

Linear Enamel Hypoplasia in the Great Apes: Analysis by Genus and Locality

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ABSTRACT Most studies report a high prevalence of linear enamel hypoplasia (LEH) in the great apes relative to other nonhuman primates and some human populations. It is unclear if this difference is a direct result of poor health status for the great apes, or if it represents differential incidence due to a lower threshold (*sensu* Goodman and Rose, 1990 *Am. J. Phys. Anthropol.* [suppl.] 33:59–110) for the occurrence of enamel hypoplasia among great apes. This study uses the Smithsonian National Museum of Natural History's great ape collection to examine the prevalence of LEH, the most common type of hypoplasia observed. Frequencies of LEH are reported, as well as analyses by taxa and provenience. The study sample consists of 136 specimens and includes 41 gorillas, 25 chimpanzees, and 70 orangutans. Analyses of frequencies

are presented for both individuals and teeth by taxonomic category and locality. Among the individuals in this study, 63.97% are affected by LEH. Overall, gorillas (29.27%) exhibit lower frequencies of LEH than chimpanzees (68.00%) and orangutans (82.86%). There is a marked difference in LEH frequencies between mountain and lowland gorillas. There is no difference in LEH frequencies between Sumatran and Bornean orangutans. A range of variation for the great apes in enamel hypoplasia frequencies is found when taxon and locality are considered. It is likely that both biological and environmental factors influence the high frequencies of enamel hypoplasia exhibited in the great apes. *Am J Phys Anthropol* 127:13–25, 2005. © 2004 Wiley-Liss, Inc.

Enamel hypoplasia is broadly defined as a deficiency in enamel thickness that results when physiological stress disrupts the formation of enamel (Goodman and Rose, 1990). Linear enamel hypoplasia (LEH), the most common and widely studied form of enamel hypoplasia, is manifested as a depressed horizontal furrow in the enamel around the circumference of the tooth crown. Because hypoplastic defects can be caused by a variety of physiological stressors, including febrile disease, parasitic infection, and nutritional deficiencies (Goodman and Rose, 1990), they have been used in numerous anthropological contexts as nonspecific indicators of physiological stress (extensively reviewed in Goodman and Rose, 1990). Although Colyer (1936) published the first comprehensive assessment of nonhuman primate enamel hypoplasia, only recently have researchers begun to explore the extent to which the study of enamel hypoplasia in nonhuman primates can provide insights into the physiological stress experienced by primate groups (Eckhardt, 1992; Eckhardt et al., 1992; Eckhardt and Protsch von Zieten, 1993; Guatelli-Steinberg, 1998; Guatelli-Steinberg and Lukacs, 1998; Guatelli-Steinberg and Skinner, 2000; Hannibal, 2000; Kelley and Buicek, 2000; Lukacs, 1999; Miles and Grigson, 1990; Moggi-Cecchi and Crovella, 1991, 1992; Newell, 1998; Skinner, 1986a,b; Skinner et al., 1995; Skin-

ner and Guatelli-Steinberg, 1997; Stottlemire, 1998; Vitzthum and Wikander, 1988; Zhang, 1987).

Most research on enamel hypoplasia in nonhuman primates has focused on establishing how LEH varies across the primate order (e.g., Guatelli-Steinberg, 2000; Newell, 1998; Schuman and Sognnaes, 1956; Skinner and Guatelli-Steinberg, 1997; Vitzthum and Wikander, 1988). These studies consistently find a high incidence of enamel hypoplasia among great apes and a low incidence in monkeys and prosimians. However, the manifestation of LEH is not only influenced by physiological stress but also by intrinsic attributes of enamel that vary systematically across taxa. Thus, this broad taxonomic pattern in the distribution of LEH is not necessarily a direct, or even an indirect, reflection of broad taxonomic differences in stress experience. For example,

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TABLE 1. Summary of LEH in common chimpanzees, gorillas, and orangutans

Study	Species or subspecies	Collections	Provinces	% of LEH-affected individuals	Method of determining LEH-affected individuals
Guatelli-Steinberg (2000)	<i>Pongo pygmaeus</i>	Museum of Comparative Zoology and Los Angeles County Museum of Natural History	Borneo, Sumatra	79 (n = 14)	Matched defects present on antimeric pair
	<i>Pan troglodytes</i>		West Africa, Uganda	85 (n = 26)	
	<i>G. gorilla gorilla</i>		Cameroon	39 (n = 23)	
Guatelli-Steinberg and Skinner (2000)	<i>Pan troglodytes</i> <i>G. gorilla gorilla</i>	Powell-Cotton Museum	Cameroon Cameroon	71 (n = 24) 66 (n = 35)	Individuals with LEH on any tooth
Newell (1998)	<i>Pongo pygmaeus</i>	American Museum of Natural History, National Museum of Natural History, Academy of Natural Sciences, Field Museum of Natural History, and Cleveland Museum of Natural History	Not reported	62.5 (n = 48)	Individuals with LEH on any tooth
	<i>Pan troglodytes</i>		Not reported	51.9 (n = 79)	
	<i>Gorilla gorilla</i> (primarily <i>G. g. gorilla</i>)		Not reported	32.9 (n = 146)	
Skinner (1986a)	<i>Pan troglodytes</i> <i>Gorilla gorilla</i>	Powell Cotton Museum	Sympatric species from Cameroon	58 (n = 110) 76 (n = 119)	Individuals with LEH on any tooth
Stottlemire (1998)	<i>Pan troglodytes</i> <i>Gorilla gorilla</i>	Cleveland Museum of Natural History	Cameroon Cameroon	80.6 (n = 98) 27.5 (n = 229)	Individuals with LEH on any tooth

there is a trend toward increasing crown formation times from prosimian to monkey to great ape grades, providing the latter with more opportunity to form enamel hypoplasia (Skinner et al., 1995). There is also a possibility that great apes may have poorer “enamel quality” than humans, making it difficult to distinguish true pathological lesions from other surface irregularities in the enamel (Lovell, 1990). Finally, great apes may exhibit more LEH than other primates because of the greater prominence of perikymata on their tooth crowns (Guatelli-Steinberg, 2001). Perikymata are tiny wave-like ridges on the enamel surface that form at regular intervals during crown formation, and their prominence as well as spacing are related to the formation and prominence of LEH defects (Hillson and Bond, 1997).

