Molar Enamel Thickness and Dentine Horn Height in *Gigantopithecus blacki*

A.J. Olejniczak,[1]* T.M. Smith,[1] W. Wang,[2,3] R. Potts,[4] R. Ciochon,[5] O. Kullmer,[6] F. Schrenk,[7] and J.-J. Hublin[1]

[1]*Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[2]*Faculty of Earth Sciences, China University of Geoscience, Wuhan, People's Republic of China*
[3]*Natural History Museum of Guangxi Zhuang Autonomous Region, Nanning, People's Republic of China*
[4]*Human Origins Program, National Museum of Natural History, Smithsonian Institution, Washington, D.C.*
[5]*Department of Anthropology, University of Iowa, Iowa City, Iowa*
[6]*Department of Paleoanthropology and Quaternary Paleontology, Senckenberg Research Institute, Frankfurt a.M., Germany*
[7]*Department of Vertebrate Paleontology, Institute for Ecology, Evolution, and Diversity, Johann Wolfgang Goethe University, Frankfurt a.M., Germany*

ABSTRACT   Absolutely thick molar enamel is consistent with large body size estimates and dietary inferences about *Gigantopithecus blacki*, which focus on tough or fibrous vegetation. In this study, 10 *G. blacki* molars demonstrating various stages of attrition were imaged using high-resolution microtomography. Three-dimensional average enamel thickness and relative enamel thickness measurements were recorded on the least worn molars within the sample (*n* = 2). Seven molars were also virtually sectioned through the mesial cusps and two-dimensional enamel thickness and dentine horn height measurements were recorded. *Gigantopithecus* has the thickest enamel of any fossil or extant primate in terms of absolute thickness. Relative (size-scaled) measures of enamel thickness, however, support a thick characterization (i.e., not "hyperthick"); *G. blacki* relative enamel thickness overlaps slightly with *Pongo* and completely with *Homo*. *Gigantopithecus blacki* dentine horns are relatively short, similar to (but shorter than) those of *Pongo*, which in turn are shorter than those of humans and African apes. *Gigantopithecus blacki* molar enamel (and to a lesser extent, that of *Pongo pygmaeus*) is distributed relatively evenly across the occlusal surface compared with the more complex distribution of enamel thickness in *Homo sapiens*. The combination of evenly distributed occlusal enamel and relatively short dentine horns in *G. blacki* results in a flat and low-cusped occlusal surface suitable to grinding tough or fibrous food objects. This suite of molar morphologies is also found to varying degrees in *Pongo* and *Sivapithecus*, but not in African apes and humans, and may be diagnostic of subfamily Ponginae. Am J Phys Anthropol 135:85–91, 2008.   © 2007 Wiley-Liss, Inc.

Since the seminal diagnosis of the extinct Pleistocene hominoid *Gigantopithecus blacki* (von Koenigswald, 1935) and its initial morphological description (von Koenigswald, 1952), the dietary proclivities of this fossil ape have been vigorously discussed (e.g., Groves, 1970; Pilbeam, 1970; White, 1975; Ciochon et al., 1990; Daegling and Grine, 1994; Kupczik et al., in review). The exceptionally large body size of *G. blacki*, its geographic context, and paleohabitat reconstructions have inspired comparisons with the giant panda (*Ailuropoda melanoleuca*), which feeds primarily on multiple species of bamboo (e.g., Ciochon et al., 1990). It has also been suggested that the diet of *G. blacki* included other species of grasses (Ciochon et al., 1990), and a study of molar microwear yielded evidence of modern chimpanzee-like frugivory (Daegling and Grine, 1994). *Gigantopithecus* molar and premolar crowns have low cusps and a relatively flat, tabular occlusal surface suitable for crushing or grinding tough and fibrous vegetation such as bamboo; absolutely thick molar enamel in *Gigantopithecus* is consistent with these dietary reconstructions.

