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Brief Communication: Dental Development and Enamel Thickness in the Lakonis Neanderthal Molar

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ABSTRACT Developmental and structural affinities between modern human and Neanderthal dental remains continue to be a subject of debate as well as their utility for informing assessments of life history and taxonomy. Excavation of the Middle Paleolithic cave site Lakonis in southern Greece has yielded a lower third molar (LKH 1). Here, we detail the crown development and enamel thickness of the distal cusps of the LKH 1 specimen, which has been classified as a Neanderthal based on the presence of an anterior fovea and mid-trigonid crest. Crown formation was determined using standard histological techniques, and enamel thickness was measured from a virtual plane of section. Developmental differences include thinner cuspal enamel and a lower periodicity than modern humans. Crown formation in the LKH 1 hypoconid is estimated to be 2.6–2.7 years, which is shorter than modern human times. The LKH 1 hypoconid also shows a more rapid overall crown extension rate than modern humans. Relative enamel thickness was approximately half that of a modern human sample mean; enamel on the distal cusps of modern human third molars is extremely thick in absolute and relative terms. These findings are consistent with recent studies that demonstrate differences in crown development, tissue proportions, and enamel thickness between Neanderthals and modern humans. Although overlap in some developmental variables may be found, the results of this and other studies suggest that Neanderthal molars formed in shorter periods of time than modern humans, due in part to thinner enamel and faster crown extension rates. Am J Phys Anthropol 138:112–118, 2009.

Studies of hominin tooth growth and enamel thickness have become quite numerous in recent decades, yielding refined assessments of the evolution of life history and taxonomic differences among hominins (reviewed in Dean, 2006; Olejniczak et al., 2007, 2008a; Smith, 2008; Smith and Hublin, 2008). Neanderthals (*Homo neanderthalensis*) have been the subject of much debate. This stems from conflicting evidence for similarities and differences relative to fossil and modern *Homo sapiens* in terms of both tooth growth (e.g., Dean et al., 1986; Stringer et al., 1990; Mann et al., 1991; Tompkins, 1996; Skinner, 1997; Stringer and Dean, 1997; Thompson and Nelson, 2000; Ramirez Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2005; Macchiarelli et al., 2006; Smith et al., 2007a) and tooth structure (e.g., Zilberman et al., 1992; Molnar et al., 1993; Constant and Grine, 2001; Grine, 2004; Olejniczak and Grine, 2005; Macchiarelli et al., 2006; Zilberman, 2007; Olejniczak et al., 2008a). These characters have taken on an important role in the continuing debate over the taxonomic status of Neanderthals, the magnitude of their anatomical differences from modern humans, and the likelihood of a Neanderthal genetic contribution to modern human origins in Europe (e.g., Stringer, 1992; Wolpoff et al., 2001; Harvati, 2003; Grine, 2004; Harvati et al., 2004; Serre et al., 2004; Smith et al., 2005a; Weaver and Roseman, 2005; Green et al., 2006; Hublin and Bailey, 2006; Harvati et al., 2007).

Tooth development is traditionally assessed from casts and thin sections of teeth, which reveal incremental structures that provide evidence for the speed and duration of crown and root formation (reviewed in Dean, 2006; Smith, 2008). Due in part to the semi-destructive nature of histological studies, only five[1] sectioned Neanderthal teeth have been reported prior to this study: a developing first molar from a Syrian infant Neanderthal (Sasaki et al., 2003); a fragment of first molar enamel from Tabun 1, Israel (Dean et al., 2001; Dean, 2007); a deciduous second molar and a permanent first molar from La Chaise, France (Macchiarelli et al., 2006); and a first molar from the Scladina Cave, Belgium (Smith et al., 2007a). Internal data on the rate of enamel development and periodicity of long-period growth lines are critical for studies of incremental features preserved on the surface of tooth crowns and roots (e.g., Dean et al.,

[1]Five likely Neanderthal teeth from the Tabun cave were sectioned for a study of dental pathology by Sognnaes (1956), but data on incremental development were not reported, and the sections are currently unavailable.

