamel secretion and extension rates, and crown formation time. Although it has been argued that the duration of tooth development might have been similar in Neandertals and modern humans (Guatelli-Steinberg et al., 2005), microstructural studies on large samples, including Scladina in particular, have shown significant developmental differences between Neandertals and modern humans (Ramirez Rozzi & Bermudez de Castro, 2004; Smith et al., 2007; Smith, 2008; Smith et al., 2010). Smith et al. (2010) conclude that the faster dental development in Neandertals does not seem to be related to ontogenetic stage, geological age or geography, albeit Scladina and Engis 2, both from Belgian sites, show a particularly rapid dental growth that is also faster than other Neandertals for the molars, while some of their incisors are slower. Moreover, Bayle et al. (2009[a]; 2009[b]) also noted a specific pattern of dental maturation in the Roc-de-Marsal child where incisors are delayed and the first molars advanced compared to a sample of modern humans. In addition to its peculiar timing of dental development, the pattern of dental maturation can be affected by the small dimensions of the Scladina's roots, that is, incisors and molars could show intra-individual differences in their relative sequence of eruption.

In contrast, very little is known about root formation. According to Macchiarelli et al. (2006) a late peak in root extension rate occurs in molars and this distinguishes Neandertals from anatomically modern humans. Smith et al. (Chapter 8) provide values for root extension rate, especially for the first molar of Scladina. A finer overview of the phenomenon would require a larger amount of comparative data. But since crown extension rates are much faster in Neandertals than in Recent Modern Humans (Smith et al., 2007; Smith et al., 2010), one could speculate that the same applies to root extension rates.

To conclude, one can speculate that the short roots of Scladina could result from a shorter period of dental development combined with an individual faster rate of root extension. Further research may investigate in more detail how the absolutely and relatively short incisor roots and contrasted overall rapid dental development in Scladina might have implications in understanding the relative differences in intra-individual dental maturation sequences within Neandertals.

4.8. Scladina I-4A in a broader comparative context

Compared to a larger sample of Neandertals, Early and Recent Modern Humans (see Kupczik & Hublin, 2010 for the first molars; see Le Cabec et al., 2013 for the anterior teeth), Scladina has among the smallest roots documented.

For the anterior dentition, the Scladina root metrics fall in the area of overlap of Neandertals and the Recent Modern Humans, or even strictly in the modern human distribution. Figures 9–14 illustrate the position of Scladina among temporally and geographically broad comparative samples: this Neandertal has the shortest roots among all Neandertals ranging from MIS 7 to 3. However, when all root and crown metrics are combined into PCA and CVA analyses, the results of the cross-validation tests show that all maxillary anterior teeth classify correctly as Neandertals, as for the I_1, while the I_2 and C, classify among Early Modern Humans (EMH,