Only a single *Gigantopithecus blacki* molar has been examined previously with regard to enamel thickness (Dean and Schrenk, 2003), and absolutely thick molar enamel was recorded in this physical section. Modern nondestructive microtomographic methods for recording enamel thickness measurements (e.g., Kono, 2004; Tafforeau, 2004; Olejniczak, 2006), however, offer the opportunity to explore enamel thickness in a larger sample of *Gigantopithecus* molars. Nondestructive microtomographic acquisition of molar sections has been shown to

have a level of accuracy similar to that of physical sectioning techniques (Olejniczak and Grine, 2006). Such methods also allow the full, three-dimensional distribution of enamel thickness to be examined rather than a single section plane. This three-dimensional approach may offer insight about how the unique tabular occlusal surface of *Gigantopithecus* molars is configured, especially with regard to aspects of enamel-dentine junction (EDJ) morphology, which has a strong influence on the shape of the outer enamel surface of molars (e.g., Korenhof, 1961; Olejniczak et al., 2004).

The goal of the study presented here is to employ nondestructive three-dimensional microtomographic techniques to examine the thickness and distribution of enamel in *Gigantopithecus* molars within the context of other hominoid taxa. An additional goal is to examine aspects of EDJ morphology (e.g., the height of dentine horns) as they relate to enamel thickness, to explore the configuration of the unique occlusal morphology evinced by *Gigantopithecus* molars.

MATERIALS AND METHODS

Ten *G. blacki* molars (from the Senckenberg Chinese drugstore collection (von Koenigswald, 1935, 1952) and the Mohui Cave locality (Wang et al., 2005, 2007)) were microCT scanned using a Skyscan 1172 system at 100 kV, 100 mA, and with an aluminum-copper filter. This sample was comprised of three maxillary and seven mandibular molars. Voxel (volumetric pixel) dimensions were kept isometric, ranging from 14 to 28 μm depending on the size of the tooth scanned. After segmenting enamel from dentine in the microCT scans, virtual models of each tooth were created for recording enamel thickness and dentine horn height measurements (Fig. 1).

Two of the molars showed little sign of attrition (Senckenberg specimen no. SMF-CA-734, a mandibular second molar, and Mohui cave specimen no. MH011, a maxillary third molar), facilitating the recording of a volumetric enamel thickness dataset (following Kono, 2004; Tafforeau, 2004; Olejniczak, 2006) including: enamel volume (mm^3), coronal dentine volume (mm^3), and the surface area of the EDJ (mm^2). On the basis of these 3D data, two enamel thickness indices were calculated. Average enamel thickness (3DAET) is the volume of the enamel cap divided by the surface area of the EDJ, yielding the average straight-line distance between the EDJ and the outer enamel surface. Relative enamel thickness (3DRET) is calculated as 3DAET divided by the cube root of the volume of coronal dentine, yielding a scale-free enamel thickness index suitable for inter-taxon comparisons.

Following methods described in greater detail elsewhere (Olejniczak, 2006), the coronal dentine volume measurement is defined to include the aspect of the pulp chamber that extends into the molar crown. The coronal pulp chamber volume is included in the dentine volume measurement in order to be consistent with the planar methods developed for measuring enamel thickness by Martin (1983). The enamel cervix of a molar is sinuous, and defining a single cervical plane (above which is crown and below which is root) is difficult in light of areas of enamel that "sleeve" towards the root apex. Following Olejniczak (2006), the most apical plane of section through the cervix that shows a continuous ring of
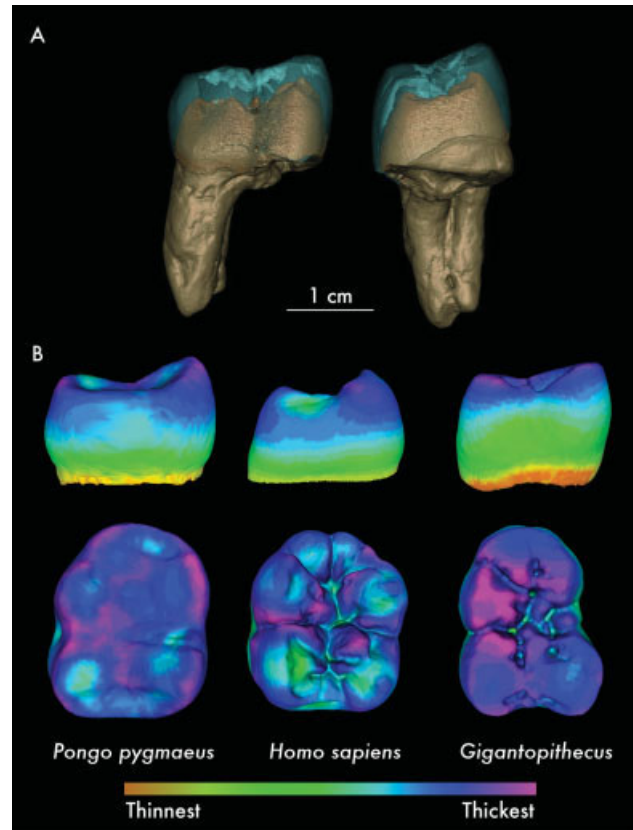