These studies of the taxonomic distribution of LEH in nonhuman primates have also revealed an intriguing pattern of LEH prevalence among the great apes, in that chimpanzees and orangutans are usually reported to have statistically significantly higher LEH frequencies than gorillas. Stottlemire (1998) found that western lowland gorillas had significantly lower LEH frequencies than chimpanzees, at 27.5% vs. 80.6% (Table 1). Guatelli-Steinberg (2000) reported an LEH frequency of 39% for western lowland gorillas, 85% for chimpanzees, and 79% for orangutans (Table 1). Likewise, Newell (1998) found that gorillas (primarily western lowland gorillas) had relatively lower LEH frequencies than orangutans and chimpanzees: 32.9% compared to

62.5% and 51.9%, respectively (Table 1). A less substantial difference of 71% for chimpanzees and 66% for gorillas was reported from Cameroon (Guatelli-Steinberg and Skinner, 2000; but for a case in which gorillas from Cameroon have significantly higher LEH prevalence than sympatric chimpanzees, see Skinner, 1986a (Table 1).

Stottlemire (1998) suggested that the distribution of LEH among great ape genera could be related to broad dietary differences among them: orangutans and chimpanzees are large-bodied fruit specialists (Martin, 1990), while gorillas have gut adaptations that facilitate leaf digestion (Chivers and Hladik, 1980; Milton, 1984). However, this simple “dietary hypothesis” requires examination at the species and subspecies levels, with special attention to bonobos and mountain gorillas, who exhibit less seasonality in food availability than common chimpanzees and western lowland gorillas, respectively (Badrian and Malenky, 1984; Basabose, 2002; Chapman et al., 1994; Doran et al., 2002; Malenky and Stiles, 1991; Malenky and Wrangham, 1994; Remis, 1997b; Rogers et al., 1990; Tutin et al., 1997; Watts, 1984; White, 1992, 1998).

While recent studies considered LEH differences among great ape genera, they did not adequately examine how enamel hypoplasia prevalence varies among great ape species, subspecies, and population samples. A more accurate assessment of the apparently large differences in LEH prevalence between great apes and other primates can be achieved by documenting the range of variation in LEH preva-

lence that exists within the great apes. The central purpose of this study is to examine how LEH prevalence varies among great ape genera, subspecies, and localities (see Materials and Methods for a definition of the latter), and to analyze this variability with respect to its consistency with the “dietary hypothesis,” as well as with respect to intrinsic attributes of enamel (such as crown formation time, “enamel quality,” and the prominence and spacing of perikymata) that may influence LEH variation at these different levels. Subspecies examined are: *P. p. pygmaeus* and *P. p. abelli* and *G. g. gorilla* and *G. g. beringei*; localities compared are, for orangutans, West Borneo and Southwest Borneo, and for chimpanzees and gorillas, Cameroon and Gabon. While these localities do not represent known populations, they are derived from different regions of a species’ range and thus allow within-species comparisons.

MATERIALS AND METHODS

The sample

The great ape collection from the Smithsonian National Museum of Natural History in Washington, DC was chosen for this study for two primary reasons: 1) the collection consists of a large number of orangutans (which were not adequately represented in previous studies of LEH), representing both subspecies and different localities; and 2) it includes both lowland and mountain gorillas. In addition, this sample had not yet been studied for LEH. The sample consists of 70 orangutans (57 *Pongo pygmaeus pygmaeus*; 13 *Pongo pygmaeus abelii*), 41 gorillas (22 *Gorilla gorilla gorilla*; 19 *Gorilla gorilla beringei*), and 25 chimpanzees (*Pan troglodytes*). There are slightly more males (52.63%) than females (47.37%), but the difference is not statistically significant. The sample consists of all individuals with at least eight original, permanent, and observable teeth present. A tooth was considered observable if less than half of the enamel crown was missing (due to either wear or damage) or obscured (by calculus and/or preservative). Many specimens had suffered postmortem damage, were heavily coated with preservative, or had at least some teeth obscured by calculus. Additionally, it was not uncommon to encounter a specimen with one or two teeth that clearly did not belong to that specimen. Some misplaced teeth were set loosely into the socket, some had been glued into place, and some had been padded with plaster, presumably to “fit” the socket. All specimens included in the sample were examined for this error, and any teeth suspected of not belonging with the specimen were coded as missing. In only one case was it necessary to exclude an entire specimen because of uncertainty as to which teeth were original and which were incorrectly assigned.

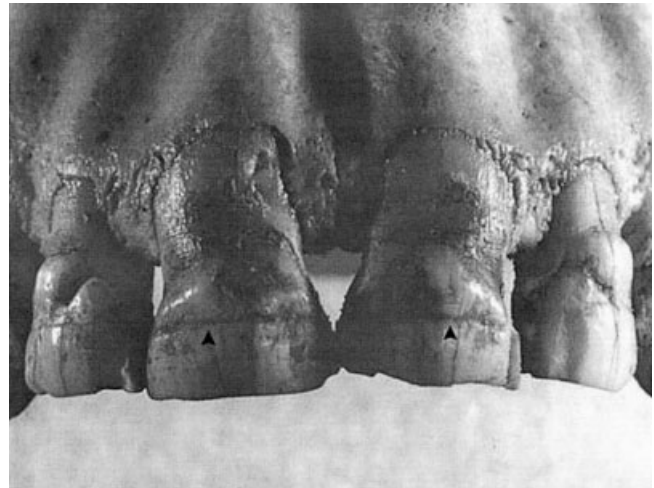


Fig. 1. Specimen 220063, LEH in *P. troglodytes*. Arrows indicate an LEH defect.

Methods of observing and scoring LEH

Data were collected by D.L.H. during August–September 1998 and again during July–August 1999, following standards set by Lukacs (1989) and Goodman and Rose (1990). All specimens were observed under diffuse lighting, with secondary oblique lighting. Initial observations were made with the naked eye, followed by closer inspection with a 10× hand lens. Therefore, only defects pronounced enough to be observed with a 10× hand lens were recorded. Presence or absence of teeth within the arcade, degree of wear, and presence or absence of enamel hypoplasia were recorded on data sheets. Additionally, the location and size of defects were drawn on dental charts included on each data sheet. Data were also collected for an intraobserver error study consisting of the reexamination of five specimens from each subspecies for a total of 25 specimens (18.4% of the sample). The intraobserver error test for the scoring of the presence or absence of LEH shows a statistically significant association between the first and second scoring sessions, indicating low intraobserver error ($\chi^2 = 20.160$, $df = 2$, $P = 0.000$).

