Enamel thickness in the Middle Miocene great apes *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*

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On the basis of industrial computed tomography, relative enamel thickness (RET) is computed in three Middle Miocene (*ca* 11.9–11.8 Ma) hominoids from Abocador de Can Mata (Vallès-Penedès Basin, Catalonia, Spain): *Pierolapithecus catalaunicus* from BCV1 and *Anoiapithecus brevirostris* from C3-Aj, interpreted as stem hominids; and *Dryopithecus fontani* from C3-Ae of uncertain phylogenetic affinities. *Pierolapithecus* displays an average RET value of 19.5, *Anoiapithecus* of 18.6 and *Dryopithecus* of 10.6. The thick-enamelled condition of *Pierolapithecus* and *Anoiapithecus* is also characteristic of afropithecids, including the more derived kenyapithecins from the early Middle Miocene of Eurasia (*Griphopithecus* and *Kenyapithecus*). Given the presence of other dentognathic and craniofacial similarities, thick enamel may be interpreted as a symplesiomorphy of the Hominidae (the great ape and human clade), which would have been later independently modified along several lineages. Given the correlation between thick enamel and hard-object feeding, our results suggest that thick enamel might have been the fundamental adaptation that enabled the out-of-Africa dispersal of great-ape ancestors and their subsequent initial radiation throughout Eurasia. The much thinner enamel of *Dryopithecus* is difficult to interpret given phylogenetic uncertainties, being either a hominine synapomorphy or a convergently developed feature.

Keywords: relative enamel thickness (RET); Hominidae; Kenyapithecini; *Anoiapithecus*; *Pierolapithecus*; *Dryopithecus*

1. INTRODUCTION

(a) *Relative enamel thickness in fossil and extant hominoids*

The teeth of primates and most other mammals are covered by a hard and durable layer of enamel that largely determines tooth wear, thus maintaining the functionality of cusps and crests, while at the same time avoiding catastrophic tooth damage (Maas & Dumont 1999). Given its relationship to crown morphology, palaeodiet and phylogeny, enamel thickness has profusely figured in the palaeoprimatological and palaeoanthropological literature during the past decades (Gantt 1976; Molnar & Gantt 1977; Martin 1985; Grine & Martin 1988; Andrews & Martin 1991; Beynon *et al.* 1991; Macho & Thackeray 1992; Macho 1994; Conroy *et al.* 1995; Dumont 1995; Schwartz *et al.* 1998; Shellis *et al.* 1998; Grine 2002, 2005; Dean & Schrenk 2003; Martin *et al.* 2003; Smith *et al.* 2003, 2004, 2005, 2006*a*,*b*; Kono 2004; Olejniczak *et al.* 2008*a*,*b*,*c*,*d*). Even though apes generally display thicker enamel than other anthropoids (Olejniczak *et al.* 2008*b*), a considerable range of variation can be observed among the former. Among living great apes, chimpanzees and, particularly, gorillas display relatively thin enamel, whereas orangutans display an intermediate thick condition (table S2, electronic supplementary material; see

also Martin 1985; Schwartz 2000; Smith *et al.* 2005, 2008; contra Kono 2004; Olejniczak *et al.* 2008*b*). With regard to fossil hominoids (table S2, electronic supplementary material and references therein), many taxa display a thick-enamelled condition that surpasses the upper range of variation displayed by extant species.

In the past, sample sizes for extinct taxa were limited by the need to section fossil teeth (e.g. Martin 1985). However, unlike studies based on histological sections, non-invasive methods based on X-ray computed tomography (CT; see review in Gantt *et al.* 2007) currently enable to accurately measure enamel thickness in extinct taxa (Chaimanee *et al.* 2003, 2006; Kono 2004; Smith *et al.* 2006*b*; Olejniczak *et al.* 2008*a*,*b*,*c*,*d*). Synchrotron X-ray microtomography has also been very successfully applied to the study of dental palaeohistology (Tafforeau *et al.* 2006), its main disadvantages being the limited access to facilities and the high associated costs (Gantt *et al.* 2007). In this paper, we rely on an industrial CT system in order to provide two-dimensional measurements of enamel thickness in three genera of Middle Miocene hominoids from Spain. Industrial scans permit the inclusion of larger fossils such as the ones studied in this paper, as well as the use of higher energy X-rays (more effective than medical scans in penetrating dense materials), which can be used at longer exposure times in order to provide higher resolution (Gantt *et al.* 2007). Although the two-dimensional results reported here must remain preliminary until other CT-scan methods can be applied to these fossils in order to retrieve

three-dimensional data, it must be stressed that two-dimensional enamel thickness measurements generally agree with three-dimensional ones (Olejniczak *et al.* 2008*b*). Moreover, three-dimensional studies have not yet been generally applied to extinct taxa, so that currently only two-dimensional enamel thickness data are available for most fossil hominoids. As such, this variable remains most useful from a comparative viewpoint within the taxonomic framework investigated in this paper.