Fig. 1. A: Microtomographic models of a *Gigantopithecus* molar ("Molar 4" described by von Koenigswald (1935); Senckenberg Museum catalogue no. SMF-CA-736). Enamel has been rendered semi-transparent to demonstrate the nondestructive segmentation of enamel from dentine, which is necessary to record enamel thickness measurements. **B**: Whole-crown enamel thickness distribution models of mandibular molars of recent *Pongo pygmaeus*, recent *Homo sapiens*, and *Gigantopithecus blacki* (not to scale). The scale of enamel thickness is relative to each tooth, facilitating comparisons between taxa with varying absolute enamel thicknesses. The *Gigantopithecus* molar, and to a lesser extent the *Pongo* molar, show a more even distribution of occlusal enamel than the *Homo* molar. The *Gigantopithecus* molar is slightly worn, which has some impact on the thickness distribution model, but reconstructing the full height of the slightly worn buccal cusps would likely not add substantial topographic complexity (e.g., as in the *Homo* molar) to the whole enamel surface.

enamel was first located; next, this plane was gradually moved apically until the most apical plane of section still containing enamel was located. The plane exactly halfway between that containing the most apical continuous ring of enamel and that containing the most apical extension of enamel was taken as the cervical plane, above which coronal measurements were recorded.

Seven molars in the sample (five mandibular and two maxillary) showed light or moderate attrition, from which planar enamel thickness measurements may be made after reconstruction of the enamel cap (following, e.g., Martin, 1983; Smith et al., 2005) (Fig. 2). For these molars, virtual planes of section coursing through the tips of the mesial cusps were created using VoxBlast software (Vaytek, Inc.). Planar enamel thickness measurements include: the area of the enamel cap (mm^2),
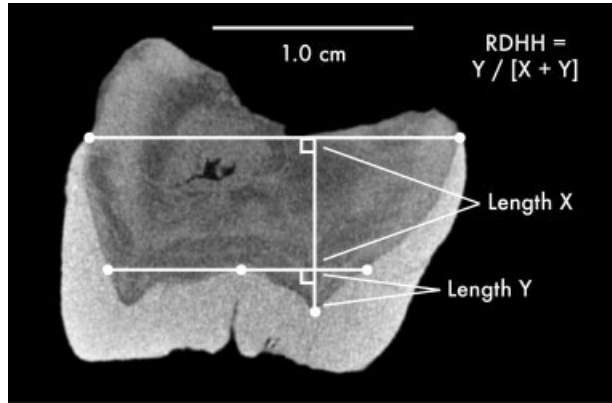
Fig. 2. Virtual mesial cross-section of a *Gigantopithecus* maxillary molar (Mohui cave specimen no. MH011) from which 2D enamel thickness measurements were taken. The method of calculating the relative height of a dentine horn tip is also depicted: the height of the dentine horn from a line parallel to the bi-cervical diameter and coursing through the lowest point of enamel in the mid-occlusal basin (length *Y*) is divided by the total height of the dentine crown measured from the bi-cervical diameter to the dentine horn tip (length *X* + *Y*), yielding the height of the dentine horn as a percentage of the total height of the dentine crown, termed here the "relative dentine horn height" (RDHH).

the area of coronal dentine (mm^2), and the length of the EDJ (mm). Two-dimensional average enamel thickness (2DAET) was calculated as the area of the enamel cap divided by the length of the EDJ, yielding the average straight-line distance from the EDJ to the outer enamel surface. Two-dimensional relative enamel thickness (2DRET) is calculated as 2DAET divided by the square root of the coronal dentine area, producing a scale-free index suitable for making interspecies comparisons.