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2001; Ramirez Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2005), in addition to the time of crown and root formation (e.g., Macchiarelli et al., 2006; Smith et al., 2007a). Recent data on crown formation time in two Neanderthal first molars (Macchiarelli et al., 2006; Smith et al., 2007a) are in conflict; in the former case Neanderthal molar formation was said to be "nearly identical" to that of modern humans, whereas in the latter case Neanderthal molars were found to form over shorter periods of time due to differences in enamel thickness and coronal extension rates. Additional data on Neanderthal molar development are necessary to resolve this disparity.

Components of tooth structure such as enamel thickness are traditionally assessed using naturally fractured teeth, occlusal wear patterns, physical sections, lateral bite-wing radiographic imaging, or X-ray computed tomography. High-resolution micro-computed tomography (micro-CT) makes it possible to quantify tooth enamel thickness nondestructively and accurately in two- and three-dimensions (2D and 3D) (e.g., Kono, 2004; Olejniczak and Grine, 2006; Smith et al., 2006a; Olejniczak et al., 2007, 2008a). Studies of hominoid enamel thickness traditionally employ measurements taken across the mesial cusp tips of molars (e.g., Martin, 1985; Shellis et al., 1998; Martin et al., 2003; Suwa and Kono, 2005; Smith et al., 2006a,b), or incorporate the entire crown when unworn or lightly worn teeth are available (e.g., Kono, 2004; Macchiarelli et al., 2006; Smith et al., 2006a; Olejniczak et al., 2008a,b). Here, we demonstrate that it is also possible to use this approach to virtually section teeth prior to physical sectioning, enabling positioning of the tooth during cutting to yield the section plane commonly employed in assessments of tooth growth and 2D enamel thickness (Smith et al., 2007a).

Recent field work at the site of Lakonis in Mani, southern Greece, has yielded the first secure evidence for the presence of Neanderthals in this region, represented by a single lower third molar (LKH 1) associated with an Initial Upper Paleolithic industry (Harvati et al., 2003; Panagopoulou et al., 2004). The taxonomic diagnosis as *Homo neanderthalensis* is based on the presence of a mid-trigonid crest, anterior fovea, and slight taurodontism, traits known to show a significantly higher frequency in Neanderthals than in Upper Paleolithic and recent humans (reviewed in Harvati et al., 2003). The aim of this study was to evaluate dental enamel thickness and the duration of crown formation in the LKH 1 molar and to compare this specimen to other previously described Neanderthals (Dean et al., 2001; Macchiarelli et al., 2006; Smith et al., 2007a; Olejniczak et al., 2008a), recent humans, and chimpanzees (Smith et al., 2005b; Reid and Dean, 2006; Smith et al., 2006b, 2007b,c). Although comparisons ideally should be made with additional fossil hominin taxa, few developmental data exist from fossil hominin histological sections, and even fewer data are available for enamel development and structure in lower third molar distal sections. Because certain developmental and structural parameters vary among cusps within a molar, and among molars within the molar row (e.g., Reid et al., 1998; Smith et al., 2005b, Suwa and Kono, 2005; Smith et al., 2006b, 2007b,c), it is important to minimize these potential sources of variation by limiting the comparative sample to homologous section planes of molars from the same tooth position. Comparisons are therefore made with chimpanzees, which represent the only hominid taxa for which comparative data are available. Although not the ideal outgroup for questions of evolution within the genus *Homo*, chimpanzee data do allow the magnitude of differences between Neanderthals and modern humans to be contextualized in light of a third sample.

