

Enamel Distribution Patterns of Extant Human and Hominoid Molars: Occlusal versus lateral enamel thickness

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Abstract Enamel thickness and distribution of the molar crown are important in the study of hominoid and hominid evolution. This is because the 3-dimensional distribution pattern of enamel within the molar crown has been recognized to have significant functional, developmental, and phylogenetic information. In order to analyze aspects of enamel distribution patterns, we quantified average enamel thicknesses separately in the occlusal basin and lateral molar crown, and compared extant great ape and modern human patterns. Interspecific comparisons show that, among modern apes and humans, chimpanzees and bonobos share a unique pattern of molar enamel distribution, in which the occlusal basin enamel is unexpectedly thin. Other taxa share a common enamel distribution pattern, greater occlusal than lateral crown average thicknesses, despite the wide range of absolute and relative whole-crown thicknesses. We hypothesize that thin occlusal enamel is a shared derived feature of the genus *Pan*, possibly an adaptation to relatively soft-fruit frugivory.

Key words: Enamel thickness, Hominoid, Molar, Occlusal fovea

Introduction

Average enamel thickness was initially defined in 2-dimensional cross sections of molars as enamel area divided by enamel-dentine junction (EDJ) length (Martin, 1983). It was devised as a convenient method of describing and comparing overall thickness of the enamel cap and has been the standard method of describing enamel thickness until recently (*e.g.*, Dean and Schrenk, 2003; Martin *et al.*, 2003; Smith *et al.*, 2003, 2004, 2005). We first reported volumetric and surface area measures of enamel and dentin portions of the crown (Kono *et al.*, 2002), and proceeded to compare modern human and extant great ape molars by means of the 3-dimensional (3D) version of Martin's (1983) average enamel thickness, that is, enamel volume divided by EDJ surface area (variable AET) (Kono, 2002; Kono, 2004). Subsequent to this work, with the rapid

increase in the application of micro-CT technology, a series of investigations has now been published that report comparable 3D measures of AET (Smith *et al.*, 2006; Olejniczak *et al.*, 2008a, b, c, d).

In these studies, AET is presented as a more appropriate measure of overall enamel thickness than the conventional 2-dimensional version of Martin (1983), a point that we agree with (*e.g.*, Kono, 2004). However, there are some differences between some of our results, such as with *Pongo*. We are not sure yet if this stems from small sample biases, different populational or subspecies representations of our respective species samples (see also discussion in Olejniczak *et al.*, 2008b), and/or methodological discrepancies such as in defining the cervix for measurement.

Aside from the 3D-based quantification of overall enamel thickness, it has been recognized

Table 1. Descriptive statistics of the 3-dimensional average enamel thickness variables.