Eight of the molars (five mandibular and three maxillary) preserved the full topography of the EDJ, and were thus suitable for comparison to previously published analyses of EDJ shape in anthropoid maxillary molars (Olejniczak et al., 2004, in press; Smith et al., 2006). A mesial plane of section was produced for each of these molars, as in the study of two-dimensional enamel thickness described earlier. In these sections, the maximum height of the dentine was recorded, measured as a line perpendicular to the bi-cervical diameter and coursing to the dentine horn tip (Fig. 2). The distance between the dentine horn tip and a line parallel to the bi-cervical diameter but coursing through the lowest point of enamel in the mid-occlusal basin was also recorded (Fig. 2). The ratio of these measurements yields the height of the dentine horn as a percentage of the total height of the dentine crown, termed here the "relative dentine horn height" (RDHH). The heights of the paracone and protocone were measured in the maxillary molars, and the heights of the protoconid and metaconid were measured in the mandibular molars. RDHH for other hominoid taxa, including *Sivapithecus sivalensis*, was culled from data previously published (Olejniczak et al., 2004, in press; Smith et al., 2006); a sample of *Pongo pygmaeus* mandibular molar dentine horn height metrics was created for the purpose of comparing the lower molars of *Pongo* to *Gigantopithecus*. Mandibular molar measurements are not available for African apes or *Sivapithecus*,

TABLE 1. *3D enamel thickness measurements (mean, minimum, and maximum)*

Taxon	Sample size	Enamel volume (mm^3)	Dentine volume (mm^3)	EDJ surface area (mm^2)	3DAET (mm)	3DRET
Gigantopithecus blacki	2	1571.06 (1552.96–1589.15)	1839.70 (1811.24–1868.15)	691.50 (690.43–692.56)	2.27 (2.24–2.30)	18.54 (18.21–18.88)
Homo sapiens[a]	39	218.91 (142.22–354.43)	226.83 (103.53–372.37)	162.56 (82.48–282.04)	1.43 (0.67–2.30)	23.97 (12.56–40.71)
Pan troglodytes[a]	26	137.00 (84.53–177.97)	166.05 (169.95–366.36)	182.67 (121.87–264.44)	0.75 (.56–0.92)	11.80 (9.03–14.72)
Gorilla gorilla[a]	9	372.01 (244.97–566.33)	1023.18 (819.89–1418.46)	375.89 (309.91–478.79)	0.98 (0.94–1.25)	9.77 (7.12–12.70)
Pongo pygmaeus[a]	12	197.91 (177.71–220.29)	336.05 (289.89–413.06)	199.75 (154.27–221.98)	1.01 (0.81–1.42)	14.49 (11.22–19.03)
Hylobates muelleri[b]	11	26.37 (16.34–35.95)	36.88 (26.17–51.80)	53.80 (44.82–69.94)	0.49 (0.36–0.60)	14.72 (11.29–18.68)
Symphalangus syndactylus[b]	17	62.29 (39.82–88.21)	119.6 (91.90–186.85)	116.21 (78.62–179.68)	0.55 (0.35–0.72)	11.15 (7.44–14.11)

[a] Olejniczak et al. (in review).
[b] Olejniczak (2006).

TABLE 2. *2D enamel thickness measurements (mean, minimum, and maximum) ordered on relative enamel thickness (greatest to least)*