Because both localized and systemic stresses can result in enamel defects and because systemic stress affects tooth germs bilaterally (Goodman and Rose, 1990), only defects present on both antimeres or on a tooth adjacent to an affected antimeric pair (Fig. 1, 2) were entered into the final data set as present. Hillson and Bond (1997) argued that it is necessary to match defects across all teeth developing at the time of metabolic insult in order to firmly establish that systemic stress has caused hypoplastic defects. These authors also argued that microscopic examination is required for the study of enamel hypoplasia, because the same stress episode may produce a defect obvious to the naked eye on an anterior tooth, but a defect on a posterior tooth that is only evident by microscopic observation. We maintain, however,

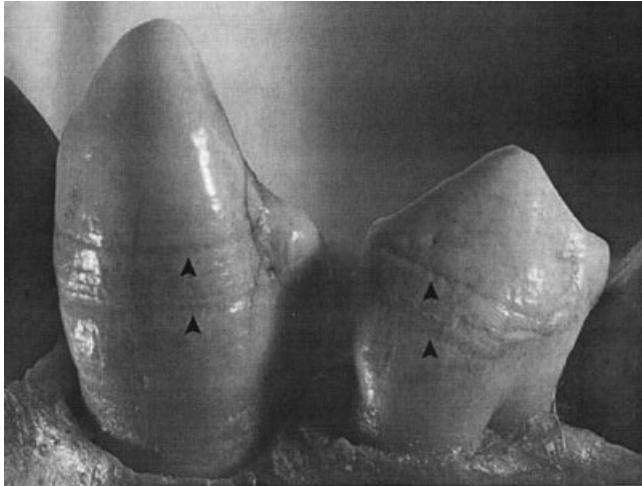


Fig. 2. Specimen 197664, LEH in *P. p. pygmaeus*. Arrows indicate an LEH defect.

that the necessity of microscopic methods in observing hypoplastic defects depends on the research question and goals of a study. The recording standard of Hillson and Bond (1997) for enamel hypoplasia limits comparison with many previous studies of enamel hypoplasias, which traditionally relied upon the FDI DDE index (Federation Dentaire Internationale, 1982, 1992) for standardizing the scoring of enamel defects. Additionally, it is usually the case that owing to time constraints, the more fine-grained the observations of each tooth, the smaller the sample size of both individuals and teeth. In this study, we chose to examine defects macroscopically in order to compare prevalence findings with those of previous studies, and to analyze relatively large samples for the purpose of generating meaningful prevalence data.

Finally, it should be noted that although Hillson and Bond (1997) argued for the use of microscopic methods to prevent underrecording of hypoplastic events, these methods do not actually allow the observer to identify all physiological disturbances recorded in the enamel. The only definitive way to identify all physiological disturbances recorded in the enamel, no matter how large or small they appear on the enamel surface, is to section the tooth and determine the presence of accentuated striae (Goodman and Rose, 1990). This method, however, is destructive and time-consuming, and is only necessary when accurate identification of all physiological disturbances in the enamel is critical to answer the research questions of a particular study. We use a conservative scoring method for recording the presence of hypoplastic defects and acknowledge that defects may be underreported, but assert that macroscopic methods are better suited to the goals of the present study.

Methods of analysis

The majority of chimpanzees, western lowland gorillas, and orangutans in the study collection were

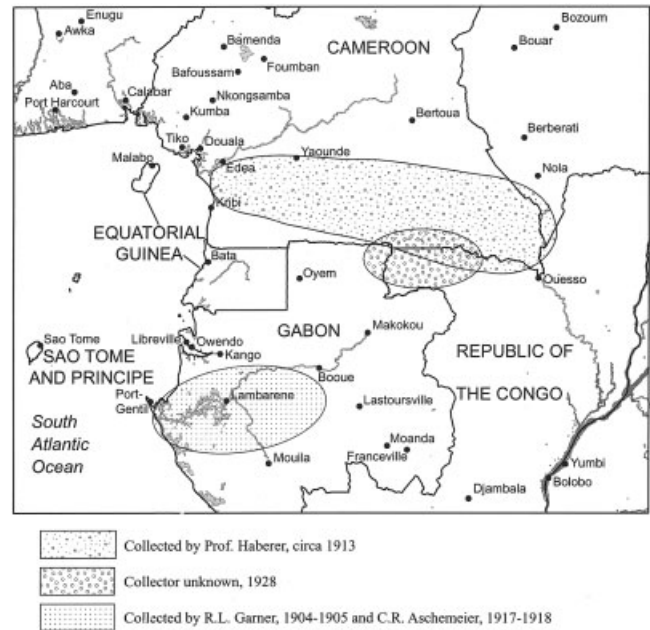


Fig. 3. Map of localities for Cameroon and Gabon.

obtained from hunting expeditions and private collectors during the early part of the 20th century. All but two mountain gorillas were recovered by researchers from the Karisoke Biological Field Station. For most specimens, information on the date and site of collection, as well as the name of the collector, are available. Field notes and maps made by collectors indicate that expeditions involved collection of a few individuals, often found around a base camp, traveling along a river system. Therefore, sites in geographic proximity to each other were grouped into localities for analyses (Fig. 3, 4). There were enough specimens from some, but not all, sites to run statistical tests by locality (Table 2).

The frequency of LEH is analyzed by taxon and by locality to determine whether LEH defects vary significantly by taxonomic category and/or locality. We use chi-square analysis to evaluate the association of LEH frequencies with taxa and with localities. For some tests, at least one expected value is below five, requiring a more conservative reporting of the results, using Yates' correction for continuity. In these cases, the corrected chi-square statistic (denoted by χ^2) is reported (Thomas, 1986). Because of postmortem damage and loss of some teeth, and because of variation in the number of LEH-affected teeth in individuals, tests are reported for both individuals and teeth. Table 3 summarizes the counts of observable teeth (at least half of the original enamel crown remained visible), the presence of LEH, and percent of LEH-affected teeth by tooth type and genus.