Species	Tooth	n	AET			OJET			LAET		
			Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
<i>Homo sapiens</i>	LM1	9	1.314	0.125	1.065–1.512	1.531	0.144	1.280–1.805	1.239	0.124	0.986–1.417
	LM2	9	1.283	0.135	1.071–1.507	1.600	0.201	1.324–1.875	1.168	0.124	0.941–1.359
	LM3	3	1.210	0.172	1.019–1.352	1.466	0.197	1.283–1.675	1.113	0.163	0.925–1.226
<i>Pan troglodytes</i>	UM1	3	1.405	0.067	1.345–1.478	1.627	0.136	1.495–1.767	1.326	0.041	1.290–1.371
	UM2	3	1.456	0.180	1.256–1.604	1.788	0.273	1.474–1.968	1.337	0.144	1.179–1.460
	UM3	3	1.195	0.114	1.064–1.266	1.479	0.124	1.350–1.598	1.095	0.102	0.981–1.177
<i>Pan paniscus</i>	LM1	9	0.787	0.058	0.709–0.869	0.738	0.110	0.546–0.863	0.809	0.054	0.710–0.880
	LM2	7	0.816	0.058	0.752–0.894	0.754	0.066	0.665–0.824	0.843	0.084	0.775–0.995
	LM3	1	0.798			0.790			0.801		
<i>Pongo pygmaeus</i>	UM1	5	0.851	0.141	0.691–1.031	0.810	0.139	0.671–0.959	0.870	0.146	0.690–1.065
	UM2	7	0.807	0.091	0.713–0.940	0.749	0.096	0.586–0.846	0.832	0.107	0.690–0.985
	UM3	1	0.904			0.963			0.875		
<i>Gorilla gorilla</i>	LM1	7	0.729	0.071	0.627–0.799	0.714	0.071	0.616–0.809	0.736	0.074	0.629–0.808
	LM2	5	0.804	0.136	0.627–0.991	0.740	0.177	0.475–0.951	0.837	0.118	0.707–1.012
	LM3	—									
<i>Pongo pygmaeus</i>	UM1	6	0.680	0.090	0.566–0.786	0.668	0.074	0.551–0.746	0.685	0.099	0.567–0.803
	UM2	4	0.726	0.085	0.610–0.814	0.711	0.106	0.558–0.791	0.734	0.080	0.633–0.824
	UM3	—									
<i>Gorilla gorilla</i>	LM1	3	0.963	0.145	0.839–1.122	1.155	0.128	1.064–1.301	0.886	0.155	0.748–1.053
	LM2	3	1.061	0.097	1.004–1.173	1.251	0.079	1.161–1.310	0.978	0.115	0.891–1.108
	LM3	—									
<i>Gorilla gorilla</i>	UM1	1	0.897			0.993			0.860		
	UM2	1	1.075			1.207			1.014		
	UM3	—									
<i>Gorilla gorilla</i>	LM1	3	0.889	0.121	0.763–1.004	1.015	0.164	0.856–1.182	0.840	0.102	0.730–0.932
	LM2	3	1.089	0.086	1.016–1.183	1.220	0.073	1.163–1.303	1.027	0.091	0.951–1.128
	LM3	1	1.232			1.359			1.164		
<i>Gorilla gorilla</i>	UM1	1	0.880			0.990			0.840		
	UM2	1	1.051			1.227			0.976		
	UM3	1	1.223			1.448			1.121		

that the 3D distribution pattern of enamel within the crown would have significant functional, developmental, and phylogenetic information (e.g., Kono *et al.*, 2002; Kono, 2004; Suwa and Kono, 2005; Suwa *et al.*, 2007; Olejniczak, 2008a, d). In contrast to earlier studies in 2-dimensions (e.g., Schwartz, 2000), we investigated 2D-based linear measures of enamel thickness in some detail, and found that occlusal and some definitions of lateral enamel thicknesses were methodologically unstable, and potentially misleading in characterizing both local and overall regional enamel thicknesses (Suwa and Kono, 2005; Kono and Suwa, 2005). Therefore, 3D-based measures of enamel thickness, of various molar regions of interest, are highly sought, which, so far, has been attempted only by the Kono (2004) study. In particular, that study quantified a contrast between enamel thickness of the occlusal fovea and the lateral crown, with *Pan troglodytes* and *Pongo pygmaeus* molars exhibiting comparatively thin and thick occlusal enamel, respectively. Recently, occlusal thickness of the enamel has gained attention from a functional standpoint, as a potential adaptation to withstanding occlusal forces induced by mastication of hard and large food objects (e.g., Lucas *et al.*, 2008; Vogel *et al.*, 2008).

In our first attempt to quantify regional enamel distribution patterns within a molar (Kono, 2002, 2004), overall enamel thickness within the occlusal fovea and the lateral face of each cusp was represented by the mean value of minimum enamel thickness from each pixel of the outer enamel surface in the adopted projected orientation of view (for details, see Kono, 2004). This was done as an alternative to the more appropriate volume to surface area ratio, defined separately for occlusal and lateral face enamel. The reason the latter method was not applied at that time was because we had not yet developed the software tools then to accurately segment enamel volume and EDJ surface area into occlusal and non-occlusal portions. Some attention is needed regarding how to 3-dimensionally define and connect the outer enamel surface occlusal fovea perimeter with the same of the internal EDJ sur-

face (see below).

In the present study, we report the values of regional AETs separated into occlusal basin and the lateral crown face portions. Comparisons are also made with the whole crown AET. The enamel distribution characteristics of the extant hominoid species will be discussed from these perspectives.

Materials

A hominoid sample consisting of permanent molars of *Pan troglodytes* (n=30), *Pan paniscus* (n=22), *Gorilla gorilla* (n=10), *Pongo pygmaeus* (n=8), and thirty permanent molars of Japanese *Homo sapiens* from Jomon (n=10), Yayoi (n=1), Kamakura (n=1), and Edo periods (n=18) were analyzed in this study. Sex is unknown for most of the specimens, since they were taken from juvenile individuals.