Recent or Extinct	Taxon	Sample size	Enamel area (mm²)	Dentine area (mm²)	EDJ length (mm)	2DAET (mm)	2DRET
Extinct	*Paranthropus robustus*[a]	1	—	—	—	—	29.6
Extinct	*Graecopithecus freybergi*[a]	1	—	—	—	—	25.9
Extinct	*Lufengpithecus lufengensis*[a]	1	—	—	—	—	24.1
Extinct	*Australopithecus africanus*[a]	2	—	—	—	—	22.4
Extinct	*Proconsul nyanzae*[a]	1	—	—	—	—	22.4
Extinct	*Gigantopithecus blacki*	7	79.76 (53.61–107.15)	122.50 (89.97–151.45)	32.59 (28.63–35.41)	2.42 (1.87–3.06)	21.77 (18.99–25.10)
Extinct	*Afropithecus turkanensis*[a]	2	—	—	—	—	21.4
Recent	*Homo sapiens*[b]	257	24.19 (16.21–38.39)	38.73 (23.75–65.71)	19.60 (15.90–24.83)	1.22 (0.80–1.95)	20.06 (11.76–31.84)
Extinct	*Griphopithecus sp.*[a]	8	—	—	—	—	19.3
Extinct	*Sivapithecus sivalensis*[a]	3	—	—	—	—	19.2
Extinct	*Proconsul heseloni*[a]	1	—	—	—	—	17.0
Recent	*Pongo pygmaeus*[c]	41	23.42 (17.42–31.86)	50.93 (31.47–70.56)	21.34 (16.12–25.79)	1.10 (0.72–1.38)	15.49 (8.60–22.50)
Recent	*Hylobates muelleri*[d]	11	4.44 (3.06–5.56)	8.47 (5.92–10.89)	10.13 (8.47–11.53)	0.44 (0.34–0.53)	15.27 (10.37–21.83)
Extinct	*Rangwapithecus gordoni*[a]	1	—	—	—	—	14.9
Extinct	*Lufengpithecus hudienensis*[a]	1	—	—	—	—	14.1
Extinct	*Proconsul major*[a]	1	—	—	—	—	13.7
Recent	*Pan paniscus*[a]	1	—	—	—	—	13.6
Recent	*Pan troglodytes*[c]	40	14.63 (9.85–18.49)	36.95 (24.11–55.80)	19.47 (14.80–23.23)	0.75 (0.61–0.95)	13.23 (8.50–16.60)
Extinct	*Oreopithecus bambolii*[d]	1	—	—	—	—	13.0
Extinct	*Dryopithecus laietanus*[a]	1	—	—	—	—	12.7
Recent	*Symphalangus syndactylus*[d]	17	7.30 (4.60–9.59)	18.50 (14.23–28.50)	13.53 (11.01–16.90)	0.54 (0.39–0.67)	12.58 (9.02–15.59)
Recent	*Gorilla gorilla*[c]	15	29.37 (22.84–39.84)	79.29 (64.28–106.05)	28.25 (24.94–32.75)	1.04 (0.83–1.38)	11.68 (9.02–15.22)
Extinct	*Proconsul africanus*[a]	1	—	—	—	—	8.5

[a] Smith et al. (2003: Table 2, and references therein).
[b] Smith et al. (2006: Appendix A).
[c] Smith et al. (2005: Table 11).
[d] Olejniczak (2006).

TABLE 3. Mean relative dentine horn height (RDHH) in hominoid taxa

Taxon	Protocone RDHH (%)	Paracone RDHH (%)	Protoconid RDHH (%)	Metaconid RDHH (%)
Gorilla gorilla	40.4%	38.2%		
Pan troglodytes	34.7%	37.3%		
Homo sapiens	35.3%	36.2%	38.3%	34.7%
Sivapithecus sivalensis	32.1%	35.8%		
Pongo pygmaeus	28.2%	27.1%	28.0%	30.7%
Gigantopithecus blacki	23.9%	22.3%	28.4%	27.2%

so comparisons of lower molars are limited to *Homo*, *Pongo*, and *Gigantopithecus*.

RESULTS

Results of 3D and 2D enamel thickness measurements are reported in Tables 1 and 2, respectively, with values for other hominoid taxa for comparison. In Table 2, relative enamel thickness data for hominoid taxa collated by Smith et al. (2003: Table 3; 2006: Table 11) are also given. In terms of absolute (mm) measurements, *Gigantopithecus blacki* has the thickest enamel of any primate (3DAET = 2.27 mm; 2DAET = 2.42 mm). In terms of relative enamel thickness, however, *G. blacki* molars (3DRET = 18.54; 2DRET = 21.77) fall between the mean value for recent *Homo sapiens* and *Pongo* when 3D data are considered, and *G. blacki* 3DRET overlaps slightly with that of *Hylobates* (Table 1). Data from 2D measurements also show overlapping enamel thickness ranges for *G. blacki*, *Homo*, *Pongo*, *Hylobates*, and several extinct hominoid taxa. *Gigantopithecus blacki* relative enamel thickness is accommodated within the "thick" enamel category defined by Martin (1983, 1985).