Even though the focus of this study is on the individual, because some individuals are not represented by all of their teeth, we feel that an analysis by tooth can provide additional insights. It must be

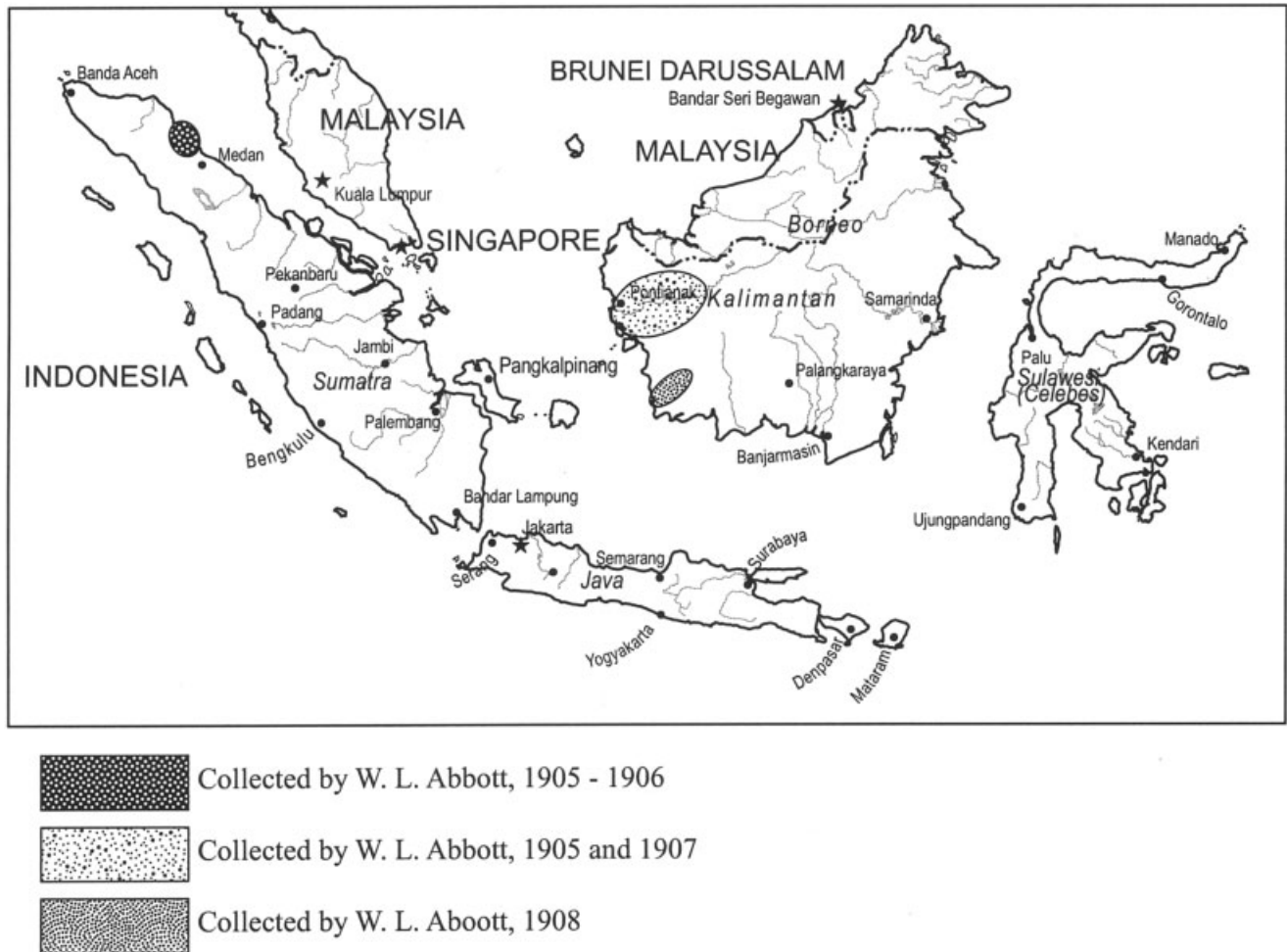


Fig. 4. Map of localities in Sumatra and Borneo.

borne in mind, however, that the by-tooth analysis has one drawback. Individuals with a large number of LEH-affected teeth (because of having more teeth present and/or because of having teeth with overlapping crown formation spans that were all affected by the same LEH-producing stress episode) could bias the teeth-affected percentages.

RESULTS

Association of LEH with genus

LEH varies significantly by genus for individuals ($\chi^2 = 32.432$, $df = 2$, $p = 0.000$), with orangutans most affected (82.86%), followed by chimpanzees (68.00%) and gorillas (29.27%), who were least affected (Table 4). The same test by teeth is also significant ($\chi^2 = 190.500$, $df = 2$, $p = 0.000$), but with slightly different results: chimpanzees have the highest frequency of affected teeth (35.91%), followed closely by orangutans (33.38%). Gorillas have a much lower frequency of affected teeth (10.25%) (Table 4).

Because LEH is disproportionately exhibited by the anterior teeth relative to the posterior teeth across primate taxa (Goodman and Armelagos,

1985; Vitzthum and Wikander, 1988), an obvious question to address is whether or not there are differences in the proportions of anterior vs. posterior teeth representing each genus. Consistent with previous studies of LEH in primates, the anterior teeth of this study sample are disproportionately affected by LEH, and although there is a disparity by genus in the number of observable teeth in the anterior vs. posterior portion of the arcade, this disparity does not explain why the results of the by-individual and by-teeth analyses differ. Gorillas have a substantially higher proportion of observable anterior teeth than the other two genera, but still have the lowest frequency of LEH (Table 4). Although chimpanzees have a higher proportion of observable anterior teeth than orangutans, the difference is not statistically significant (Table 5). It is reasonable to conclude that these differences in the analyses by individual and by teeth reflect real differences in the number of teeth affected vs. the number of individuals affected by LEH among genera. In other words, both the analyses by individual and by teeth are reliable, but provide different information about the prevalence of LEH: although more orangutan indi-