The chimpanzee, gorilla, and orangutan teeth are mostly from the collection of the Cleveland Museum of Natural History. The bonobo specimens are from the collection of the Royal Museum of Central Africa, Tervuren. A small part of the chimpanzee and orangutan molars are housed either at the University of California, Berkeley, The University Museum, The University of Tokyo, or National Museum of Nature and Science, Tokyo. The Jomon Japanese molars were taken from the skeletal collection housed in The University Museum, The University of Tokyo. The Yayoi, Kamakura and Edo period specimens derive from the skeletal collections housed in the National Museum of Nature and Science, Tokyo.

Molars were chosen to have no wear, or slightest wear. With the non-human hominoid species, molars with slight occlusal wear and/or small chipping of enamel around the cervical region were included. In some cases where these losses were noticeable, digital interpolation and/or reconstruction was attempted to virtually approximate the original conditions.

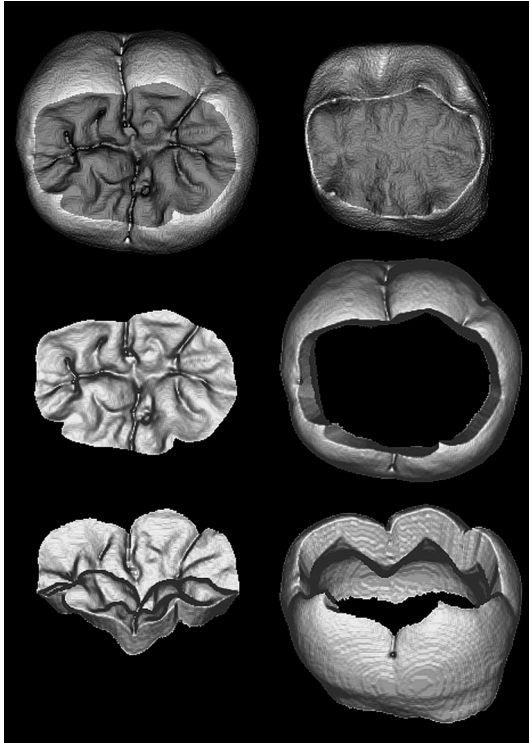


Fig. 1. Methods of obtaining occlusal enamel volume. Top row, surface rendered occlusal views of OES (left) and EDJ (right); the masked fovea regions are shaded. Bottom two rows, the same 3-dimensional volume data after separating the occlusal fovea (left) and lateral crown (right) enamel portions, shown in different orientations.

Methods

Explanations have been given elsewhere regarding our micro-CT based digitization, 3D reconstruction, and metric quantification methods (Kono, 2004; Suwa and Kono, 2005). In the present study, details of two new variables are presented, in addition to the original, whole crown average enamel thickness (AET) (Kono, 2004). OAET is defined as the average enamel thickness of the occlusal fovea, calculated as the occlusal enamel volume divided by the EDJ surface area of the occlusal fovea. Average thickness of the lateral molar crown, LAET, is defined as the mutual complement of the OAET, lateral enamel volume divided by the lateral crown face EDJ

surface area, with both volumes and surface areas non-overlapping and summing to whole crown enamel volume and EDJ surface area. These variables correspond to the previous study's OAMT and LAMT (Kono, 2004), but are different as described above.

Occlusal enamel volume was measured as follows (Fig. 1). First the entire volume data of the tooth is rotated so that the projected area of the EDJ occlusal fovea region (which is well defined by sharp margins) is maximized. The optimal amount of rotation is calculated iteratively and empirically determined (see Suwa and Kono-Takeuchi, 1998; Suwa and Kono, 2005). Once the orientation of the entire volume is adjusted, the topographic boundaries of the EDJ and outer enamel surface (OES) are determined in 3-dimensional space in order to digitally reconstruct the enamel cap morphology of the tooth crown. Next, in standardized projection (EDJ occlusal fovea maximized), the occlusal foveae of both the EDJ and the OES are delineated. This is done by defining the fovea region on the rendered occlusal view surface images with the aid of contour lines drawn at the elevation intervals of about 100 or 200 microns. The space between these two surfaces is 3-dimensionally filled, by bridging the gap between the perimeters of the two occlusal surfaces with triangle panels. The "shortest diagonal" algorithm (Christiansen and Sederberg, 1978) is employed in the triangulation; when adding a new triangle, the shorter one of the two diagonals between the two contours is selected as the side of the triangle. This algorithm is applicable when the numbers of points on the two contour loops are not equal, such as in the present case (the OES perimeter usually contains more points than the EDJ).

