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Nombre et distribution des périkymaties sur les dents des premiers hommes modernes : le cas de Qafzeh (Israël)

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**PERIKYMATA NUMBER AND SPACING ON EARLY MODERN HUMAN TEETH:
EVIDENCE FROM QAFZEH CAVE, ISRAEL**

**NOMBRE ET DISTRIBUTION DES PÉRIKYMATIES SUR LES DENTS
DES PREMIERS HOMMES MODERNES : LE CAS DE QAFZEH (ISRAËL)**

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ABSTRACT

The microscopic anatomy of dental enamel has been employed in numerous studies of fossil hominin teeth. This research has focused on the use of microstructure, primarily perikymata and, when available, their internal manifestations, in the construction of phylogenetic relationships as well as in the reconstruction of hominin patterns of growth and development. The literature on perikymata numbers and packing as reported over the last 20 years, shows a huge range of variation within modern humans. The variation is so large in fact that virtually every fossil hominin species can be encompassed within the range except for some but not most of the robust australopithecines. The sample of Mousterian level hominins from the site of Qafzeh, in northern Israel represents some of the earliest recognized members of *Homo sapiens sapiens*. Included in this sample are a number of immature individuals (N = 5) whose permanent incisor crowns have observable perikymata. The number of perikymata on complete and unworn teeth is within the range of variation of other hominins and does not provide specific evidence for attributing these specimens to one hominin taxon or another. Similarly, the pattern of perikymata compaction toward the cemento-enamel junction of the Qafzeh specimens is compared to published sources.

Keywords: teeth, perikymata, Qafzeh children, Neandertals, growth and development.

RÉSUMÉ

La structure microscopique de l'émail dentaire est employée dans de nombreuses études des dents des Homininés fossiles. Cette recherche se concentre sur l'emploi de la microstructure et, en premier, celui des périkymaties et de leur disposition interne quand cela est possible, pour traiter des relations phylogénétiques et reconstruire des processus de croissance et de développement au sein du groupe. Depuis une vingtaine d'années, les travaux publiés sur le nombre et la distribution des périkymaties permettent de dégager une variation importante dans les populations actuelles, qui intègre pratiquement toutes les espèces d'Homininés fossiles, à l'exception peut-être de quelques-uns des Australopithèques robustes. Les niveaux moustériens du site de Qafzeh au Nord d'Israël ont livré un large échantillon des plus anciens représentants des Homo sapiens sapiens, dont un grand nombre de sujets non adultes. Parmi ces derniers, se trouvent des individus (N = 5) dont les germes d'incisives permanentes portent des périkymaties observables. Le nombre de périkymaties sur les couronnes complètes et non usées s'intègre dans la variation connue des Homininés. La distribution, sur ces quelques dents, des périkymaties le long de la couronne jusqu'à la jonction cémento-énamélaire, est comparée aux données publiées.

Mots-clés : dents, périkymaties, enfants de Qafzeh, Néanderthaliens, croissance et développement.

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INTRODUCTION

Dental enamel microstructures have been widely employed in paleoanthropology to reconstruct patterns of growth and development in earlier members of the human lineage (for a sample of articles see: Dean *et al.* 1986; Stringer *et al.* 1990; Dean *et al.* 1992; Dean, Reid 2001; Mann *et al.* 1991a, b; Bermúdez de Castro *et al.* 2003; Ramirez-Rozzi, Bermúdez de Castro 2004; Guatelli-Steinberg *et al.* 2005). In addition, variations in the form and pattern of certain features have been used to distinguish species from each other and even to construct phylogenetic relationships. Among the components of dental microstructure used in these specific contexts are perikymata, enamel surface manifestations of internal

structures known as striae of Retzius. These structures, external and internal, are thought to be deposited in a time ordered sequence and to provide an indication of the time frame of development of lateral or cervical enamel. It should be noted that only on this one part of a tooth are perikymata visible on the surface of the enamel and thus subject to examination and counting (only cervical or imbricational enamel). Because perikymata do not reach the surface of cuspal enamel, in order to estimate perikymata formation on this part of the crown, either naturally fractured enamel must be present or purposeful destructive sections must be made. Since the ultimate calculation of crown formation times demands a count of both cuspal and cervical enamel perikymata increments, as well as the periodicity in which these increments are