TABLE 2. Counts of specimens by taxa, region, and site

Genus and species	Subspecies	Region/country ¹	Site ¹	Total
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Gatinga-Uganda	1
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Mt. Muhavura	1
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Mt. Sabinyo	1
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Mt. Visoke	1
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Tsudura	3
<i>Gorilla gorilla</i>	<i>beringei</i>	Rwanda	Virunga	10
<i>Gorilla gorilla</i>	<i>beringei</i>	Zaire	Kivu central	1
<i>Gorilla gorilla</i>	<i>beringei</i>	Zaire	Mt. Karisimbi	1
<i>Gorilla gorilla</i>	<i>beringei</i> subtotal			19
<i>Gorilla gorilla</i>	<i>gorilla</i>	Unknown	Unknown	2
<i>Gorilla gorilla</i>	<i>gorilla</i>	French Congo ²	Unknown ³	6
<i>Gorilla gorilla</i>	<i>gorilla</i>	French Congo ²	Fernan Vaz ³	3
<i>Gorilla gorilla</i>	<i>gorilla</i>	French Congo ²	Moambe ³	1
<i>Gorilla gorilla</i>	<i>gorilla</i>	French Congo ²	Nkami River ³	1
<i>Gorilla gorilla</i>	<i>gorilla</i>	Cameroon	South Kamerun ³	3
<i>Gorilla gorilla</i>	<i>gorilla</i>	Cameroon	Souanke-Goko ³	6
<i>Gorilla gorilla</i>	<i>gorilla</i> subtotal			22
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Unknown ³	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Fernan Vaz ³	4
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Lake Fernan Vaz ³	5
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Lame Nkami ³	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Ogouma ³	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	French Congo ²	Pembanyambi Ngovi ³	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	Ivory Coast	Niebe	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	Liberia	Tarstown, Grand Gedeh	2
<i>Pan troglodytes</i>	<i>troglodytes</i>	Uganda	Budongo Forest	1
<i>Pan troglodytes</i>	<i>troglodytes</i>	Cameroon	South Kamerun ³	8
<i>Pan troglodytes</i>	<i>troglodytes</i> subtotal			25
<i>Pongo pygmaeus</i>	<i>abelli</i>	Sumatra	Adji	1
<i>Pongo pygmaeus</i>	<i>abelli</i>	Sumatra	Aru Bay	12
<i>Pongo pygmaeus</i>	<i>abelli</i> subtotal			13
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Unknown	4
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Batu Jurong ³	1
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Kendawangan River ³	13
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Mambuluh River ³	4
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Sakaiam River ³	15
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Semandong River ³	5
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Sempang River ³	12
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Sungei Menganne ³	1
<i>Pongo pygmaeus</i>	<i>pygmaeus</i>	Borneo	Sungei Samma ³	2
<i>Pongo pygmaeus</i>	<i>pygmaeus</i> subtotal			57
Grand total				136

¹ Country and site names are as recorded in NMNH records, except Souanke-Goko. These are French Congo specimens grouped with specimens from southern Cameroon (see Materials and Methods).

² All French Congo sites are in what is now called Gabon.

³ Indicates use in locality analysis.

viduals are affected by LEH, chimpanzees tend to have a greater number of LEH-affected teeth than orangutans.

Association of LEH with subspecies

There is no association between subspecies of orangutans and LEH when analyzed by individuals for the presence of LEH ($\chi^2 = 0.048$, $df = 1$, $0.90 > p > 0.75$) (Table 6). There is, however, a significant association when analyzed by teeth ($\chi^2 = 7.310$, $df = 1$, $p = 0.007$) (Table 6). Bornean orangutans have a higher frequency of affected teeth (35.18%) than Sumatran orangutans (27.50%), even though Sumatran orangutans have a significantly higher proportion of observable anterior teeth than Bornean orangutans ($\chi^2 = 111.604$, $df = 1$, $p = 0.000$) (Table 6). The distribution of observable teeth in the anterior vs. posterior portion of the arcade might have caused an artificially low frequency of

defects by individual for Bornean orangutan individuals. In this case, the analysis by teeth should be regarded as more reliable than the analysis by individuals. In this case, because Bornean and Sumatran individuals differ in the percentage of anterior vs. posterior teeth that represent them, the analysis by teeth may be a more reliable indicator of subspecies LEH differences than the analysis by individual.

There is a significant association between gorilla subspecies and LEH when analyzed by both individuals and teeth (individuals: $\chi^2 = 9.856$, $df = 1$, $p = 0.002$; teeth: $\chi^2 = 53.751$, $df = 1$, $p = 0.000$) (Table 7). Relative to mountain gorillas, western lowland gorillas have both higher frequencies of LEH-affected individuals (50.00% vs. 5.26%) and higher frequencies of LEH-affected teeth (16.48% vs. 1.96%). There is no significant difference between the mountain and western lowland gorilla samples

TABLE 3. LEH and observable teeth by tooth type and genus

Jaw/position	Tooth	Pan			Gorilla			Pongo		
		Observable teeth (n)	LEH-affected teeth		Observable teeth (n)	LEH-affected teeth		Observable teeth (n)	LEH-affected teeth	
			+	%		+	%		+	%
Maxillary right	11	16	10	62.50	31	3	9.68	32	16	50.00
	12	16	11	68.75	32	4	12.50	35	15	42.86
	C	18	10	55.56	30	3	10.00	35	17	48.57
	P3	21	9	42.86	37	3	8.11	55	26	47.27
	P4	14	4	28.57	39	0	0.00	58	20	34.48
	M1	20	0	0.00	33	0	0.00	62	3	4.84
	M2	19	2	10.53	27	1	3.70	62	12	19.35
Maxillary left	M3	16	0	0.00	14	2	14.29	36	13	36.11
	11	15	10	66.67	29	3	10.34	35	17	48.57
	12	17	12	70.59	32	4	12.50	40	15	37.50
	C	16	10	62.50	24	3	12.50	34	17	50.00
	P3	18	8	44.44	34	3	8.82	53	26	49.06
	P4	15	4	26.67	34	0	0.00	54	19	35.19
	M1	17	0	0.00	30	0	0.00	63	3	4.76
Mandibular right	M2	20	2	10.00	30	1	3.33	63	11	17.46
	M3	14	0	0.00	22	4	18.18	43	11	25.58
	11	14	11	78.57	25	3	12.00	43	19	44.19
	12	14	10	71.43	30	6	20.00	46	29	63.04
	C	12	8	66.67	27	10	37.04	37	22	59.46
	P3	18	10	55.56	35	8	22.86	51	32	62.75
	P4	17	5	29.41	36	3	8.33	56	20	35.71
Mandibular left	M1	16	0	0.00	32	0	0.00	51	2	3.92
	M2	16	1	6.25	29	0	0.00	56	6	10.71
	M3	16	0	0.00	25	2	8.00	39	6	15.38
	11	13	11	84.62	24	4	16.67	39	18	46.15
	12	15	11	73.33	25	5	20.00	45	28	62.22
	C	14	9	64.29	30	9	30.00	35	19	54.29
	P3	17	11	64.71	37	8	21.62	55	34	61.82
Total	P4	15	5	33.33	35	4	11.43	58	20	34.48
	M1	17	1	5.88	30	0	0.00	58	2	3.45
	M2	15	1	6.67	33	0	0.00	62	6	9.68
	M3	17	0	0.00	25	2	8.00	40	7	17.50
	Total		518	186	35.91	956	98	10.25	1531	511