A new volume file is created that consists of only the voxels inside the occlusal fovea. Occlusal enamel volume is calculated as the number of voxels multiplied by voxel size. In order to obtain average occlusal enamel thickness (OAET), this volume is divided by EDJ occlusal fovea surface area (as delineated above).

The volume of the lateral crown face enamel is

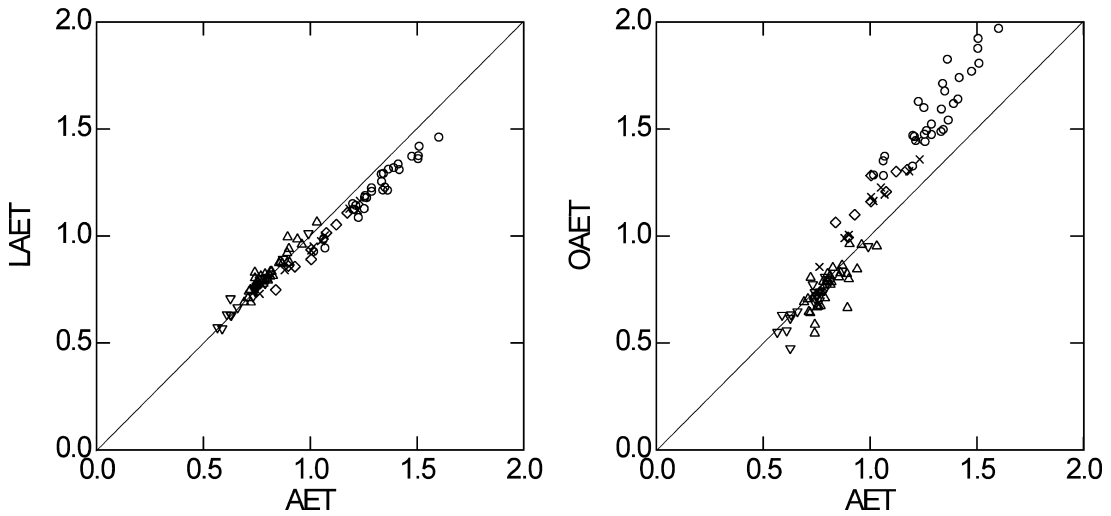


Fig. 2. Regional average enamel thicknesses, LAET and OAET, are plotted against the whole crown AET, respectively. The line of equality between the two variables is shown as the diagonal. Open circles, *Homo sapiens*; open triangles pointing upwards, *Pan troglodytes*; open triangles pointing downwards, *Pan paniscus*; diamonds, *Pongo pygmaeus*; crosses, *Gorilla gorilla*.

obtained by subtracting the occlusal portion described above from the entire crown enamel volume. The denominator of LAET, lateral crown face EDJ surface area, is obtained in the same way (subtracting occlusal EDJ surface area from whole crown EDJ surface area).

The measurements were obtained by use of the 3D image analysis software (3D- and CT-Rugle, Medic Engineering Inc., Kyoto), in part developed through our research project. Specifically, for the present study, a special routine was coded by Toyohisa Tanijiri to generate the above defined occlusal fovea volume file.

Results

The basic statistics of AET, OAET, and LAET of the five species are summarized in Table 1. When comparing the values of these variables, in most cases, the whole crown AET values are in between those of the two partial AETs. In other words, OAET is the largest, AET follows this, and LAET is the smallest. This is not surprising based on the fact that the lateral crown average enamel thickness includes the cervical part

where the enamel becomes thinner and finally terminates. In the case of the two species of *Pan*, however, the mean values of LAET surpass those of OAET in all tooth types examined except for the single UM3 of the common chimpanzee.

To depict this pattern more clearly, the two partial average enamel thickness values were plotted against the whole-crown AET (Fig. 2). In the individual molars of *Homo*, *Gorilla*, and *Pongo*, OAET and LAET values lie, respectively, above and beneath the line that represent equality with the AET. To the contrary, both OAET and LAET are nearly equal to AET in the molars of the two *Pan* species, with OAET being slightly (or substantially, in several specimens) smaller than AET. This confirms that the molars of both species of *Pan* share a unique pattern of unexpectedly thin occlusal fovea enamel.