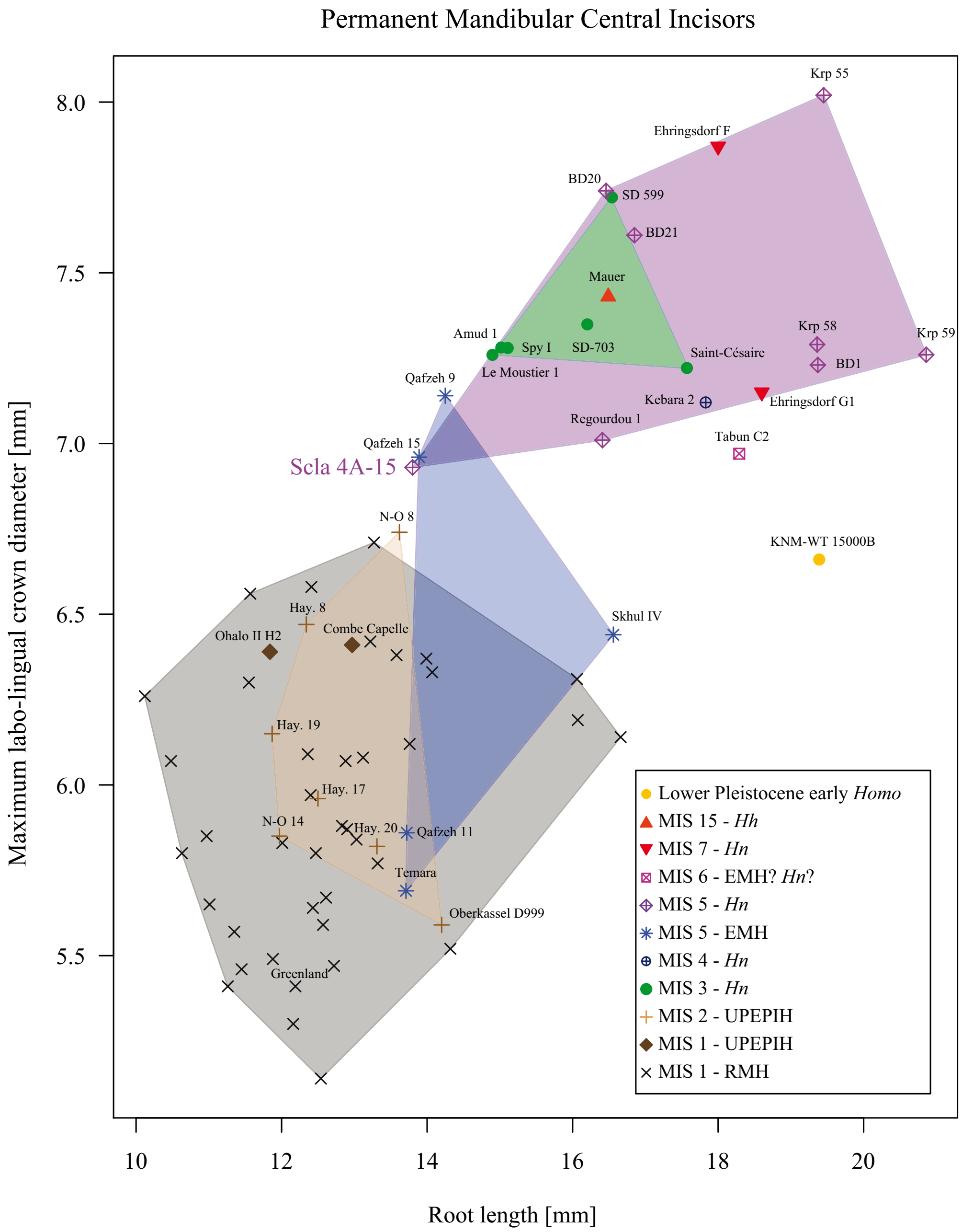


Figure 9: Scla 4A-15 in the broader context of permanent mandibular central incisors. The observed pattern suggests a chronological trend in our crown and root size data. A gradient is clearly visible, from the older specimens (at the right) toward the more gracile Recent Modern Humans (at the very left). Note the smaller variability of MIS 3 Neandertals (this is possibly due to small sample size). Adapted from Le Cabec et al., 2013.