TABLE 4. Analysis by genus

Taxon	Individuals			Teeth			Observable anterior teeth		
	%	+	n	%	+	n	%	+	n
Gorilla	29.27	12	41	10.25	98	956	68.90	339	492
Pan	68.00	17	25	35.91	186	518	60.00	180	300
Pongo	82.86	58	70	33.38	511	1,531	54.29	456	840
Total	63.97	87	136	26.46	795	3,005	59.74	975	1,632
	$\chi^2 = 32.432, df = 2, P = 0.000$			$\chi^2 = 190.500, df = 2, P = 0.000$			$\chi^2 = 27.572, df = 2, P = 0.000$		

TABLE 5. Pan Pongo, and observable anterior teeth

Taxon	Observable anterior teeth		
	%	+	n
Pan	60.00	180	300
Pongo	54.29	456	840
Total	55.79	636	1,140
	$\chi^2 = 2.926, df = 1, P = 0.087$		

in the number of observable anterior vs. posterior teeth ($\chi^2 = 1.922, df = 1, p = 0.166$) (Table 7).

Association of LEH with locality

Most of the Bornean orangutans were collected in either western Borneo or southwestern Borneo. There is no significant association of LEH and locality for Bornean orangutan individuals ($\chi^2 = 2.79, df = 1, 0.10 > p > 0.05$) (Table 8). However, oran-

gutans from southwestern Borneo have a higher frequency of LEH-affected teeth than those from western Borneo (48.95% vs. 26.09%; $\chi^2 = 58.512, df = 1, p = 0.000$) (Table 8). There is no significant difference between the Bornean and Sumatran orangutan samples in the distribution of observable anterior teeth ($\chi^2 = 2.278, df = 1, p = 0.131$) (Table 8). The size of the sample of individuals is rather small, requiring Yates' correction for continuity, and thus yields a test of low power. A larger sample size of orangutan individuals might produce a result consistent with the analysis by teeth. In this case, the analysis by teeth should be regarded as more reliable.

The chimpanzee and western lowland gorilla samples from southern Cameroon (formerly German Kamerun) and west Gabon (formerly the French Congo) are of sufficient size (see Table 2) to

TABLE 6. Analysis by orangutan subspecies

Taxon	Individuals			Teeth			Observable anterior teeth		
	%	+	n	%	+	n	%	+	n
<i>P. p. abelli</i>	84.62	11	13	27.50	99	360	92.31	144	156
<i>P. p. pygmaeus</i>	82.46	47	57	35.18	413	1,171	45.61	312	684
Total	82.86	58	70	33.38	511	1,531	54.29	456	840
	$\chi^2 = 0.048, df = 1, 0.90 > P > 0.75$			$\chi^2 = 7.310, df = 1, P = 0.007$			$\chi^2 = 111.604, df = 1, P = 0.000$		

TABLE 7. Analysis by gorilla subspecies

Taxon	Individuals			Teeth			Observable anterior teeth		
	%	+	n	%	+	n	%	+	n
<i>G. g. beringei</i>	5.26	1	19	1.95	8	410	65.79	150	228
<i>G. g. gorilla</i>	50.00	11	22	16.48	90	546	71.59	189	264
Total	29.27	12	41	10.25	98	956	68.90	339	492
	$\chi^2 = 9.856, df = 1, P = 0.002$			$\chi^2 = 53.751, df = 1, P = 0.000$			$\chi^2 = 1.922, df = 1, P = 0.166$		

TABLE 8. Analysis by locality for Bornean orangutans

Taxon	Individuals			Teeth			Observable anterior teeth		
	%	+	n	%	+	n	%	+	n
W Borneo	73.53	25	34	26.09	191	732	46.08	188	408
SW Borneo	95.24	20	21	48.95	187	382	40.08	101	252
Total	81.82	45	55	33.93	378	1,114	43.79	289	660
	$\chi^2 = 2.79, df = 1, 0.10 > P > 0.050$			$\chi^2 = 58.512, df = 1, P = 0.000$			$\chi^2 = 2.278, df = 1, P = 0.131$		

TABLE 9. Analysis by locality for West African apes

Taxon	Individuals			Teeth			Observable anterior teeth		
	%	+	n	%	+	n	%	+	n
Cameroon	27.27	3	11	6.01	14	233	68.63	140	204
Gabon	66.67	20	30	29.96	210	701	61.81	178	288
Total	56.10	23	41	23.98	223	934	64.63	318	492
	$\chi^2 = 14.951, df = 1, P = 0.000$			$\chi^2 = 126.820, df = 1, P = 0.000$			$\chi^2 = 2.431, df = 1, P = 0.119$		

pool the two genera and test for an association of locality and LEH. Six western lowland gorilla specimens from the border area of Cameroon, Gabon, and Congo were included with the Cameroon specimens because the collection site is considerably closer to the Cameroon specimens than the Gabon specimens (Fig. 3). The sample sizes of the two ape genera in Cameroon (chimpanzees, $n = 8$; western lowland gorillas, $n = 9$) and Gabon (chimpanzees, $n = 13$; western lowland gorillas, $n = 11$) are about equal in proportion (Table 2). It is therefore unlikely that any observed differences in LEH frequencies between apes from the two locations are confounded by intrinsic enamel differences or dietary differences between the two genera. Relative to apes from Cameroon, those from Gabon have higher frequencies of LEH-affected individuals (Gabon, 66.67% vs. Cameroon, 27.27%; $\chi^2 = 14.951, df = 1, p = 0.000$) (Table 9). When analyzed by teeth, the Gabon sample again has a higher frequency than the Cameroon sample (Gabon, 29.96% vs. Cameroon, 6.01%; $\chi^2 = 126.820, df = 1, p = 0.000$) (Table 9). The number of observable anterior teeth in the Gabon sample is slightly less than expected, while the number of observable anterior teeth in the Cam-

eroon sample is slightly more than expected, but these differences are not significant ($\chi^2 = 2.431, df = 1, p = 0.119$) and are the opposite of what would be expected if they were influencing differences in LEH frequencies (Table 9).