(b) *Three Middle Miocene Spanish hominoids*

The fossil remains investigated in this paper were recovered from several sites of the Abocador de Can Mata section (els Hostalets de Pierola, Catalonia, Spain; Alba *et al.* 2009), corresponding to the following taxa: *Pierolapithecus catalaunicus*, *Anoiapithecus brevirostris* and *Dryopithecus fontani* (Moyà-Solà *et al.* 2004, 2009*a*,*b*; Alba & Moyà-Solà 2009). *Pierolapithecus* is recorded by a face and partial skeleton from a single individual, whereas *Anoiapithecus* is recorded by a partial face and associated mandible, and *Dryopithecus* by a lower face. Cranially, *Pierolapithecus* shows a plesiomorphic prognathic facial profile but an essentially modern great-ape-like morphology displaying several synapomorphies of the Hominidae or great ape and human clade (Moyà-Solà *et al.* 2004). *Anoiapithecus* shares several hominid facial synapomorphies, but further displays an autapomorphically very orthognathous face coupled with several kenyapithecine-like primitive retentions (Moyà-Solà *et al.* 2009*b*). Finally, *Dryopithecus* displays a derived-hominid, gorilla-like facial morphology, interpreted as indicating that it is either a stem hominine or a stem hominid convergent with gorillas (Moyà-Solà *et al.* 2009*a*). Until recently, *Dryopithecus* included the Middle Miocene *D. fontani* and several Late Miocene taxa from Europe, but the previously unknown cranial morphology shown by the Spanish remains recently led Moyà-Solà *et al.* (2009*a*) to restrict this genus to the type species and resurrect the genus *Hispanopithecus* for Late Miocene taxa. Most recently, Begun (2009) has suggested that both *Pierolapithecus* and *Anoiapithecus* are junior synonyms of *Dryopithecus*, but this taxonomic opinion is not followed here given the striking craniofacial differences shown by these taxa.

2. MATERIAL AND METHODS

(a) *Fossil sample*

The fossil specimens investigated in this paper include the face of *P. catalaunicus* (IPS21330, holotype; see Moyà-Solà *et al.* 2004) from ACM/BCV1, the maxillary fragments of *A. brevirostris* (IPS43000, holotype; see Moyà-Solà *et al.* 2009*b*) from ACM/C3-Aj and the partial face of *D. fontani* from ACM/C3-Ae (IPS35026; see Moyà-Solà *et al.* 2009*a*). These localities are situated in the local stratigraphic series of Abocador de Can Mata in els Hostalets de Pierola (Vallès-Penedès Basin, Catalonia, Spain), with an estimated age of 11.9, 11.9 and 11.8 Ma, respectively (Moyà-Solà *et al.* 2009*a*,*b*).

(b) *Computed tomography*

The samples were scanned with high-resolution CT (Xylon Compact) at Burgos University (Spain). IPS21330 was scanned at 210 kV and 2.20 mA, obtaining 0.123 mm of pixel size and an output of 1024×1024 pixels per slice,

with an inter-slice space of 0.2 mm. IPS43000 was scanned at 180 kV and 2.20 mA, obtaining 0.08 mm of pixel size and an output of 1024×1024 pixels per slice, with an inter-slice space of 0.2 mm. Finally, IPS35026 was scanned at 225 kV and 2.20 mA, obtaining 0.04 mm of pixel size and output of 2048×2048 pixels per slice, with an inter-slice space of 0.2 mm. The slices from the 13 teeth included in the present study were obtained using the CT software Mimics (Materialise, Belgium) and imported into ImageJ 1.36b software, developed at the U.S. National Institute of Health (NIH) and available from the Internet at http://rsb.info.nih.gov/ij/. To segment the enamel crown, two thresholds were performed: one across the air–enamel boundary and another across the enamel–dentine boundary. We used recent threshold protocol (Fajardo *et al.* 2002) to interpret the images that resulted from the CT scanning.