Reference	Tooth Type/Number	Total/Average
Bromage, Dean 1985	10 incisors (various)	188 (range 165-202)
Dean <i>et al.</i> 2001	19 UI1	165
	16 UI2	134
	15 LI1	133
	13 LI2	130
Beynon, Dean 1991	LI1s	132 (range 111-154)
	LI2s	141 (range 110-164)
	UI1s	160 (range 135-208)
	UI2s	139 (range 123-153)
Dean <i>et al.</i> 1992	LI1 (Spitalfields)	197
	LI2	224
	UI2	162
Beynon 1992	LI1s	133 +/- 15.5
Dean, Reid 2001*	115 "modern human anterior teeth"	136 (average)
Ramirez Rozzi, Bermudez de Castro 2004**	UI1 (14)	156
	UI2 (15)	147
	LI1 (13)	148
	LI2 (9)	158
Guatelli-Steinberg <i>et al.</i> 2005***	UI1 (Inuit, Newcastle, South Africa)	170, 165, 115
	UI2 (Inuit, Newcastle, South Africa)	151, 130, 113
	LI1 (Inuit, Newcastle, South Africa)	128, 130, 107
	LI2 (Inuit, Newcastle, South Africa)	140, 128, 110

* origin of teeth described in Reid and Dean (2006).

** extrapolated average from figure 1. Average includes estimated 7 perikymata in decile 1 as shown in figure 1b.

*** extrapolated average from figure 2.

Table I—Perikymata counts reported in the literature on sample of modern human teeth.

Tabl. I - Décomptes des périkymaties sur des dents humaines actuelles disponibles dans la littérature.

laid down, it is not possible to estimate crown formation times except as an expression of relative number of perikymata representing only a portion of tooth formation time. Thus, on undamaged fossil hominin teeth, counts of perikymata number are limited in the total amount of data they can provide (see for example, Smith 2004 for a plea to section a sample of fossil teeth).

Complicating all these studies, however, are the results of studies of enamel structure in samples of recent human populations (*table 1*) derived for comparative purposes. These have demonstrated wide variations in the number of observable perikymata, variations broad enough to encompass reported perikymata numbers in virtually every fossil hominin species reported in the literature. For this reason, there has been a recent emphasis away from simple counts of perikymata numbers to more focused investigations of the pattern of perikymata on the lateral or cervical enamel. These examinations have been primarily directed toward the packing or compaction of large numbers of perikymata near the Cemento-Enamel Junction (CEJ), which has been suggested as a reflection of a more prolonged period of maturation and thus an attribute of modern humans (*i.e.* Ramirez-Rozzi, Bermúdez de Castro 1993, 2004; Dean, Reid 2001; Ramirez-Rozzi 2005).

At the present time, however, there are no published data describing enamel surface features on early *Homo sapiens sapiens* fossil samples. The cave site of Qafzeh (northern Israel) has yielded a large sample of individuals recovered from Mousterian layers dated to ca 92,000 +/- 5,000 years B.P. (Schwarcz *et al.* 1988; Valladas *et al.* 1988; Hovers 1997; Bar-Yosef 2000; Bar-Yosef, Vandermeersch 1981; Tillier 1999) and identified, on the basis of numerous morphological attributes found on both the adult (Vandermeersch 1981) and immature specimens (Tillier 1999), as early modern humans. The total of eight immature individuals recovered from the site is the largest number of immature Mousterian remains from a single site in the Levant (Tillier 1999). Thus, a comparison of the external morphology of the dental enamel of the Qafzeh sample to these structures in living modern humans as well as in samples of other Late Pleistocene fossil hominins, especially European Neandertals, has the potential to provide data of interest in the continuing assessment of evolutionary relationships amongst all these forms.

Here we test the hypothesis that perikymata counts on incisors can be used to distinguish fossil hominin species from each other both by using perikymata counts

alone, and in conjunction with the packing of perikymata across the tooth crown. We further question the use of perikymata numbers, as represented here and in the substantial literature on this point, to estimate crown formation times.