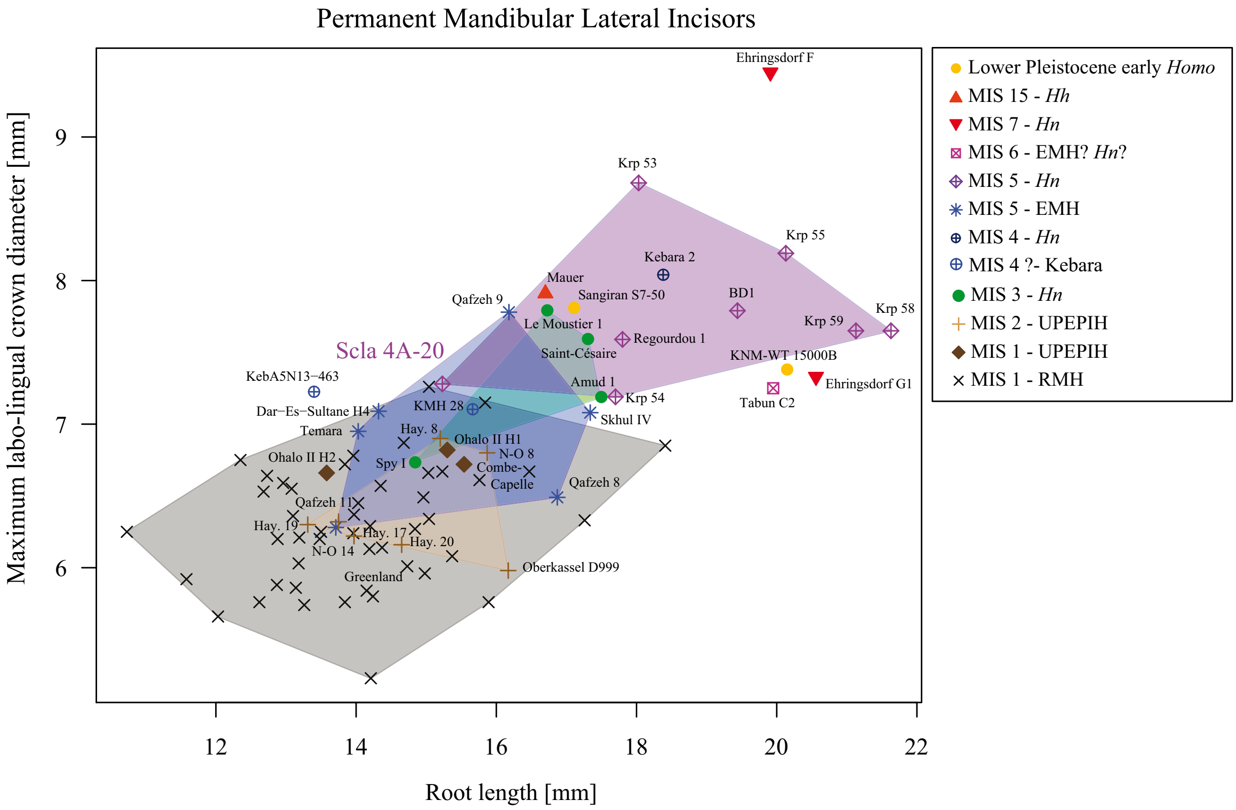


Figure 10: Scla 4A-20 in the broader context of permanent mandibular lateral incisors. Same possible gradient in size and chronological trend as in Figure 9.