Recent studies indicate that relative enamel thickness increases from anterior to posterior molar positions in hominoid taxa (e.g., Smith et al., 2005, 2006), indicating that molar position should be taken into account in inter-taxon enamel thickness comparisons. The 2D enamel thickness data recorded for *Gigantopithecus blacki* represent only one or two teeth from each molar position, rendering any anterior-to-posterior gradient difficult to assess. The characterization of an enamel thickness gradient in *Gigantopithecus* awaits larger samples, and molars from all tooth positions are therefore grouped in Tables 1 and 2.

The relative height of *G. blacki* dentine horns is given in Table 3, along with data from other taxa for comparison. *Gigantopithecus blacki* has the relatively shortest dentine horns among the taxa examined. Although there is little difference between the mean values obtained for the maxillary molars of *Homo sapiens* and *Sivapithecus sivalensis*, it is notable that the lowest values of RDHH are found in apes commonly attributed to subfamily Ponginae. Previous studies of EDJ shape metrics indicate that metameric variation in the molar row (i.e., differences in EDJ configuration between M1, M2, and M3) are unlikely to contribute to the overall variation within each taxon's dentine horn height measurements (Smith et al., 2006; Olejniczak et al., in press), and molars from all three positions are combined in Table 3 (although maxillary and mandibular molars are treated separately).

DISCUSSION

Average enamel thickness has a tendency towards either positive allometry with body weight or an isometric relationship with body weight in extant anthropoid primates, depending on the tooth position examined (Martin, 1983; Shellis et al., 1998). *Gigantopithecus blacki* has the thickest molar enamel of any primate (in mm units), which is consistent with large body weight estimates for this species. However, body weight and aspects of molar size do not predict one another perfectly [e.g., McHenry's (1984) estimates of relative megadontia in hominins]; since *Gigantopithecus blacki* is known only from dental and mandibular remains, corroboration of large body size estimates for this taxon awaits the recovery of skeletal elements that are not directly related to the dento-gnathic system. The measurement employed in this study, relative enamel thickness, relies only on information from the tooth being measured, avoiding estimates of body weight (the volume or area of coronal dentine is used as a scalar for enamel thickness in inter-taxon comparisons). Previous studies have demonstrated the efficacy of the relative enamel thickness measurement for taking size into account (e.g., Martin, 1983; Shellis et al., 1998), and this measurement is especially useful when other estimates of size are lacking, as is the case for *G. blacki*. When scaled in this manner, *Gigantopithecus blacki* molar relative enamel thickness (Table 2) falls within the ranges of a several thick-enameled Miocene, Pliocene, and recent hominoids, despite large tooth size and absolutely thick enamel in this taxon (Tables 1 and 2). *Gigantopithecus blacki* molars are characterized by relatively "thick" enamel (i.e., not relatively "hyperthick" enamel).

Dietary reconstructions of *Gigantopithecus blacki* typically focus on tough or fibrous vegetation (such as bamboo) supplemented with fruits and seeds (e.g., Ciochon et al., 1990; Daegling and Grine, 1994; Kupczik et al., in review). Low molar cusps with thick enamel are indicative of the grinding and crushing behavior associated with processing such vegetation. The microtomographic data presented in this study clarify the dietary molar adaptations of *G. blacki* through depictions of enamel thickness distribution. Figure 1 shows the three-dimensional distribution of enamel thickness in molars of recent *Pongo pygmaeus*, recent *Homo sapiens*, and *Gigantopithecus blacki*. *Gigantopithecus blacki* molar enamel is spread uniformly across the tooth crown compared to the variation in occlusal enamel thicknesses in the molar of recent *H. sapiens*. The *P. pygmaeus* molar also has more uniformly distributed enamel than the *H. sapiens* molar (see also Kono, 2004), but its enamel is not distributed as evenly over the occlusal surface as in *G. blacki*.