MATERIALS, SAMPLE AND METHODS

The immature specimens from the Qafzeh site that possess anterior teeth potentially suitable for analysis of their perikymata include 5 individuals (Qafzeh 4, Q10, Q12, Q15, and Q21). Of the remaining individuals with permanent dentition, Qafzeh 11, aged at about 13 years, has no visible perikymata over the entire crown surface and is assessed as too old at the time of death for this study. All these specimens have been described in detail by Tillier (1999).

The sample of immature incisors (N = 20) were molded and cast employing methods discussed in previous publications (Mann *et al.* 1991). Qafzeh 15 was considered unsuitable for analysis; few perikymata were visible on the labial surfaces of these teeth, the result of its chronological age. At 8-10 years (Tillier 1999), all of the incisor teeth had complete root formation and had been in occlusion for several years. In addition, there has been some alteration of the external surface of the enamel (origin unknown) but most probably caused by post-mortem damage.

Qafzeh 12 possesses central incisors suitable for perikymata analysis, with a complete tooth crown on the upper central incisors and with virtually the entire labial surface preserved. Based on both cranial features and teeth, Qafzeh 12 seems to be best aged at 3 to 3.5 years at death, an age consistent with the Moorrees *et al.* (1963a, b) standards of radiological dental development. There is some abrasion on the exposed labial surfaces, but perikymata were visible over the entire crown surface. Perikymata counts on this specimen, however, have not been included in this study because of its obvious pathologies assessed from other aspects of skeletal anatomy. This specimen was not considered useful in the study of normal variation in the dentition of *Homo sapiens* (Tillier *et al.* 2001).

Finally the central and lateral incisors of Qafzeh 21 were far from approaching crown complete although perikymata were clearly visible over the section of tooth crowns mineralized at the time of death of the individual. The Qafzeh 21 teeth could not be included in the study.

Of the remaining specimens, only Qafzeh 4 and 10 have incisors that possess perikymata over the entire crown and have achieved crown complete status: Qafzeh 10 has incisors staged at root inception (Ri) and Qafzeh 4,

at 1/3 root development. Total perikymata counts as well as the number of perikymata in each decile of these two individuals are summarized in table II and figure 1.

Individual	Tooth	h	n
Qafzeh 10	Right upper central incisor	12.5	131
	Left upper central incisor	12.7	127
Qafzeh 4	Right lower central incisor	10.5	142
	Left lower central incisor	10.6	139

Table II—Immature incisors from the Mousterian levels at Qafzeh with complete crowns suitable for the study. Crown heights (h) in mm and perikymata counts (n).

Tabl. II - Incisives d'enfants provenant des niveaux moustériens de Qafzeh avec couronnes complètes sélectionnées pour l'analyse. Hauteur coronaire (h) en mm et nombre de périkymaties (n).

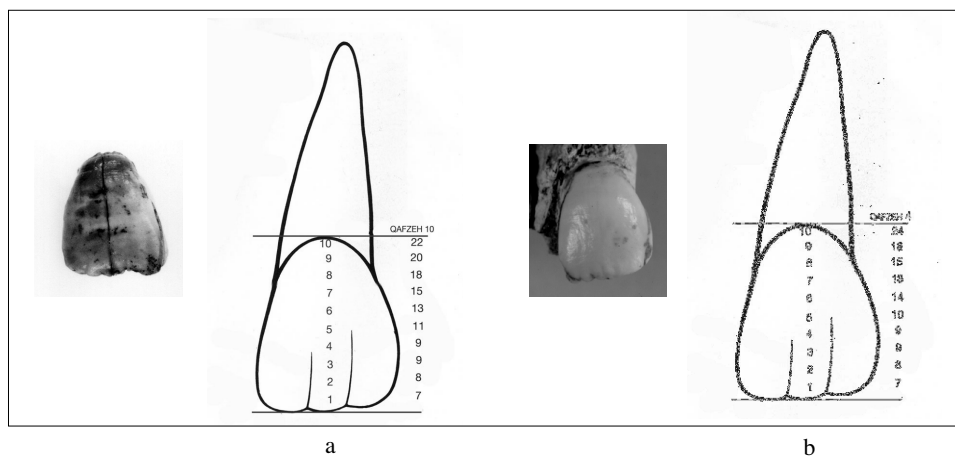


Fig. 1—Upper central incisors of Qafzeh 10 (a) and 4 (b) in labial views and perikymata packing pattern.