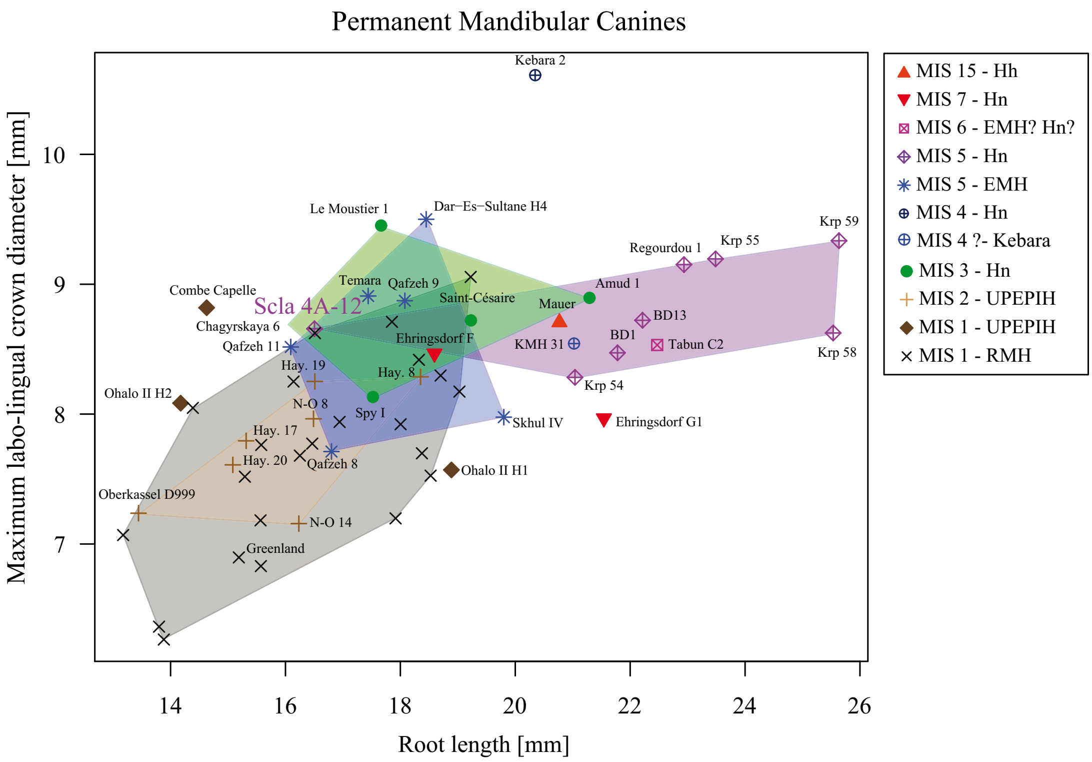


Figure 11: Scla 4A-12 in the broader context of permanent mandibular canines. Same possible gradient in size and chronological trend as in Figure 9.