Occlusal enamel that is thick and evenly distributed, coupled with short dentine horns and a narrow and shallow central fossa, gives the *G. blacki* molar its characteristic tabular (i.e., large and flat) grinding surface. By contrast, the thick enamel of modern human molars is coupled with taller dentine horns with broad and deep basins (more similar to those of African apes; Table 3), and is distributed in such a way that the occlusal surface shows several different areas of thicker and thinner enamel. Modern human molars show a more complex distribution of enamel thickness, resulting not in a tabular occlusal surface, but in a less homogeneous topography. Thus, although *G. blacki* and

H. sapiens may both be characterized by having relatively thick enamel compared to African apes (and also relatively thicker than *Pongo*), the distribution of this relatively thick enamel over dentine horns of different height results in substantially different occlusal morphologies.

Short dentine horns and more uniformly distributed enamel also occur in *Pongo pygmaeus* molars, albeit to a lesser extent than is seen in *Gigantopithecus blacki*. Microtomographic data are lacking for *Sivapithecus*, but the thickness of enamel in *Sivapithecus* molars (reported by Martin, 1983; Smith et al., 2003), and similarly bunodont molars with low occlusal relief among *Sivapithecus, Pongo*, and *Gigantopithecus* have led previous scholars to conclude that these taxa are closely related (e.g., von Koenigswald, 1935, 1952; Andrews and Cronin, 1982). Data presented here also show a similarity in the overall molar morphology in *Pongo* and *Gigantopithecus*, in which evenly distributed intermediate to thick enamel is combined with short dentine horns to varying degrees, resulting in broad and flat occlusal surfaces relative to African apes and humans. This similarity in molar morphology relative to African apes and humans might indicate a phylogenetic affinity linking *Pongo* and *Gigantopithecus* (and perhaps also *Sivapithecus*); Heizmann and Begun (2001) noted, however, that thick enamel and low "dentine penetrance" (i.e., the rate of dentine exposure during tooth attrition, which is likely indicative of dentine horn height) characterize many Miocene large-bodied hominoids, dating to as early as the *Griphopithecus* molar from Engelswies (16.5–17.0 Ma). The combination of thick enamel and low-dentine horns appears to be plesiomorphic for large-bodied hominoids, and is insufficient evidence to link *Gigantopithecus* and *Pongo* to the exclusion of other apes. Nonetheless, *G. blacki* molars show the most extreme variation of this morphology.

The molars studied here may indicate a hyper-masticatory adaptation relative to other hominoids; an alternative to a phylogenetic explanation for the morphology of *Gigantopithecus* molars can thus be considered. Although, microCT measurements of other dentally similar fossil hominoid taxa (Table 2) are lacking (e.g., *Paranthropus robustus*, *Graecopithecus freybergi, Afropithecus turkanensis*), these thick-enameled hominoids (Grine and Martin, 1988; Smith et al., 2003, 2004) represent intriguing analogues to *Gigantopithecus*. If *Gigantopithecus* and these other taxa have similarly short dentine horns and evenly distributed enamel in three-dimensional perspective, then hyper-masticatory adaptations may account for overall molar morphological similarity in these taxa. Cursory examination of published molar sections (e.g., Smith et al., 2003: Fig. 2; Smith et al., 2004: Fig. 1) show that these taxa do appear to have short dentine horns, but the uniformity of enamel thickness distribution is difficult to assess in cross-section. Future work on the relationship between enamel thickness distribution and aspects of EDJ shape may clarify whether the condition seen in *Gigantopithecus* is typical of all hyper-masticatory adapted hominoids, or if this condition represents a unique variation of a Ponginae molar morphological pattern.

ACKNOWLEDGMENTS

LITERATURE CITED

Andrews P, Cronin JE. 1982. The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. Nature 297:541–546.

Ciochon RL, Piperno DR, Thompson RG. 1990. Opal phytoliths found on the teeth of the extinct ape *Gigantopithecus blacki*: implications for paleodietary studies. Proc Natl Acad Sci USA 87:8120–8124.

Daegling DJ, Grine FE. 1994. Bamboo feeding, dental microwear, and diet of the Pleistocene ape *Gigantopithecus blacki*. S Afr J Sci 90:527–532.