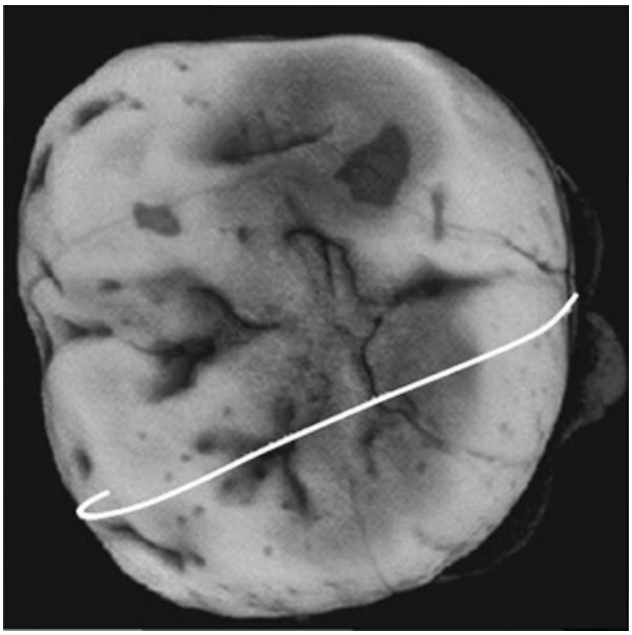

Fig. 1. Virtual 3D model indicating the orientation of the virtual section plane (white line) shown in Figure 2. This model was also used to orient the tooth prior to physical sectioning.

MATERIALS AND METHODS

Section preparation

Prior to physical sectioning, both virtual and physical copies of the LKH 1 molar were generated. The tooth was scanned with a high resolution micro-CT system (Skyscan 1172) at the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany), using 100 kV, a copper and aluminum filter, and isometric voxels of 14.04 μm^3. High-resolution molds and casts of the tooth crown were made using Coltene President impression materials and Epo-Tek 301 epoxy resin. A histological section was generated after casting and micro-CT scanning (detailed later). Because of the advanced degree of attrition of the mesial cusps, which prohibits comparison with the majority of published data, we restricted study to the less worn distal cusps. To create a plane of section, a virtual model was first generated with VoxBlast Software (Vaytek, Inc.), the tips of the dentine horns were located, and a plane of section was virtually located coursing through the distal cusp tips and perpendicular to the best-fit plane through the dentine horns of the major cusps (Figs. 1 and 2) (further description of this method is available in Olejniczak, 2006; Smith et al., 2006a, 2007a; Olejniczak et al., 2008a,b). This virtual 3D model was used to orient the tooth prior to sectioning and facilitated the production of a virtual section similar to the resulting physical section (Fig. 3). The compatibility of physical sections and micro-CT sections has been established elsewhere (Olejniczak and Grine, 2006).

The tooth was embedded in methylmethacrylate resin for stability, and then sectioned with a Logitech annular

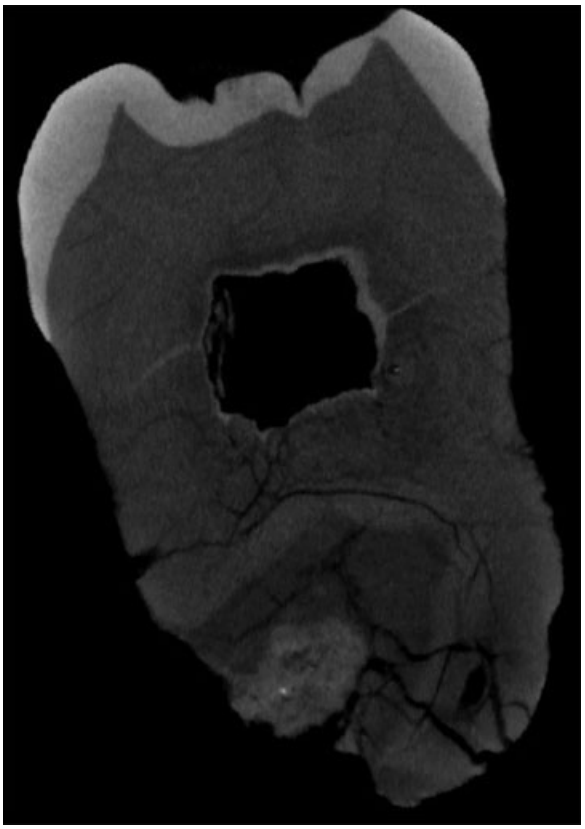

Fig. 2. Virtual section through the distal cusps used for measurement of the average and relative enamel thickness.