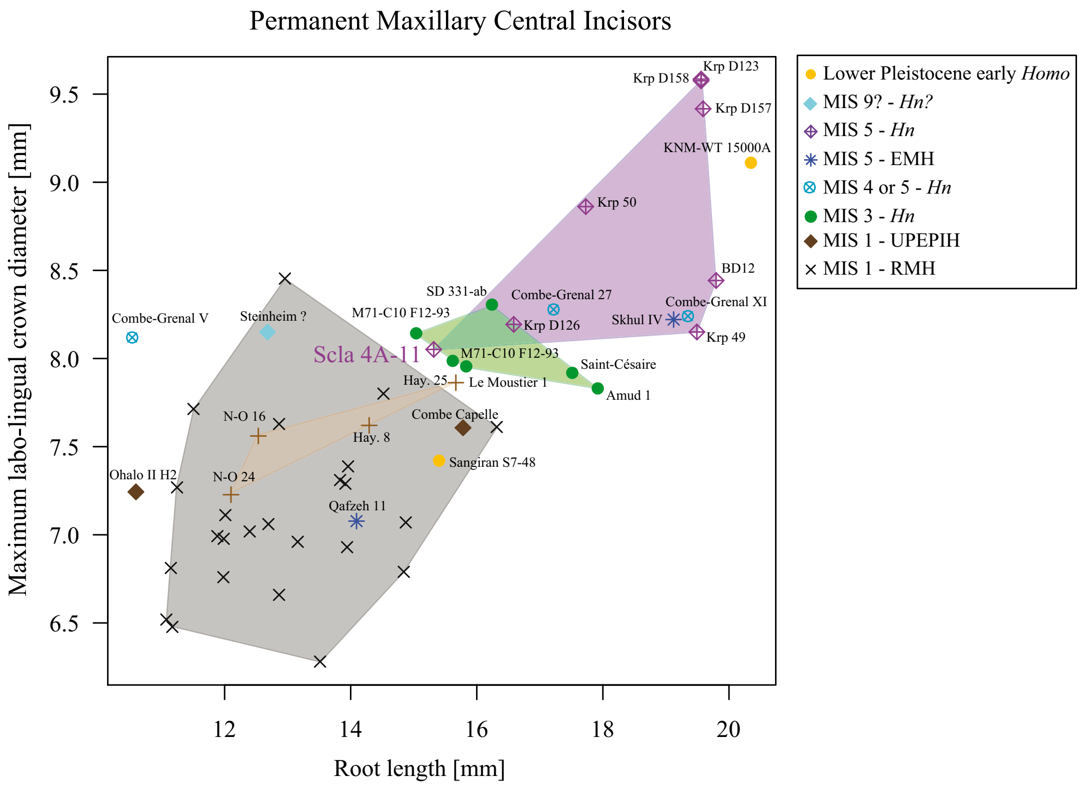


Figure 12: Scla 4A-11 in the broader context of permanent maxillary central incisors. Same possible gradient in size and chronological trend as in Figure 9.

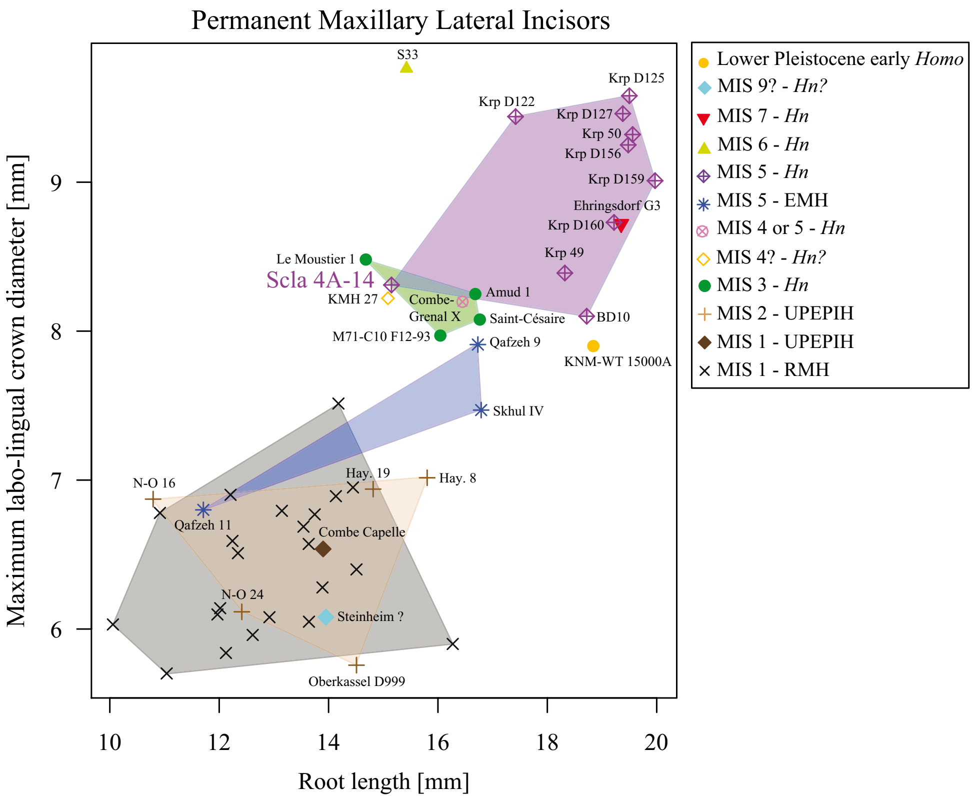


Figure 13: Scla 4A-14 in the broader context of permanent maxillary lateral incisors. Same possible gradient in size and chronological trend as in Figure 9.