(c) *Enamel thickness measurements*

In order to compute enamel thickness, we measured the following variables (see Smith *et al.* 2005, fig. 1): enamel cap area (*c*), length of the enamel–dentine junction (*e*) and dentine area (*b*). Following Smith *et al.* (2005; after Martin 1983, 1985), two-dimensional average enamel thickness (AET) was computed as c/e, whereas two-dimensional relative enamel thickness (RET) was computed as $[(c/e)/(b)^{1/2}] \times 100$.

The RET index is a dimensionless variable that was developed by Martin (1983, 1985) to compare enamel thickness among species of different body size, whereas comparisons among teeth of a single individual must be based instead on AET (Smith *et al.* 2005). The three variables (*b*, *c* and *e*) employed to compute AET and RET were measured on a coronal plane of the maxillary molars: the six upper molars of *Pierolapithecus*, the five upper molars of *Anoiapithecus* (all but the left M3/) and the two upper molars (the left M2/ and M3/) of *Dryopithecus* were employed (the right and left M1/ of this taxon were too damaged and/or worn to provide reliable measurements). The coronal section was taken through the two mesial cusps, except in the right M1/ of *Anoiapithecus*, where a distal section had to be employed owing to preservational reasons. The latter measurement should be taken with care, given the fact that differences between mesial and distal sections have been sometimes reported (Smith *et al.* 2005). The results for the several measured teeth are reported separately because a trend towards increasing enamel thickness from first to third molars has been reported for humans and other hominoids (Grine & Martin 1988; Macho 1994; Grine 2002, 2005; Smith *et al.* 2005, 2006*a*). Nevertheless, the mean value for each taxon is also employed for making interspecific comparisons, given that RET values for each molar separately are rarely reported for fossil taxa, and given the fact that the small samples sizes currently available for most taxa preclude an analysis of each tooth locus separately.

3. RESULTS

Tooth-specific measurements of AET and RET for *Pierolapithecus* (figure 1*a*), *Anoiapithecus* (figure 1*b*) and *Dryopithecus* (figure 1*c*) are reported in table 1. *Anoiapithecus* displays an average RET value of 18.6 (range 16.7–20.6; $n = 5$, s.d. = 1.46), *Pierolapithecus* an average value of 19.5 (17.3–21.8; $n = 6$, s.d. = 1.65) and *Dryopithecus* a mean of 10.6 (9.6–11.6; $n = 2$, s.d. = 1.42). No trend of increasing RET values towards
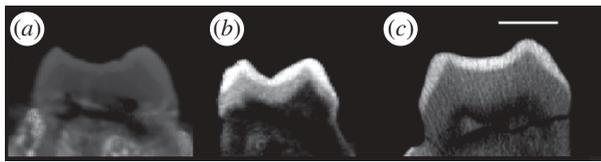
Figure 1. CT-scan coronal sections of the left second upper molars of (*a*) *P. catalaunicus* IPS21350 (holotype), (*b*) *A. brevirostris* IPS43000 (holotype) and (*c*) *D. fontani* IPS35026. Scale bar, 5 mm.

the distal molars can be discerned, although the sample size is admittedly too small to reach any conclusion in this regard. Although the small size of the samples also precludes a sound statistical analysis, the reported values suggest that there are no significant differences between *Anoiapithecus* and *Pierolapithecus*—which display largely overlapping maximum–minimum ranges— whereas *Dryopithecus* clearly shows much lower values. Differences in RET among fossil and extant hominoids (table S2, electronic supplementary material and references therein) must be interpreted with caution owing to the generally small sample sizes for the former. However, the RET values reported here for both *Pierolapithecus* and *Anoiapithecus* surpass the upper range of variation of extant species, by showing a thick-enamelled condition most comparable to *Afropithecus* (21.4), *Griphopithecus* (19.3), *Sivapithecus parvada* (18.9) and *S. sivalensis* (19.2), and less accentuated than in *Proconsul nyanzae* (22.4), *Ouranopithecus* (25.5), *Lufengpithecus lufengensis* (24.2), *Gigantopithecus* (21.8) and all available Hominini except Neandertals. *Dryopithecus*, on the contrary, displays a thin-enamelled condition, which is on average even slightly thinner than the condition displayed by extant African apes.