saw. An initial cut ~0.3-mm wide was made and the two faces of the tooth block were examined. The distal posterior block was judged to contain the more ideal developmental plane, and thus it was coated with cyanoacrylate for stability and remounted; the saw was advanced 1.1 mm, and a "thick" section of ~0.8 mm was removed. Total tissue loss was estimated to be 1.5–2.0 mm. The thick section was then mounted to a microscope slide with dental sticky wax, and the more ideal (less oblique) face was lapped on a grinding machine with 3 μm alumina, ultrasonicated, and finished with a 1 μm alumina suspension. This face was then fixed to a microscope slide with Logitech ultraviolet curing resin under pressure. After curing, the section was lapped to an approximate 0.12-mm thickness, ultrasonicated, and finished with a 1 μm polishing suspension. The section was then ultrasonicated, dehydrated in an alcohol series, cleared in xylene, and a cover slip was mounted with DPX mounting media. For comparative purposes, histological sections of the distal cusps of 10 unworn lower third molars extracted from German dental practices were prepared according to procedures that are described in Reid et al. (1998).

Samples were taken from the two parts of the embedded tooth block for ancient DNA and isotopic analyses by micro-drilling dentine and enamel from the exposed internal surfaces (Richards et al., 2008). After sampling, the tooth was removed from methylmethacrylate by immersion in dichloromethane. During this process, the originally fragile tooth root subsequently fractured; however, the crown was reconstructed with a dental restorative color-matched to the tooth (Fig. 4). Although the restoration approximates the original crown dimensions, the mesial-distal dimension is not exact, and we suggest that any future metric assessments should be taken from the virtual model or the high resolution cast.

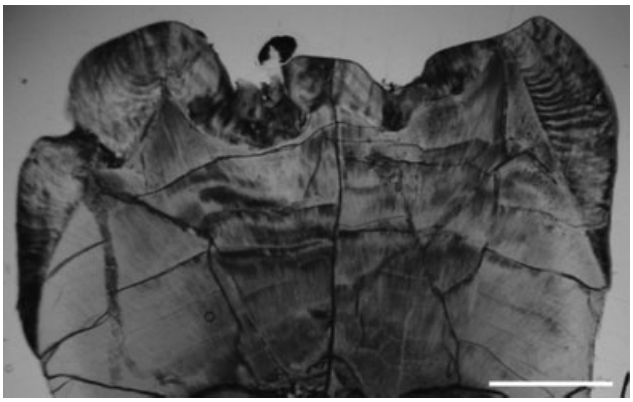

Fig. 3. Histological section through the distal cusps used for reconstruction of crown formation time. The scale bar is equal to 2 mm.

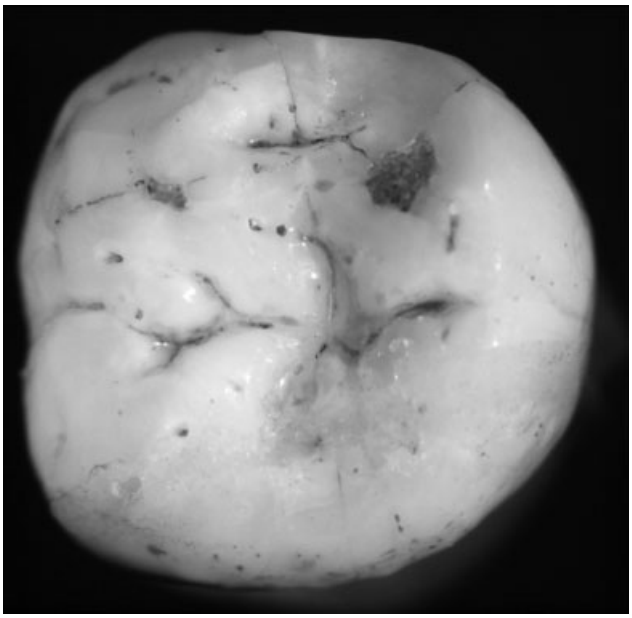

Fig. 4. The reconstructed crown of LKH 1 after sectioning. Mesial is to the top, distal to the bottom. The plane of section runs at a slight diagonal across the two distal cusps.