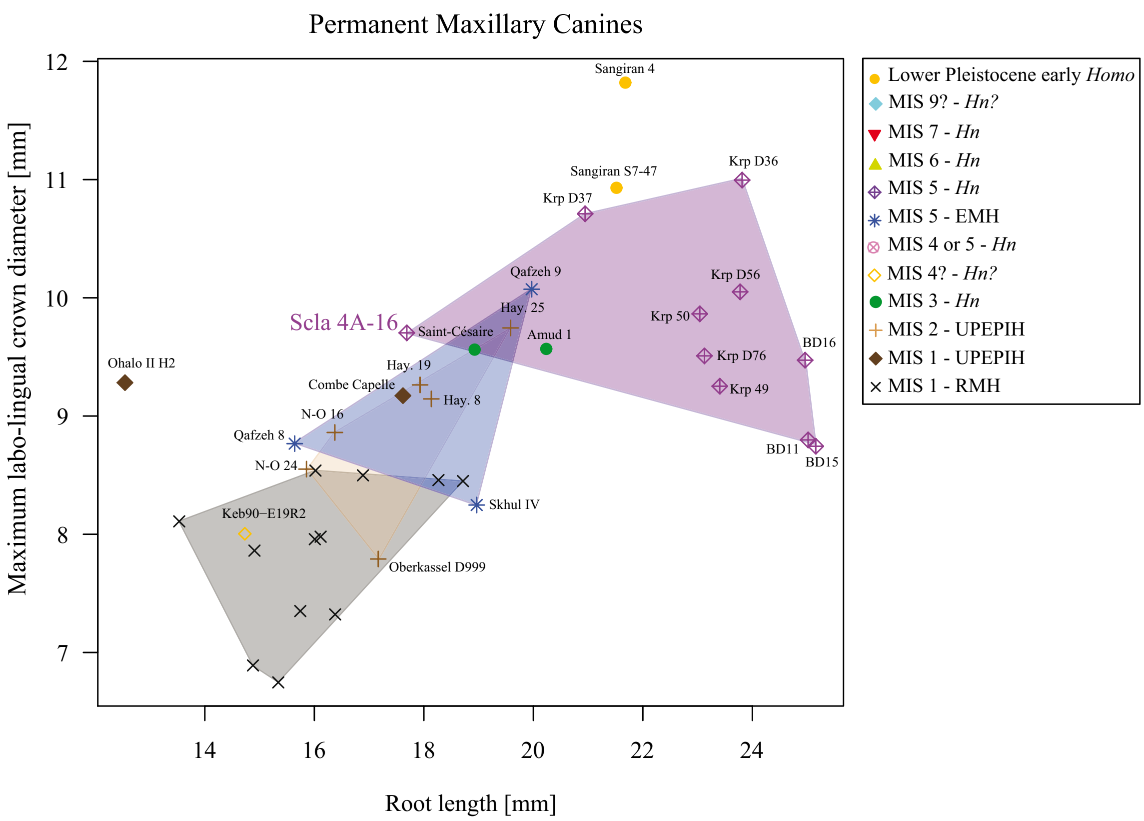


Figure 14: Scla 4A-16 in the broader context of permanent maxillary canines. Same possible gradient in size and chronological trend as in Figure 9.

see Figure 6 and supplementary information Figure 1 in Le Cabec et al., 2013). This later result can be easily explained, since most of the classification is driven by size, the smaller Neandertals will have a higher probability to be classified as EMH. Le Cabec et al. (2013) have demonstrated that long roots in Neandertals likely result from the retention of an ancestral condition. The EMH are not yet as specialized as the Recent Modern Humans, whence their overlapping position between Neandertals and extant humans. As pointed out earlier with Sima de las Palomas and, here with Scladina, Neandertals have a broader variability in root dimensions than previously thought, although they remain overall significantly larger than extant humans. The shape of the anterior roots of the Scladina Juvenile (see Figure 2, after Le Cabec et al., 2013, see this publication for details) are typically Neandertal, involving a supero-inferior labial convexity of the root surfaces.

The lack of any degree of taurodontism in the mandibular first molars of Scladina could be taxonomically misleading (Figure 15). Kupczik & Hublin (2010) provide a larger comparative context for the M_1. The root pulp volume of the Scladina M_1 falls within the lower half of the Neandertal descriptive statistics reported (mean ± standard deviation). Regarding root length, surface and volume, the Scladina M_1 falls below the distribution reported, but should be equal or close to the minimal values. All the Scladina M_1 root dimensions fall within the Recent Modern Human variation described by Kupczik & Hublin (2010).