4. DISCUSSION
(a) *Palaeodietary inferences*
Extant hominoids display a frugivorous diet, with a variable emphasis on soft and hard fruits depending on the species (Andrews & Martin 1991). Sclerocarpic foraging, which involves the consumption of hard-food items such as hard seeds and the mesocarp of unripe fruit (Kinzey & Norconk 1990; Martin *et al.* 2003; Vogel *et al.* 2008), has been related to thick dental enamel (Jolly 1970; Kay 1981; Martin 1985; Dumont 1995; Schwartz 2000). This is supported by microwear and shearing crest analyses (Andrews & Martin 1991; Ungar & Kay 1995; Ungar 1996), although the underlying selection pressures are subject to several interpretations (Shellis *et al.* 1998). Thick enamel may be related to hard-object feeding because of its usual correlation with low cusp relief and reduced shearing crests, which are functionally related to powerful chewing (Andrews & Martin 1991), while on the contrary thin enamel is thought to be suitable for maintaining the sharp crests required by folivorous taxa to shear tough vegetal foods (Kay 1981; Schwartz 2000). Thick enamel might also prevent abrasion by delaying dentine exposure (Jolly 1970; Molnar & Gantt 1977; Schwartz 2000), although the tendency of enamel thickness to increase from M1 to M3 (Grine & Martin 1988; Macho 1994; Grine 2002, 2005; Smith *et al.* 2005, 2006*a*) is not consistent with abrasion being its

Table 1. Tooth-specific measurements of two-dimensional AET and RET in *Anoiapithecus*, *Pierolapithecus* and *Dryopithecus*. (Measurements based on upper molars and mesial sections, except in one tooth, where this was not possible owing to preservational reasons. L, left; R, right).

taxon	section	tooth	AET	RET
A. brevirostris	mesial	L M1/	0.67	20.6
	distal	R M1/	0.63	17.9
	mesial	L M2/	0.73	19.3
	mesial	R M2/	0.74	16.7
	mesial	R M3/	0.86	18.4
P. catalaunicus	mesial	L M1/	0.67	21.8
	mesial	R M1/	0.61	17.3
	mesial	L M2/	0.74	20.3
	mesial	R M2/	0.86	20.5
	mesial	L M3/	0.75	18.3
	mesial	R M3/	0.81	18.8
D. fontani	mesial	L M2/	0.47	9.6
	mesial	L M3/	0.66	11.6

main selective factor (Macho & Berner 1993). On the contrary, this tendency is consistent with biomechanical models predicting higher masticatory loads towards the distal molars (Macho & Berner 1993, 1994; Spears & Macho 1998; Macho & Spears 1999; Schwartz 2000). In accordance with this, it has been recently suggested that thick enamel could prolong tooth life in hard-object feeders by preventing the propagation of radial cracks from the enamel–dentine junction that are caused by the high stresses produced during the mastication of hard foods (Lucas *et al.* 2008; Vogel *et al.* 2008).

Following the latter interpretation, according to which thick enamel would be an adaptation to withstand and/or dissipate high masticatory loads, differences in enamel thickness between the thin-enamelled chimpanzees and the thick-enamelled orangutans have been related to their respective dietary preferences: thus, chimpanzees become seasonal folivores when ripe fruit is not available, whereas orangutans habitually consume tougher and harder items as fallback foods (Vogel *et al.* 2008). This correlation between thicker enamel and hard-object feeding must be applied with care to fossil taxa, given that there is no threshold value for distinguishing hard-object feeders on this single basis alone (Dumont 1995; Maas & Dumont 1999). Moreover, thick enamel is not a necessary prerequisite for hard-object feeding, as shown by pitheciins, which employ the anterior dentition for breaking hard-food items and the posterior (thin-enamelled) dentition to process softer foods (Martin *et al.* 2003). Hence, other anatomical aspects such as gnathic morphology, enamel microstructure, incisor morphology and dental microwear should also be taken into account for making reliable palaeodietary inferences.