Fig. 1 - Incisives centrales supérieures de Qafzeh 10 (a) et 4 (b) en vue vestibulaire et mode de distribution des périkymaties.

Thus if perikymata could not be counted over the whole surface, the tooth was not used in this study. This method is distinct from two recent studies that focused on perikymata packing (Dean, Reid 2001; Ramirez-Rozzi, Bermúdez de Castro 2004) where all teeth were used, worn teeth included, by partitioning each tooth's labial surface into deciles (an equal measure of 10th along an entire tooth crown) and counting perikymata only on the portions of each tooth where the structures are visible. Guatalli-Steinberg *et al.* (2005), using a sample of Neandertal teeth, include counts over the entire crown surface, and only on teeth that are unworn or are

moderately worn (where over 80% of the crown is intact). Even minimal wear effects the appearance of perikymata and it is unknown if the scoured effect of wear limits the ability to make accurate counts even on surfaces that retain some measure of perikymata structure. Further, in our opinion, it is extremely difficult to accurately assess the division of a crown into 10ths when only a portion of the crown remains. Estimations of this sort can markedly influence conclusions about the biology of a tooth, and a population, without the certainty that an accurate division has been achieved.

DISCUSSION

Since the work of Bromage and Dean (1985), it has been normal practice for microscopic examination of the teeth to be incorporated into the study of fossil specimens. On occasion, these types of studies have been used, in conjunction with the examination of dental calcification, to speculate on the pattern and rate of dental development in fossil specimens. Without a consideration of both internal and external dental microstructure, and without an analysis of possible differences in root formation times, it is difficult to conclude anything substantive about the meaning of differences between fossil specimens and species. Thus, most of the earlier studies were naïve in the use of these techniques to provide insight into the dental development of extinct forms. For example, if these structures are indeed time-ordered dental manifestations, then if daily incremental rates (represented as cross-striations) were different, the same number of more gross structures like perikymata could have actually formed in a longer time frame. Fortunately, more recent studies have refined much of this earlier work (see for example Dean and Reid 2001) and have focused on the association of enamel microstructure to tooth development times, not with speculative aspects associated with overall growth and development patterns, but with a possible correlation to modifications in overall crown height and changes in food preparation techniques.

In addition, as noted earlier, there has been a shift from mere counts of perikymata to evaluations of the total pattern of dispersion of perikymata over the tooth crown (Dean, Reid 2001; Ramirez-Rozzi, Bermúdez de Castro 2004). Without the ability to evaluate other microstructural details, as for example, daily enamel periodicity rate, it is not possible to speculate on overall crown formation times (see for example Dean *et al.* 2001 and Reid, Dean 2006). Still others continue to speculate on overall crown formation times based solely on perikymata counts even though they represent only a portion of crown formation time (Ramirez-Rozzi, Bermúdez de Castro 2004).

In the present study, both the number of perikymata and the compactness of these structures over the entirely unworn tooth crowns of Qafzeh 10 and 4 immature specimens are presented. No such report is present in the literature of the very earliest of modern human fossil specimens. Interestingly, there has been remarkably little data presented on modern human teeth although much focus has been directed towards fossil hominin

specimens. Indeed the data are a bit confusing since the numbers reported span every single fossil hominin species including the early hominins in the genus *Australopithecus*.

Perikymata numbers

Perikymata numbers are summarized in table 1 for all published samples of modern humans. Often specimen numbers are not reported; sometimes the range is not reported. Between 1985 and 2001, the numbers of reported perikymata appear to have decreased in modern human samples as compared to the numbers originally reported by Bromage and Dean (1985). In part this is explained by differences in samples or in the use of mixed anterior teeth (Beynon, Dean 1991; Dean, Reid 2001). In 1985, for example, the average was 188; in 1991 the range was reported as being between 132 and 160; in 2001, projected from a graph, the average is 136. Because in general mean and range are not reported, and because it is not usual to report the population from which these numbers derive, it is impossible for us to compare the statistical significance of these differences to the Qafzeh sample. One recent and significant publication on modern human perikymata counts, is Guatelli-Steinberg *et al.* (2005) where a sample was presented for specimens derived from Inuit, South African, and English samples.