Enamel thickness and development

Because of the degree of attrition of the LKH 1 crown, it was decided to restrict analyses of enamel thickness to a single plane of section (that could be corrected for wear), as opposed to a 3D analysis that requires unworn or lightly worn teeth (e.g., Olejniczak et al., 2008a). Relative enamel thickness (RET) was measured from the virtual section of LKH 1 through the distal dentine horn tips produced from the micro-CT data (Fig. 2), and this was compared with a modern human comparative sample of physical sections. Following Martin (1983, 1985), several variables were measured on each cross-

Fig. 5. The hypoconid of LKH 1 showing the cuspal enamel (upper left) and a pair of accentuations (dashed and solid lines) used to reconstruction the formation time of the enamel associated with the fissure. To determine this, cross-striation spacing was measured along a prism path between the accentuated lines (indicated with white dotted line), and the length of the prism path was divided by the average cross-striation spacing (secretion rate). See text for description of total cusp-specific formation time estimation. The scale bar is equal to 1 mm. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

section: area of the enamel cap (*c*), length of the enamel-dentine junction (*e*), and dentine area (*b*) (illustrated in Martin, 1985; Smith et al., 2005b, 2006b). Using Martin's formulae, average enamel thickness (AET) is calculated as [*c*/*e*] (in mm), and RET is calculated as $[([c/e]/\sqrt{b}) \times 100]$ (a unitless measurement). When necessary, slight reconstructions were made prior to measurement in regions that showed light wear or a minimal amount of missing cervical enamel, based on the profile of the enamel cap in unworn teeth. To be consistent with previous studies, sections that showed heavy wear, marked obliquity, or two missing cervices were excluded. For each tooth, multiple planes of section were compared, and the section with the lowest RET was used in the analysis in order to minimize the effects of obliquity (illustrated in Smith et al., 2004).

Enamel development was assessed from visualization of histological thin sections viewed under transmitted light microscopy. The LKH 1 molar showed attrition on the entoconid (distolingual cusp), in addition to pronounced prism decussation, making accurate assessment of crown formation time difficult. The hypoconid (distobuccal cusp) showed less attrition and more distinct incremental features, thus it was chosen for assessment of incremental development. Due to the slight attrition and a mid-lateral fissure, the cusp-specific formation time was determined from three regions of the crown and then summed. Cuspal enamel thickness was first measured from the virtual and physical sections. The daily secretion rate in the cuspal enamel was assessed by measurements of daily cross-striations in the inner, middle, and outer cuspal enamel. Measurements were made with a minimum of three cross-striations in at least three areas within each zone. Cuspal enamel formation time was estimated by dividing the cuspal enamel thickness by the average daily secretion rate, yielding a minimum estimate of formation time. This value was then multiplied by a correction factor of 1.15 to correct for marked decussation of the cuspal enamel prisms (Risnes, 1986), yielding a maximum formation time estimate.

A pair of accentuated lines was identified lateral to the cusp tip (Fig. 5) and the corresponding prism length and mean daily secretion rate were determined (from local cross-striations). Division of the prism length by the mean daily secretion rate yielded the time of formation in days.

Long-period lines known as Retzius lines were counted from the second accentuated line to the tooth cervix, their periodicity was determined by counting the number of cross-striations between successive lines, and the formation time (in days) was calculated by multiplying the number of lines by their periodicity.

For the modern human sections, cuspal daily secretion rates and crown formation times were determined as detailed in Reid et al. (1998) and Smith et al. (2007b,c). Sections that showed cuspal obliquity were excluded. Cusp-specific extension rates were determined by division of the formation time by the enamel-dentine junction length.

RESULTS

Values of the components of enamel thickness are given in Table 1. The AET calculated from the distal 2D

TABLE 1. Average components of enamel thickness in lower third molar distal sections

Sample	*N*	*a* (mm^2)	*b* (mm^2)	*c* (mm^2)	*e* (mm)	AET (mm)	RET
LKH 1	1	47.79	31.73	16.05	17.47	0.92	16.31
Modern *H.s.*	8	55.87	29.23	26.65	16.28	1.63	30.44

Components–*a*, area of the total section (enamel plus dentine); *b*, area of dentine enclosed by the enamel cap; *c*, area of the enamel cap; *e*, length of the enamel-dentine junction; AET, average enamel thickness (*c*/*e*); RET: relative enamel thickness ($([c/e]/\sqrt{b}) \times 100$).