The results reported in this paper for *Pierolapithecus* and *Anoiapithecus* indicate that these taxa, like afropithecids (*Afropithecus*, *Griphopithecus*) and stem pongines, display thicker enamel than orangutans, albeit to a lesser degree than other fossil taxa such as *Ouranopithecus*, *Gigantopithecus* and *Paranthropus* (see table S2, electronic supplementary material). The high RET values of *Ouranopithecus* are consistent with microwear analyses
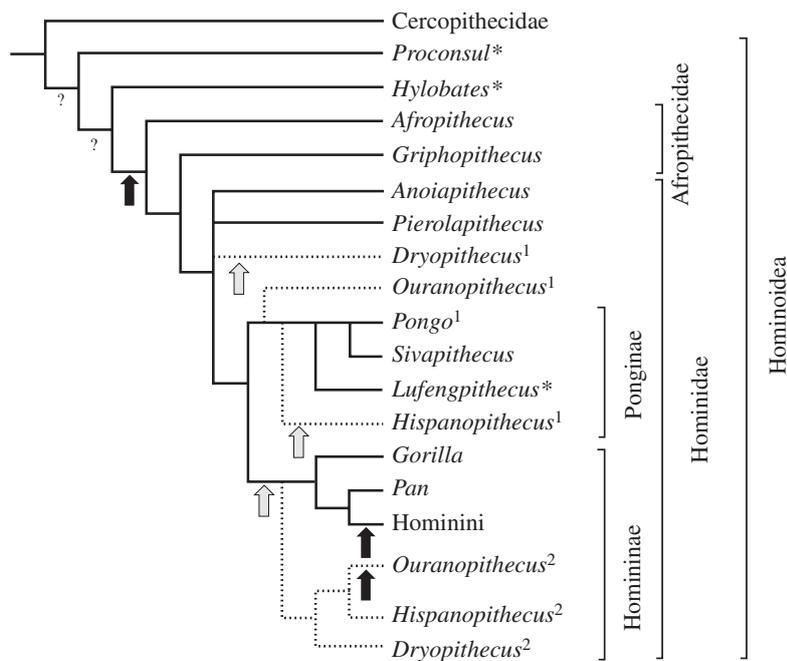
Figure 2. Simplified phylogenetic scheme of the Hominoidea indicating the main changes in RET (from intermediate thin or thin to intermediate thick or thick, and vice versa). Two different topologies are depicted for the three most problematic taxa (*Ouranopithecus*, *Dryopithecus* and *Hispanopithecus*); see text for further explanations. RET values reported in table S2, electronic supplementary material. Black arrow, (int.) thick; grey arrow, (int.) thin, question mark, uncertain; asterisk, variable; 1, our preferred hypothesis; 2, Begun (2009).

indicating that, unlike any living ape, this taxon was probably a hard-object specialist (Ungar 1996; King 2001). In the past, kenyapithecines such as *Kenyapithecus* and *Equatorius* were considered sclerocarpic foragers owing to dentognathic similarities to pitheciins (McCrossin & Benefit 1997; Palmer *et al.* 1999). The former, however, lack the similarities in the anterior dentition shared between pitheciins and *Afropithecus* (Deane 2009), thus more closely resembling the condition displayed by *Cebus*, in which hard-food items are processed by the thick-enamelled molars, presumably adapted to dissipating the associated high stresses (Martin *et al.* 2003). In the case of *Griphopithecus*, dental microwear analyses indicate that this taxon consumed hard fruits at least as often as orangutans do (King *et al.* 1999; King 2001). The possession of other kenyapithecine-like dentognathic features in the taxa studied in this paper, particularly in *Anoiapithecus* (Moyà-Solà *et al.* 2009*b*), supports the interpretation of their thick-enamelled condition as an adaptation to feeding on hard or unripe fruits, at least as fallback foods. The much thinner enamel of *Dryopithecus*, on the contrary, would suggest a much greater reliance on soft fruits, or alternatively a different strategy able to cope with hard fruits without possessing thick-enamelled molars (as in pitheciins). The significance of these differences in enamel thickness from a palaeodietary perspective, without additional evidence, must remain tentative until other analyses based on microwear and occlusal morphology are performed in the future. Nevertheless, it clearly emerges that, contrary to Begun's (2009) contention, not all the Middle Miocene dryopithecins from Spain display a thin-enamelled condition, further suggesting that *D. fontani* must have displayed important palaeodietary differences with regard to the remaining taxa.