To summarize, our results highlight the very small root dimensions of the Scladina Juvenile. Krapina shows a large intra-populational variability and has the largest dental dimensions. Specimens from Abri Bourgeois-Delaunay fall in the Krapina variability and also exceed Scladina in root dimensions. The same is true for the Regourdou 1 specimen which has relatively small teeth. In addition, the relatively small teeth of Regourdou 1 and the short roots of Scladina go against the assumption that Krapina can reliably be taken as representative of the dental variation of MIS 5 Neandertals.

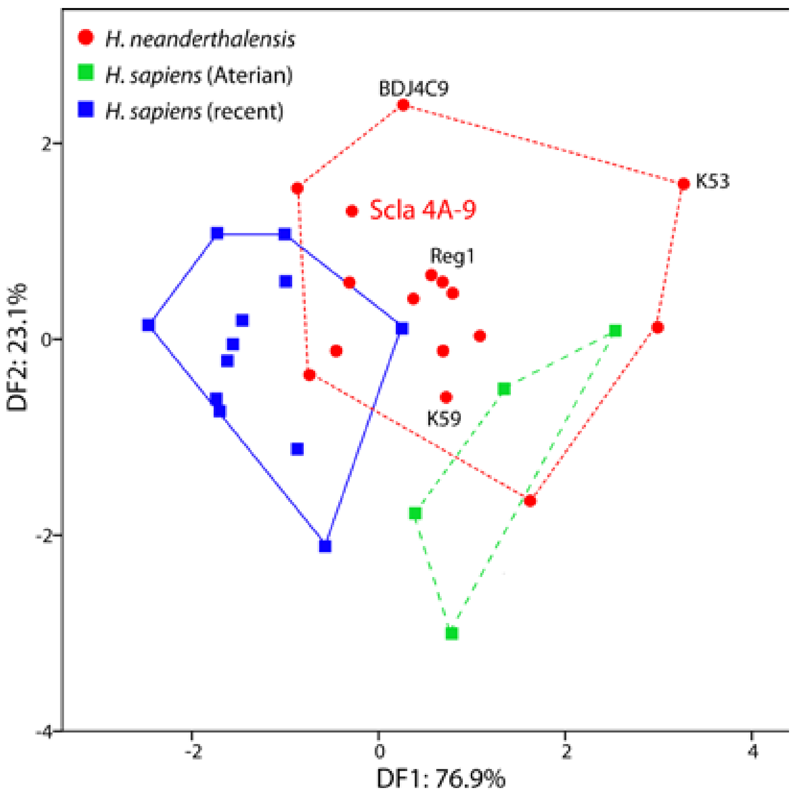


Figure 15: Molar root morphology and taurodontism. Plot of the first two principal components calculated from the covariance matrix of five linearised root variables (root length, cervical plane area, pulp volume, root stem volume, root apex volume) in the first mandibular molar (modified after Kupczik & Hublin, 2010).

5. Conclusion

Using micro-computed tomography, the present study documents the external and cross-sectional root morphology in all teeth of the Scladina Child. Moreover, we compare the Scladina crown and root, external and internal dimensions, to a sample of MIS 5 Neandertal teeth from central Europe (Krapina) and southwestern France (Bourgeois-Delaunay and Regourdou 1). While the crown and root dimensions of Bourgeois-Delaunay and Regourdou 1 are well within the range of the Krapina sample, the teeth of the Scladina Juvenile have relatively short tooth roots with large pulp cavities. These differences in root form among MIS 5 Neandertals may be due to geographic variability, sexual dimorphism, individual variability in dental development, and age modifications of the dental tissues. Furthermore, our results suggest that taxonomical diagnosis based on root metrics alone has to be considered carefully, as shown by the outlier short-rooted Scladina.

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