DISCUSSION

Association of LEH with genus

Consistent with most previous studies (see introduction), this study also finds that gorillas exhibit LEH frequencies at around one-third to half of that exhibited by chimpanzees and orangutans. The combined evidence of this and previous studies strongly suggests that LEH is discernible among other enamel irregularities, evident in the differing frequencies of LEH by taxon and by locality, and is not simply the result of generalized poor enamel quality. However, the generic differences in LEH frequencies reported here could potentially result from several other factors. Here, we will first consider to what extent intrinsic factors of enamel may be affecting the observed intergeneric pattern of LEH prevalence. Then we will turn to examining this pattern

with respect to potentially relevant environmental variables, with special attention to the “dietary hypothesis.”

In terms of relevant intrinsic features of enamel, one possibility is that crown formation times vary among great ape genera, affecting the amount of time available for recording enamel growth disruptions (as first suggested by Skinner et al., 1995). This factor, however, while likely to be relevant to LEH frequency differences between great apes and monkeys (Guatelli-Steinberg, 2001; Skinner et al., 1995), is unlikely to be involved in the intergeneric LEH frequency differences found here for the following reasons. Reid et al. (2000) studied the duration of imbricational enamel formation in great ape anterior tooth crowns. LEH can only form in the imbricational enamel, where internal dark bands known as striae of Retzius “outcrop” onto the enamel surface as perikymata (Hillson and Bond, 1997). Reid et al. (2000) found the following canine imbricational enamel formation times in the great apes. These are: 5 years for orangutan females, 7.96 years for orangutan males, 5.12 years for chimpanzee females, 5.86 years for chimpanzee males, 4.75 years for gorilla females, and 7.02 years for gorilla males. These imbricational enamel formation times do not parallel the LEH frequency differences found here, as, for example, gorilla females do not take substantially less time than chimpanzee and orangutan females to form their imbricational enamel. In addition, although gorilla male canine imbricational enamel formation time is longer than that of chimpanzee males, gorilla male canines in the present study are less affected by LEH than those of chimpanzees. The results of this study provide an exception to the general trend across the primate order (Guatelli-Steinberg, 2001) that longer imbricational enamel formation times are associated with higher rates of LEH.

Hillson and Bond (1997) explained that the prominence of LEH defects may be affected by the prominence and spacing of perikymata on tooth crowns. The authors of the present study (based on their subjective assessment) did not find that perikymata were any more or less prominent on the crowns of different great ape genera. Thus the prominence of perikymata, while likely to be relevant to the difference in LEH prevalence among great ape, monkey, and prosimian grades, is not likely to be involved in LEH prevalence differences among great ape genera.

Hillson and Bond (1997) also argued that, where perikymata are more closely spaced on a tooth crown (such as near the cervix of anterior teeth), defects are more sharply defined, and so are more easily detected by the observer. In addition, Hillson and Bond (1997) argued that in areas of the tooth crown where Retzius planes are acutely angled with respect to the dentin-enamel junction (DEJ) and where perikymata are thus more widely spaced, defects are more difficult to perceive because they ap-

pear as undefined, shallow depressions on the tooth surface. A possible implication of this argument for the present study is that if perikymata are more closely spaced in one genus relative to another, then LEH defects might also be easier to identify in the genus with the more densely packed perikymata. Dean and Reid (2001) indeed showed that perikymata are more closely packed in chimpanzee teeth than they are in gorilla teeth in comparable regions of the crown. In the lower half of the tooth, the average density of perikymata in chimpanzee anterior teeth reaches a high of 20 perikymata per mm, while it reaches only 15 perikymata per mm in gorilla teeth. Thus, the spacing of perikymata is one possible factor contributing to the observed LEH frequency difference between *Pan* and *Gorilla*. An obvious test of this possibility would entail comparing the perikymata spacing in orangutans with that of chimpanzees and gorillas, with the prediction that orangutans would also have more closely packed perikymata than gorillas.

Goodman and Armelagos (1985) suggested that enamel thickness might be a relevant variable in LEH occurrence. These authors argued that ameloblasts with high enamel secretion rates may be more vulnerable to disruption than ameloblasts with less taxing enamel production schedules. We do not have the relevant data to evaluate this possibility, as it requires specific information about enamel secretion rates in orangutans, gorillas, and chimpanzees. However, Guatelli-Steinberg (2001) noted that the general pattern of minimal LEH presence in prosimians, low LEH frequencies in monkeys, and relatively high LEH frequencies in great apes cannot be explained simply by differences in their enamel thickness, because there is considerable taxonomic overlap in primate enamel thickness. For example, Shellis et al. (1998) showed that *Daubentonia*, *Cebus apella*, *Theropithecus*, and *Homo* all have similar enamel thickness relative to body weight.

Considering potential environmental variables influencing LEH, it is interesting that the differences in frequency exhibited among the genera in this study are consistent with differences in great ape dietary strategy found in the literature. Both chimpanzees and orangutans are highly frugivorous (Galdikas, 1988), and are indeed large-bodied fruit specialists (Martin, 1990; Tutin et al., 1997). Although fruit is a “high-quality” food (high in simple carbohydrates), it is also very patchy in space and time and thus relatively scarce (Martin, 1990). Knott (1998) showed in Bornean orangutans, that fluctuations in fruit availability are associated with physiological stress, evident in the metabolism of fat stores. No such data are available in the published literature for Sumatran orangutans or for chimpanzees. However, immature chimpanzees from Gabon show a lack of weight gain from February to June during seasonal low fruit productivity (Hladik, 1981). Wrangham et al. (1998) found that chimpanzees in Kibale National Forest, Uganda, experience

seasonality in the availability of ripe fruit, relying on piths as their “fallback” food during ripe-fruit scarcity.