(b) *Taxonomic implications*

Both *Pierolapithecus* and *Anoiapithecus* have been recently considered junior synonyms of *Dryopithecus* by Begun (2009). This issue cannot be discussed here at length, and the reader is referred to the original descriptions of the two former taxa (Moyà-Solà *et al.* 2004, 2009*b*), as well as to the description of the *D. fontani* palate IPS35026 (Moyà-Solà *et al.* 2009*a*), for further details on the morphological features that justify a taxonomic distinction at the genus level between the three taxa. The results of RET reported in this paper, however, are relevant regarding the recent erection of the subtribe Dryopithecina and the emended diagnosis of the genus *Dryopithecus* by Begun (2009). According to the latter author, both taxa would be characterized by thin-enamelled teeth (Begun 2009, pp. 794–795). This is clearly contradicted by the results published in this paper, which suggest that both *Pierolapithecus* and *Anoiapithecus* (further lacking other putatively diagnostic features of the Dryopithecina, such as a large maxillary sinus) should be removed from this subtribe.

(c) *Phylogenetic hypotheses and biogeographic scenarios*

Thick enamel has been postulated to be ancestral for the Hominidae as a whole (Martin 1985), a hypothesis that was disputed by Beynon *et al.* (1991). Testing this hypothesis is hampered by the numerous uncertainties regarding the phylogeny of Miocene hominoids. In figure 2, we have mapped the evolution of enamel thickness on a simplified phylogenetic scheme of fossil and extant hominoids (RET data reported in table S2, electronic supplementary material). Unfortunately, while the phylogeny of extant hominoids is well resolved, the phylogenetic position

and systematic status of many fossil hominoids is far from being definitively settled. This is attributable to several reasons, including the pervasive nature of homoplasy in hominoid evolution, the fragmentary nature of several key fossil taxa and disagreements among researchers regarding character selection and definition (e.g. compare Moyà-Solà & Köhler 1995; Begun *et al.* 1997; Harrison & Rook 1997: their fig. 2; Finarelli & Clyde 2004: their fig. 2*b*; and Grehan & Schwartz 2009). This is further complicated by the fact that the specimens studied in this paper were published quite recently, so that the morphological evidence that they provide has not yet been incorporated into any formal cladistic analysis. As such, regarding the position of *Anoiapithecus* and *Pierolapithecus*, we follow the previously proposed hypothesis that these taxa are stem hominids (Moyà-Solà *et al.* 2004, 2009*b*), while considering that *Sivapithecus* and *Lufengpithecus* are stem pongines (e.g. Harrison & Rook 1997; Finarelli & Clyde 2004). On the contrary, alternative phylogenetic positions are depicted in figure 2 for the most problematic taxa (*Dryopithecus*, *Ouranopithecus* and *Hispanopithecus*). The consensus cladogram of Finarelli & Clyde (2004: their fig. 2*b*) did not resolve whether *Ouranopithecus* is a pongine or hominine, further placing *Dryopithecus* s.l. (i.e. including *Hispanopithecus*) in a more basal position. On the contrary, these taxa were considered stem pongines by Moyà-Solà & Köhler (1995; which is our preferred hypothesis) and stem hominines by Begun *et al.* (1997; see also Begun 2009). Regarding *Dryopithecus*, in the description of the first palate ever attributed to its type species, *D. fontani*, Moyà-Solà *et al.* (2009*a*) proposed two alternative hypotheses: to consider it a stem hominine (on the basis of its gorilla-like facial morphology), in agreement with Begun (2009); or to consider it a stem hominid convergent with the gorilla condition (which is currently our preferred hypothesis).

The basal position within the Hominidae of the two thick-enamelled hominoids studied in this paper is supported by the retention of several primitive, kenyapithecine-like traits (anterior position of the zygomatic root, strong mandibular torus and extreme reduction of the maxillary sinus) in this taxa (Moyà-Solà *et al.* 2009*b*). According to this hypothesis, kenyapithecin afropithecids (*Kenyapithecus* and *Griphopithecus*) would be recognized as hominid's sister taxa. This phylogenetic hypothesis had been previously suggested by other researchers (Pickford 1986; Harrison 1992; Harrison & Rook 1997; McCrossin & Benefit 1997; Begun 2001, 2005, 2007; Güleç & Begun 2003), and some authors had even included *Kenyapithecus* and *Griphopithecus* as a distinct subfamily (Kenyapithecinae) within the Hominidae (Ward & Duren 2002; Cameron 2004). That would imply two separate dispersal events from Africa into Eurasia (one for hylobatids and the other for the ancestors of hominids), and a third dispersal event back into Africa, irrespective of whether *Dryopithecus*, *Ouranopithecus* and *Hispanopithecus* are considered stem hominines (e.g. Begun 2009) or not. The palaeobiogeographic scenario advocating a Eurasian origin of the Hominidae and a later back-to-Africa dispersal of African ape and human ancestors had been previously proposed by several researchers (Begun *et al.* 1997, 2003; Begun 2001, 2003, 2005, 2009; Begun & Nargolwalla 2004; Andrews & Kelley 2007; Alba & Moyà-Solà 2009; Moyà-Solà *et al.* 2009*b*) and is also consistent with the