Discussion

The present results on the distribution pattern of enamel within the molar crown correspond to our previous results and interpretations based on a cruder method (OAMT and LAMT of Kono,

2004). The bonobo is investigated for the first time, and it is clearly shown that the pattern of molar enamel distribution is similar to that of the common chimpanzee. This implies that the uniquely thin occlusal enamel is a derived feature of the genus *Pan*. Both species of *Pan* are known to be a frugivore strongly dependent on ripe fruits (e.g. White, 1992; Tutin and Fernandez, 1993).

Vogel *et al.* (2008) has recently shown that the fruits actually consumed by common chimpanzees at Kibale are indeed softer than those consumed by the Kalimantan orangutans. Kono (2004) previously noted that the thin occlusal enamel of the common chimpanzee molar has the effect of emphasizing the EDJ occlusal topography at the OES, with the combined effect of simultaneously forming a capacious occlusal fovea and retaining prominent cuspal topography. It was proposed that the capacious occlusal fovea may be advantageous in ripe fruit frugivory, while the retention of salient cusps may be effective in some degree of shear (Kono, 2004). Vogel *et al.* (2008) compared the actual food items and their physical properties of *P. troglodytes* and *Pongo pygmaeus*. They interpreted the broad occlusal basin of *Pan* molars endowed by thin enamel as an adaptation to relatively soft and juicy fruits, but also noted that the common chimpanzee do in fact rely on leaves as fallback food items.

However, Vogel *et al.* (2008) differ from our interpretations in considering *Pongo* molars to have higher cuspal topography (after Ungar, 2006), and therefore better shearing capabilities than in *Pan*. We ourselves view *Pongo* as in fact having reduced cusp saliency (Kobayashi, 2000, and data not shown), perhaps because of hard-fruit eating. In a large primate with absolutely large masticatory forces (Lucas *et al.*, 1994) and documented dependency on not only tough but also hard food objects (Vogel *et al.*, 2008), we hypothesize that salient cusps would be prone to breakage. Selection to reduce cuspal topography might then override selection to retain saliency, despite the need for shearing tough foodstuff (as

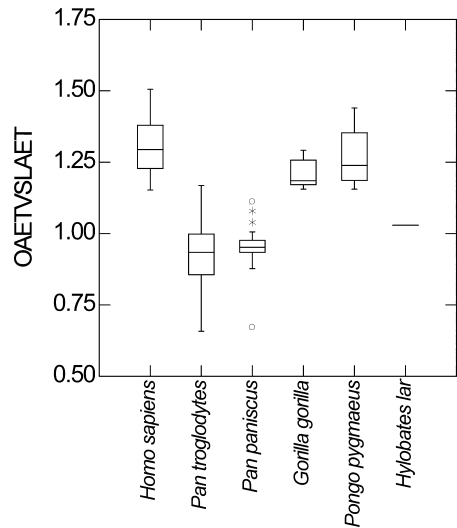


Fig. 3. Box plot of the index OAET divided by LAET. Lower and upper molars are pooled. A single *Hylobates* specimen is added for reference.

was also probably the case in *Australopithecus*).

Our results on enamel distribution of the bonobo molars are instructive in this regard. The *Pan paniscus* molars show the same occlusal fovea pattern as seen in those of the common chimpanzee, but has actually a more enhanced cusp saliency (Yamaguchi, 2008, and data not shown). Kinzey (1984) had previously noted qualitative difference in the details of molar cresting pattern and interpreted the bonobo condition to be better suited for shearing. It is known that the bonobo relies more heavily on THV for their non-fruit part of the diet (e.g. Malenky and Wrangham, 1994). This suggests that cusp saliency in *Pan* is in fact related to their partial reliance on fibrous food items.