TABLE 2. Average daily secretion rates in the hypoconid of LKH 1 and modern humans (in μm/day)

	N	Inner	Middle	Outer	Overall
LKH 1	1	3.46	3.73	4.33	3.84
Modern *H.s.*	7	2.99	3.74	4.11	3.61

Inner, middle, and outer zones refer to equal divisions of the cuspal enamel as illustrated in Beynon et al. (1991).

plane of section of LKH 1 is 0.92. The RET is 16.31, which is outside of the range of modern human third molar values (mean = 30.44, n = 8, range = 24.93–35.50).

The periodicity (long-period line repeat interval) of the LKH 1 tooth was determined to be 7 days. Cuspal enamel thickness in LKH 1 was estimated as 1.15–1.20 mm, although the thickness used for local formation time estimation was 1.02 mm (see Fig. 5). Human hypoconids show much thicker cuspal enamel (mean = 2.19 mm, n = 8, range = 1.68–2.80 mm). Average daily secretion rates are quite similar between the Lakonis hypoconid and modern humans (Table 2), although humans may show slower rates at the beginning of formation. Cuspal formation time in the LKH 1 hypoconid could not be estimated precisely due to attrition, but can be estimated to have been just less than or equal to 1 year, which is much shorter than modern human times (mean = 1.80 years, n = 7, range = 1.35–2.29 years). The total number of Retzius lines could not be counted directly due to wear, although ~86 lines were counted after the second accentuation (see Fig. 5), which is likely to be close to the total number. Retzius line number in four human hypoconids ranged from 70 to 88 with a mean of 78. Crown formation time in the LKH 1 hypoconid was estimated from three regions: 266–306 for the cuspal enamel preserved, 94 days for the region between accentuated lines, and 602 days for the remaining lateral/cervical enamel (86 Retzius lines × 7 days). The sum of these three regions yields a cusp-specific crown formation time of 2.64–2.74 years (962–1,002 days), which is shorter than modern human values (mean = 3.53 years, n = 4, range = 3.15–3.96 years). By using a mean hypoconid formation time of 982 days, we estimated the cusp-specific extension rate to be 5.63 μm/day, which is greater than modern human values (mean = 4.14 μm/day, n = 4, range = 3.72–4.79 μm/day).

Numerous accentuated lines were found associated with the fissure apparent in the thin section, beginning ~300 days after hypoconid initiation and continuing for 100–150 days (see Fig. 5). Based on the position of an accentuated line in the cuspal enamel, it could be determined that the entoconid initiated formation ~1–3 months after the hypoconid. A number of hypoplastic defects were noted on the surface of the crown, and a number of thin tunnel-like holes were found in the deeper enamel, possibly connected to pit-type defects on the surface. In addition to these unusual developmental features, the tooth shows marked decussation, interglobular dentine, and an extremely scalloped enamel-dentine junction in certain areas. Interpretation of these features is difficult given the lack of systematic comparative data. It is clear that LKH 1 shows several signs of developmental stress (hypoplasias and accentuated lines); however, it is unlikely that this would impact assessments of enamel secretion rate or total formation time.

DISCUSSION

AET in the Lakonis distal section is slightly lower than a distal section of the right lower third molar of Le Moustier (1.23: Smith, unpublished data), but is similar to mean AET values from a temporally diverse sample of mesial sections of Neanderthal molars, which range from 0.99 to 1.22 (Olejniczak et al., 2008a). Enamel thickness in LKH 1 may best be described as intermediate/thick relative to other hominoid primates (*sensu* Martin, 1985), which is consistent with the results of a study of Neanderthal whole crown and mesial enamel thickness (Olejniczak et al., 2008a). The value of RET for LKH 1 (16.31) is only slight greater than corresponding distal section planes of chimpanzee third molars (mean = 14.92, n = 5, range = 11.37–16.48) (Smith et al., 2005b). Modern humans have the thickest enamel among extant hominoids (e.g., Martin, 1985; Shellis et al., 1998), demonstrating a significant increasing trend from first to third molars (Smith et al., 2006b), possibly due to dental size reduction in the molar row (Grine, 2002; also see discussions in Smith et al., 2006b; Olejniczak et al., 2008a).