evidence provided by other mammals (Andrews 2007; Folinsbee & Brooks 2007).

The wide range of interspecific variation displayed within several fossil and extant genera (*Proconsul*, *Hylobates* and *Lufengpithecus*) suggests that the phylogenetic signal of RET must be interpreted with care, being subject to homoplasy, presumably owing to convergent dietary adaptations (Andrews & Martin 1991; Hlusko *et al.* 2004; Kono 2004). Given the phylogeny of extant and extinct hominoids, it seems clear that both thick and thin enamel independently arose several times, probably in response to similar environmental conditions (Andrews & Martin 1991). Thus, thin enamel would have originated from a thicker enamelled condition, at least in the ancestor of the African ape and human clade, and perhaps also in *Hispanopithecus* and/or *Dryopithecus*, if they were not stem hominines. Similarly, thick or even hyperthick enamel would have re-evolved from a thin-enamelled condition at least in the ancestor of the Hominini (australopiths and humans) and maybe also in *Ouranopithecus* if it were a stem hominine. Regarding the earliest origin of thick enamel, hominoids generally display thicker enamel than cercopithecoids, but the variable thickness in both stem hominoids (*Proconsul*) and hylobatids precludes deciphering the ancestral condition for the Hominoidea total group and crown group. Nevertheless, the most parsimonious explanation regarding the thick-enamelled condition displayed by *Anoiapithecus* and *Pierolapithecus* is that it was inherited from their afropithecid ancestors. The thick-enamelled kenyapithecin afropithecids are the earliest hominoids recorded outside Africa, where they are represented by a single tooth tentatively attributed to cf. *Griphopithecus* from the MN5 (*ca* 15 Ma) of Europe (Heizmann & Begun 2001), several remains of *Griphopithecus darwini* from the MN6 of Europe (Steininger 1967) and by the specimens from the MN5 or MN6 (*ca* 15–13 Ma) of Turkey attributed to *Griphopithecus alpani* and *Kenyapithecus kizili* (Alpagut *et al.* 1990; Andrews & Harrison 2005; Andrews & Kelley 2007; Kelley *et al.* 2008). Their thick-enamelled condition would have been not only inherited by the stem great apes *Anoiapithecus* and *Pierolapithecus* at *ca* 11.9 Ma—suggesting that thick enamel might be symplesiomorphic for the great ape and human clade—but also to some degree (intermediate thick to thick enamel) by Asian pongines, first recorded by *Sivapithecus* at *ca* 12.5 Ma (Kappelman *et al.* 1991).

From a palaeoecological perspective, whereas Early Miocene African stem apes inhabited tropical wet evergreen forests and displayed a mainly frugivorous diet, the increasing abundance of thick-enamelled hominoids towards the Middle Miocene is in accordance with the presence of more seasonal, open and drier environments in Africa by this time (Andrews 1992, 1996). The acquisition of thick enamel in the afropithecid lineage was coupled with the evolution of other adaptations related to hard-object feeding, such as low cusps, enlarged incisors and massive jaws, which would have enabled afropithecids to exploit food resources unavailable to other catarrhines that relied on softer fruits that require a lesser amount of processing (Andrews & Martin 1991). Southern European habitats were quite similar to African ones during the Middle Miocene, although Turkish ones were probably somewhat more open and with more deciduous taxa, owing to greater seasonality (Andrews 1990; Andrews *et al.* 1997; Andrews & Bernor 1999).