Dean MC, Schrenk F. 2003. Enamel thickness and development in a third permanent molar of *Gigantopithecus blacki*. J Hum Evol 45:381–387.

Grine FE, Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 3–42.

Groves CP. 1970. *Gigantopithecus* and the mountain gorilla. Nature 226:973–974.

Heizmann EPJ, Begun DR. 2001. The oldest Eurasian hominoid. J Hum Evol 41:463–481.

Kono R. 2004. Molar enamel thickness and distribution patterns in extant great apes and humans: new insights based on a 3-dimensional whole crown perspective. Anthropol Sci 112:121–146.

Korenhof CAW. 1961. The enamel-dentine border: a new morphological factor in the study of the (human) molar pattern. Proc Koninklijke Nederlands B 64:639–664.

Kupczik K, Dean MC, Spoor F. Tooth root morphology and dietary specialisation in *Gigantopithecus blacki* and extant hominids. J Hum Evol, in review.

Martin LB. 1983. Relationships of the later Miocene hominoidea. Ph.D. dissertation, University College, London.

Martin LB. 1985. Significance of enamel thickness in hominoid evolution. Nature 314:260–263.

McHenry HM. 1984. Relative cheek-tooth size in *Australopithecus*. Am J Phys Anthropol 64:297–306.

Olejniczak AJ. 2006. Micro-computed tomography of primate molars. Ph.D. dissertation, Stony Brook University.

Olejniczak AJ, Gilbert CC, Martin LB, Smith TM, Ulhaas L, Grine FE. Enamel-dentine junction morphology in anthropoid maxillary molar sections. J Hum Evol, in press.

Olejniczak AJ, Grine FE. 2006. Assessment of the accuracy of dental enamel thickness measurements using microfocal X-ray computed tomography. Anat Rec A 288:263–275.

Olejniczak AJ, Martin LB, Ulhaas L. 2004. Quantification of dentine shape in anthropoid primates. Ann Anat 186:479–485.

Olejniczak AJ, Tafforeau P, Feeney RNM, Martin LB. Three-dimensional primate molar enamel thickness. J Hum Evol, in Review.

Pilbeam D. 1970. *Gigantopithecus* and the origins of hominidae. Nature 225:516–519.

Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variation in molar enamel thickness among primates. J Hum Evol 35:507–522.

Smith TM, Martin LB, Leakey MG. 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. J Hum Evol 44:283–306.

Smith TM, Martin LB, Reid DJ, de Bonis L, Koufos GD. 2004. An examination of dental development in *Graecopithecus freybergi* (= *Ouranopithecus macedoniensis*). J Hum Evol 46:551–577.

Smith TM, Olejniczak AJ, Martin LB, Reid DJ. 2005. Variation in hominoid molar enamel thickness. J Hum Evol 48:575–592.

Smith TM, Olejniczak AJ, Reid DJ, Ferrell RJ, Hublin J-J. 2006. Modern human molar enamel thickness and enamel-dentine junction shape. Arch Oral Bio 51:974–995.

Tafforeau P. 2004. Phylogenetic and functional aspects of tooth enamel microstucture and three-dimensional structure of modern and fossil primate molars. Ph.D. dissertation, Université de Montpellier II.

von Koenigswald GHR. 1935. Eine fossile Säugetierfauna mit Simia aus Südchina. Proc Kon Nederl Akad Weten Ser C 38:872–879.

von Koenigswald, GHR. 1952. *Gigantopithecus blacki*, a giant fossil hominid from the Pleistocene of southern China. Anthropol Pap Am Mus Nat His 43:295–325.

Wang W, Potts R, Baoyin Y, Huang W, Cheng H, Edwards RL, Ditchfield P. 2007. Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China. J Hum Evol 52:370–379.

Wang W, Potts R, Hou Y, Chen Y, Wu H, Yuan B, Huang W. 2005. Early Pleistocene hominid teeth recovered in Mohui cave in Bubing Basin, Guangxi, South China. Chin Sci Bull 50:2777–2782.

White TD. 1975. Geomorphology to paleoecology: *Gigantopithecus* reappraised. J Hum Evol 4:219–233.