It would seem from these data that the number of perikymata on the anterior teeth of modern humans is very variable. Indeed, the range of variation in perikymata numbers in one individual can be broad. At the site of Spitalfields, for example, specimen number 2179 has perikymata counts between 162 and 224 (Dean *et al.* 1986). In conjunction with previous counts made by two of us (JMM and AEM) (Mann *et al.* 1991) on a sample of modern human teeth, the range of modern humans appears to be from a low of 75 in an archaeological specimen from the third Millennium Iron Age site of Hasanlu in North Central Iran (Hasanlu VIE B19) (Mann *et al.* 1990b critiqued by Beynon and Dean 1991), to a high in the lower I2 of the Spitalfields child of 224.

The range is so large in fact that it encompasses virtually all *Australopithecus* forms including some *Australopithecus robustus* specimens. Beynon and Dean (1991) reported an average perikymata count on 5 *Australopithecus* teeth with an average of 146.2; in 2001, Dean and Reid report a sample of 22 *Australopithecus* (not including the robust australopithecines

which are characterized by very low perikymata numbers), with a projected average of 116. Certainly, at least some of the very earliest hominins have perikymata numbers that are within the range of modern human samples.

Perikymata Packing

Because of the issues involving the use of perikymata numbers to characterize species and rates of developmental maturation, emphasis more recently has been placed on not just perikymata numbers, but the packing and placement of perikymata over the entire tooth crown. Since it is practically impossible to routinely section teeth and examine the internal microstructural details of enamel form, total perikymata number is used in conjunction with perikymata counts or packing in each equal division of tenths over the enamel.

According to Dean and Reid (2001), packing patterns in living *Homo sapiens sapiens* is characterized by a general increase in perikymata number in the 8th and 9th decile followed by a decrease in the 10th decile of crown development. *Pan* and *Gorilla* are characterized a steeper rise in number in the early deciles followed by a distinct peak in the 6th and 7th decile, with a precipitous drop in deciles 9 and 10. Total perikymata numbers in both *Pan* and *Gorilla* (extrapolated from the figure 1 in Dean and Reid 2001) appear much higher than the mean presented in that publication for *Homo sapiens* but still overlapping at least one individual modern human (from Spitalfields). Finally, in both gracile and robust *Australopithecus* perikymata packing appears to be evenly distributed over the entire crown surface, without peak numbers in any specific decile.

Ramirez-Rozzi and Bermúdez de Castro (2004) have presented comparative data on *Homo sapiens*, Neandertals and specimens from Atapuerca (referred to as "*Homo heidelbergensis*"). Here, the decrease in perikymata number in the 10th decile recorded by Dean and Reid (2001) for *Homo sapiens* was not observed in the sample of modern humans used here. Ramirez-Rozzi and Bermúdez de Castro (2004) do not record a drop in perikymata packing in the 10th decile of enamel development.

Within the context of this rather confusing array of possible variations of fossil hominin and modern human perikymata counts, Qafzeh specimens 4 and 10 (table II) appear to be within the range of the modern human

sample presented by Dean and Reid (2001) and within the modern human, Neandertal and Atapuerca samples presented in Ramirez-Rozzi and Bermúdez de Castro (2004). In terms of the distribution of the perikymata across the tooth crown surface (perikymata packing) from cuspal to cervical areas, however, the Qafzeh specimens are similar to the results reported for non-modern hominins. The distribution of perikymata for Qafzeh 4 and 10 presented in figure 1 shows a gradual rise in perikymata number towards the cervix rather than showing a peak between the 8th and 9th deciles. This pattern appears more like the modern humans presented in Ramirez-Rozzi and Bermúdez de Castro (2004) (unfortunately about 50% of specimens reported in this research were wrongly attributed to an Upper Paleolithic and Mesolithic time) than in the sample presented in Dean and Reid (2001) (undisclosed sample of modern teeth).