The evidence reviewed above therefore supports the adaptive scenario (Begun 2003) in which thick enamel might have been the key innovation that facilitated the out-of-Africa dispersal of hominoids as well as the early radiation of Eurasian great apes. In other words, this dispersal event would have been possible thanks to a previous adaptive shift in Early Miocene African hominoids, which were initially forest dependent (living in multi-canopied, evergreen forests) but progressively became adapted to more open, seasonal woodland and forest environments, more similar to those that they encountered when dispersed into Eurasia (Andrews & Kelley 2007). Once in this continent, the ancestral thick-enamelled condition displayed by kenyapithecins would have been inherited not only by the stem great apes *Pierolapithecus* and *Anoiapithecus*, but also (at least to some lesser degree) by several Asian pongines (*Lufengpithecus*, *Khoratpithecus* and *Pongo*), which would have benefited from this condition for exploiting hard fruits at least as fallback foods. Environmental conditions in Eurasia during the late Middle and early Late Miocene, however, were probably more favourable to hominoids than the conditions that they encountered when first dispersing into this continent, which would explain their subsequent adaptive radiation into different adaptive types. This is exemplified by the thinner enamelled condition of the Middle Miocene *Dryopithecus* and the Late Miocene *Hispanopithecus*, presumably owing to the adaptation to a more generalized frugivorous diet, which in the latter taxon is confirmed by both dental microwear and shearing crests analyses (Ungar & Kay 1995; Ungar 1996; Galbany *et al.* 2005).

5. SUMMARY AND CONCLUSIONS

The study of dental enamel has played an important role in studies of hominoid evolution. On the basis of non-invasive techniques (industrial CT scans), we investigated two-dimensional AET and RET in the Middle Miocene great apes *P. catalaunicus*, *A. brevirostris* and *D. fontani*, which have been recovered from three similarly aged (*ca* 11.9–11.8 Ma) localities of Abocador de Can Mata. Our results indicate that both *Pierolapithecus* and *Anoiapithecus* display thick enamel (mean RET of 18.6 and 19.5, respectively), whereas *Dryopithecus* displays a thin-enamelled condition (mean RET of 10.6).

Hominoids generally display thicker enamel than other primates, and among extant great apes, orangutans display a thicker condition than African apes. Many fossil great apes, however, display a thicker enamelled condition than orangutans. From a palaeobiological viewpoint, the thick-enamelled condition shared by Early Miocene afropithecines, Middle Miocene African and Eurasian kenyapithecines, the Middle Miocene European putative stem hominids *Pierolapithecus* and *Anoiapithecus* and many Middle to Late Miocene Asian pongines might be indicative of hard-object feeding and its biomechanical requirements. Other studies (microwear and shearing crest analyses), however, would be required in order to confirm this hypothesis, as well as to decipher whether the taxa investigated in this paper were habitual sclerocarpic foragers (as inferred for the thicker enamelled, fossil great ape *Ouranopithecus*) or whether they only seasonally consumed hard-food items as fallback foods (as in

orangutans). The much thinner enamelled condition displayed by *Dryopithecus*, in any case, is highly suggestive of dietary differences relative to the two other taxa included in this study, thereby suggesting that the Middle Miocene evolutionary radiation of great apes in Europe did not merely consist of a taxonomic diversification, but was also accompanied by some degree of feeding niche divergence.

It is difficult to reconstruct the evolutionary history of enamel thickness, given current uncertainties regarding the phylogeny of Miocene apes. When taken as a whole, and despite the numerous uncertainties, hominid phylogeny indicates that thin enamel must have independently evolved several times. The retention of kenyapithecine features in *Pierolapithecus* and *Anoiapithecus*, interpreted as stem hominids (Moyà-Solà *et al.* 2004, 2009b), is consistent with chronological and palaeobiogeographical evidence favouring the view that kenyapithecins (*Griphopithecus* and *Kenyapithecus*) are the most likely sister taxa of hominids. From the viewpoint of enamel thickness evolution, this phylogenetic link indicates that thick enamel may be a symplesiomorphy of the great ape and human clade, having been inherited from their African afropithecid ancestors. This suggests that thick enamel (and its associated dentognathic features) might have been the fundamental adaptation that facilitated the out-of-Africa dispersal of large-bodied apes, by enabling them to inhabit the relatively drier and seasonal environments that they must have encountered on their way into Eurasia. This condition might have been inherited by the earliest pongines, but later modified in hominine ancestors, although both thick enamel and thin enamel must have convergently evolved several times along different lineages (perhaps including *Dryopithecus* and *Hispanopithecus*, depending on their correct phylogenetic position).

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