Olejniczak et al. (2008a) found that dental tissue conformation (i.e., the percentage of the tooth crown that is dentine) distinguishes Neanderthal molars from those of modern humans and is better suited to intra-generic comparisons than enamel thickness. Data recorded for the Lakonis molar show that dentine comprises 66.41% of the total crown area, whereas the modern human average for distal sections is 52.31%. This difference exceeds that found for mesial sections by Olejniczak et al. (2008a). Average and relative enamel thickness and cross-sectional tooth conformation each lend support to Harvati et al.'s (2003) taxonomic assignment of LKH 1 to *Homo neanderthalensis* and underscore that Neanderthal enamel thickness and dental tissue conformation are different than those of modern humans.

Data on dental development in the LKH 1 lower third molar is consistent with other histological studies of Neanderthal molars (Dean et al., 2001; Macchiarelli et al., 2006; Smith et al., 2007a). Neanderthal long-period line periodicity ranges from 7 to 8 days (mean = 7.5, n = 4), which is higher than chimpanzee values (mean = 6.4, n = 61, range = 6–7) and lower than modern human values (mean = 8.3, n = 365, range = 6–12) (Smith et al., 2007b,c). In general, fossil hominin periodicity values range from 6 to 9 days, with mean values between 7 and 7.5 (reviewed in Smith, 2008). Differences

in cuspal enamel thickness are consistent with trends in larger samples of mesial sections of Neanderthal molars. Smith et al. (2007a) found the enamel thickness of Neanderthal mesial molar cusps to be ~60–90% as thick as modern humans. Cuspal enamel thickness in LKH 1 is similar to a reported value for chimpanzees; Smith et al. (2007c) found a cuspal enamel thickness of 1.06 mm for a single third molar hypoconid. Daily secretion rates in LKH 1 follow a similar pattern to those reported in Dean et al. (2001) and Macchiarelli et al. (2006). Relative to modern humans, cuspal enamel formation in Neanderthals may begin slightly faster, but overall mean values are quite similar (see Macchiarelli et al. 2006: Fig. 3), which is also the case when compared with chimpanzees (Smith et al., 2007c). This implies that cuspal enamel formation time is shorter in Neanderthals than in modern humans (Smith et al. 2007a).

Crown formation time in the LKH 1 hypoconid was shorter than values for respective modern human cusps, which is similar to trends in two other Neanderthal permanent molars (Macchiarelli et al., 2006; Smith et al., 2007a). Macchiarelli et al. (2006) reported formation times of 1,041 and 865 days for the protoconid and metaconid of the La Chaise lower first molar, which are shorter than values for northern European modern humans (1,188 ± 39 days and 1,012 ± 51 days, respectively) and southern African modern humans (1,117 ± 55 days and 936 ± 55 days, respectively) (Reid and Dean, 2006). Smith et al. (2007a) reported formation times of 872 and 811 days for the protocone and paracone of the Scladina upper first molar, which are also shorter than values for northern European modern humans (1,210 ± 58 days and 1,097 ± 51 days, respectively) and southern African modern humans (1,096 ± 60 days and 1,047 ± 77 days, respectively) (Reid and Dean, 2006). Finally, differences were also found in comparisons of cusp-specific extension rates, with the LKH 1 hypoconid value (5.63 μm/day) exceeding the modern human range and showing some similarity with a single chimpanzee value of 5.10 μm/day (Smith et al., 2007c). Smith et al. (2007a) also found a similar pattern of rapid coronal extension rates in the La Chaise and Scladina first molars.

CONCLUSIONS

The Lakonis molar shows a degree of enamel thickness and developmental patterns similar to other Neanderthal molars. Neanderthals molars are distinct from modern humans; noteworthy differences are found in the cuspal enamel thickness and rate of coronal extension, leading to shorter crown formation times in Neanderthals (see also Smith et al., 2007a). It is unclear if this represents evidence of a faster life history profile for Neanderthals and would be more conclusively assessed with data on root extension. Coupled with shorter crown formation times, faster rates of root extension would likely lead to earlier ages of molar eruption, events that are correlated with the timing of primate life history (e.g., weaning, age at first reproduction: Smith et al., 1994). Evidence from Neanderthal first molar root extension is contradictory (Macchiarelli et al., 2006; Smith et al., 2007a). Data from additional Neanderthal dentitions are needed to clarify if life history differences also distinguish Neanderthals and modern humans.

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