The other three genera lack the characteristic enamel distribution pattern seen in *Pan*. This was most clearly seen when comparing the relationship of occlusal versus lateral enamel thicknesses (Fig. 3). *Gorilla* is known to have the thinnest molar enamel among the extant great apes in relative enamel thickness, while modern humans have the thickest, and orangutans have intermediate enamel thicknesses. It is striking that the oc-

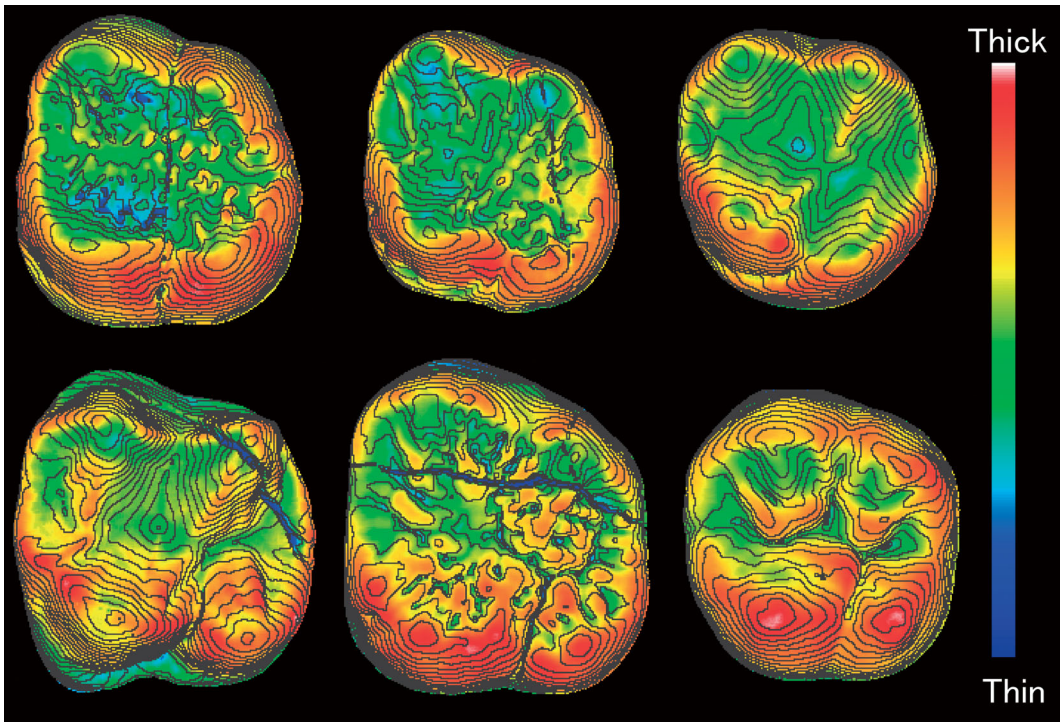


Fig. 4. Enamel thickness color maps of the upper second molar. Thickness is measured as the minimum distance from a given point on the OES to the EDJ surface. Color scale is adjusted so that the maximum thickness of the specimen approximately corresponds to the maximum value of the scale. Size is also adjusted for comparison. Top row, from left to right, *Pan troglodytes*, *Pan paniscus*, *Hylobates lar*; bottom row, from left to right, *Gorilla gorilla*, *Pongo pygmaeus*, *Homo sapiens*.

clusal versus lateral enamel distribution pattern is common to the three genera, despite the large differences among the three in both absolute and relative (size adjusted) AET values (Martin, 1983; Kono, 2004; Olejniczak *et al.*, 2008b). Furthermore, 3D-data of *Australopithecus* (data not shown) and Miocene apes such as *Gigantopithecus* (Olejniczak *et al.*, 2008a), *Chororapithecus* (Suwa *et al.*, 2007), *Dryopithecus*, *Lufengpithecus*, *Ouranopithecus* (data not shown) as well as 2D-cross section imagery of a wide range of Miocene apes (*e.g.* Andrews and Martin, 1991; Beynon *et al.*, 1998; Smith *et al.*, 2003, 2004; Chaimanee *et al.*, 2003, 2006; Pickford and Kunimatsu, 2005; Kunimatsu *et al.*, 2007) strongly suggest that the *Pan* condition is the rarer and derived condition.

Among the hominoids we have examined so

far, only the hylobatids share the derived condition with chimpanzees and bonobos (Fig. 3 and 4). Since hylobatids are phylogenetically an outgroup of all the taxa examined in this study and most if not all of the above cited Miocene ape genera, the most parsimonious hypothesis would be that *Hylobates* evolved the derived *Pan*-like pattern independently, perhaps in response to similar dietary and masticatory needs. According to our interpretations above, this would involve relatively soft-fruit frugivory and some amount of fibrous leaves. Hylobatid species more dependent on leaves should tend to have more salient cusps. Clearly this should be evaluated from larger samples of hylobatid species with divergent dietary dependencies.

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