CONCLUSIONS

The anterior permanent dental sample from the Qafzeh site available for study possesses perikymata numbers characteristic of modern humans but also well within the range of all fossil hominins. The pattern of perikymata distribution, however, is different from that previously reported by Dean and Reid (2001) for modern *Homo sapiens*, but not from the results presented by Ramirez Rozzi and Bermúdez de Castro (2004). Given the range of perikymata numbers and the differences reported in perikymata packing, it would be questionable to assert that the Qafzeh specimens are more like modern humans than any other fossil hominin. Although it is possible that similarities (or differences) exist in dental development timing (or pattern), it is impossible to explore this question more fully using perikymata structure.

Beyond this, we have argued (Mann *et al.* 1991 a, b; Lampl *et al.* 1993) that even if it was ethical to cut fossil teeth to more fully explore the question, it appears that a simple conversion of any micro-structural feature or a sum of all features inside both the enamel and dentin would not yield overall time frames of tooth development or growth and development pattern and/or rate of species. Variation in human growth pattern is well documented and huge and easily altered by a variety of conditions. Although much variation was known to exist in human populations (Eveleth, Tanner 1990; Liversidge 2003), it was only recently that Zihlman *et al.* (2004) increased our knowledge of chimp maturation rates. Using a small

sample of known-age at death wild *Pan troglodytes* (12 immature specimens and 1 young adult), they report a much slower rate of dental maturation than had been previously reported on captive animals of known-age (Anemone *et al.* 1996; Kuykendall 1996). This study significantly expands the range of chimp maturation and appears to come close to or overlap the overall time frame of development reported within human populations. Additionally, extrapolated perikymata numbers on *Pan* and *Gorilla* from Dean and Reid (2001), appear to show that chimpanzees (16 animals) have an average of approximately 220 perikymata with gorilla specimens (14 animals) showing approximately 30 less than chimps. Although the researchers did not report the provenience of these animals, the overall perikymata numbers reported on these species also overlaps with the known human range. If a 7 day periodicity is applied to the time of dental calcification of the crowns of the anterior teeth, the both chimps and gorillas appear to have a much slower dental calcification pattern than has been reported in the literature.

Thus, it appears that perikymata counts on the anterior teeth of hominin specimens are very variable and that these counts fail to distinguish species from each other. In addition, the pattern of compactness of perikymata towards the cervical margins of the anterior teeth, while showing a general trend to increase in quantity in later hominin species, does appear also quite variable especially in the last one tenth of the tooth crown development.

The total number of perikymata on the Qafzeh immature teeth appear to place this sample, as represented by this small number of specimens, into the range of modern humans, and into the range of Neandertals as reported by Ramirez-Rozzi and Bermúdez de Castro (2004) but outside of the range of Neandertals as reported for both Krapina 90 (Mann *et al.* 1991b), Montgaudier (Mann, Vandermeersch 1997) and Chateaufort 2 (Lampl

et al. 1995 ; Tillier *et al.* 1995) specimens. In the sample of mixed anterior teeth of Neandertals analyzed by Guatelli-Steinberg *et al.* (2005), the average number of perikymata, while smaller than the previously reported Neandertal number, is higher than that reported for their South African modern human comparative sample, overlaps the range of specimens from England, and is lower than the Inuit sample presented.

Thus, it would appear that the biology of incisor perikymata is not very useful in making species level or phylogenetic conclusions. Given that the range of some modern human samples overlaps the range of some australopithecines, in particular, *Australopithecus afarensis*, it seems clear that enamel histomorphology may prove to be useful in fossil analysis, perikymata counts alone cannot be used to identify species or lineages. Further confounding these problems, the database on both humans and the African Great Apes developmental rates, seems to indicate that simple extrapolation of perikymata numbers to maturation, as reported in Ramirez-Rozzi and Bermúdez de Castro (2004), must be abandoned. However, as Reid and Dean (2006) point out, the incisors are the most variable tooth type, and perhaps more useful information can be accrued using molar microstructures.

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