Gorillas, in contrast to chimpanzees and orangutans, have gut adaptations that enable them to more easily digest leaves and extract their nutritive content (Chivers and Hladik, 1980; Milton, 1984). Leaves are a “low-quality” food (high in complex carbohydrates and fiber that require an energy investment to digest) but are relatively abundant (Martin, 1990). Remis (1997b) stated that western lowland gorillas prefer fruit, have considerable dietary overlap with chimpanzees, and only fall back on leaves when fruit availability is low. Chimpanzees, however, continue to specialize in fruit consumption, even when fruit is scarce (Remis, 1997b). Comparing her data from Bai Hokou, Central African Republic, with data from other studies, Remis (1997a) showed that across sites, western lowland gorilla diets are 26.6–63.0% fruit, while eastern lowland gorilla diets are 0.0–25.0% fruit and mountain gorilla diets are 0.3–10.0% fruit. Owing to their ability to digest leaves, gorillas may be more “buffered” against seasonality in fruit availability and thus less nutritionally stressed than chimpanzees and orangutans.

In sum, the LEH prevalence differences among the chimpanzee, gorilla, and orangutan samples in this study may result from intrinsic differences in enamel, differences in stress experience, or a combination of both. The LEH prevalence differences cannot be explained by generic differences in imbricational enamel formation times, as discussed above, because these imply a generic pattern of LEH frequencies contrary to that found in this study. In addition, perikymata are not more prominent in one genus relative to another, such that this potential factor can be discarded. On the other hand, it was noted (based on Dean and Reid, 2001) that in comparable regions of the crown, perikymata in anterior teeth are more closely packed in chimpanzees than they are in gorillas. This may mean that defects are easier to identify on chimpanzee teeth than on gorilla teeth. As mentioned, if this explanation is correct, then orangutan teeth, which are also highly affected by LEH, would be expected to have a density of perikymata packing similar to that of chimpanzees. Finally, broad dietary differences among chimpanzees, orangutans, and gorillas, especially with respect to the seasonality of food resources, are consistent with the LEH differences among genera found in this study. Clearly, however, further assessment of the “dietary hypothesis” requires discussion of the LEH subspecies data, as addressed below.

Association of LEH with subspecies and with locality

This study demonstrates significant LEH frequency differences among great ape subspecies and locality. Thus, as with LEH frequency differences

found among genera, the differences among subspecies and localities indicate that all great apes are not equally affected by LEH because of any apparent intrinsic difference in the enamel (i.e., quality, crown formation times, or perikymata spacing) of great apes relative to other primates.

One of the most notable aspects of this study is the low prevalence of LEH among mountain gorillas relative to western lowland gorillas, in the analyses by individual and by teeth. As with generic LEH frequency differences, the duration of imbricational enamel formation and the spacing of perikymata should be considered as relevant explanatory factors. However, to the authors’ knowledge, published data comparing imbricational enamel formation and the spacing of perikymata in mountain vs. lowland gorillas do not yet exist. While the dietary flexibility of western lowland gorillas relative to chimpanzees may explain, in part, the lower LEH frequency in western lowland gorillas compared to chimpanzees, it is not clear that this flexibility explains why western lowland gorillas have a higher frequency of LEH than mountain gorillas in this study. Both subspecies can rely on leaves, which are more abundant and predictable than fruit. It is possible that exposure to pathogens in lowland vs. highland habitats, or proximity to human populations (increase in disease and other encroachment stresses), plays a role in the differential prevalence of LEH between gorilla subspecies in this sample, and these factors should be further explored. Whatever the cause(s), LEH prevalence is extremely low in this sample of mountain gorillas relative to the samples of western lowland gorillas, chimpanzees, and orangutans. Thus, the generalization that great apes have higher rates of enamel hypoplasia than other primates is somewhat misleading. Mountain gorillas, at least in this study, do not share this high prevalence.

Given the low prevalence of LEH in mountain gorillas and the lower prevalence of LEH in western lowland gorillas relative to chimpanzees and orangutans, it is interesting to note that Tsukamoto (2001) reported an LEH prevalence of 98.8% in a sample of bonobos. Her sample derived from the Royal Museum for Central Africa in Tervuren, Belgium. She included only linear defects in her LEH prevalence figure for this sample, used a 5–20× pocket hand lens to identify defects, and rated defects on a scale from mild to severe.

Like chimpanzees, bonobos include terrestrial herbaceous vegetation (THV) in their diet, but most studies of seasonality in bonobo diets (Badrian and Malenky, 1984; Kano and Mulavwa, 1984; Malenky and Stiles, 1991; White, 1998) and one study on nearest-neighbor distances (White and Chapman, 1994) suggest that bonobos are generally under less dietary stress and feeding competition than common chimpanzees. In a study linking the presence of female sociality in bonobos with reduced feeding competition relative to chimpanzees, White (1998) found that at the Lomako study site, while there was some

seasonality in rainfall and fruit availability, seasonality was not as distinct as that found at other *Pan* study sites and did not result in seasonal changes in food-type consumption or in the use of THV or figs specifically as fallback foods. In an earlier study, Badrian and Malenky (1984) also found no noticeable seasonality of foods eaten by bonobos at Lomako. According to Kano and Mulavwa (1984) and Malenky and Stiles (1991), bonobos at the respective sites of Wamba and Lomako consume THV throughout the year, regardless of fruit availability. Malenky and Stiles (1991) further reported that at Lomako, fruit does not become markedly scarce at any time of the year. White and Chapman (1994), in a study comparing nearest-neighbor distances among chimpanzees at Kibale and among bonobos at Lomako, argued that chimpanzees maintain greater distances from their nearest neighbor, especially between same-sex individuals during feeding activities, and that bonobos are more tolerant of shorter nearest-neighbor distances, preferring slightly greater distances (but still smaller than with chimpanzees) between same-sex individuals during feeding as opposed to other activities. According to the “dietary hypothesis” and in light of the above-cited comparative studies of *Pan* feeding ecology, bonobos should clearly be buffered against fluctuations in fruit availability. If the results of Tsukamoto (2001) are directly compared to those in this study, they suggest that dietary differences are not a distinctly important cause of LEH in great apes. Without the inclusion of other great ape taxa in the study by Tsukamoto (2001), however, it is problematic to make such direct comparisons, given the high interobserver error rates for LEH.

The higher prevalence of LEH in specimens from Gabon vs. Cameroon seem to be the result of differences in the experience of stress for great apes from these two different areas. Chimpanzees and gorillas from each location were pooled for this particular analysis (Table 7), and the sample sizes of the two ape genera in Cameroon (chimpanzees, $n = 8$; western lowland gorillas, $n = 9$) and Gabon (chimpanzees, $n = 13$; western lowland gorillas, $n = 11$) are about equal. It is therefore extremely unlikely that patterns of perikymata spacing or crown formation systematically vary between the two locations such that LEH frequencies in both chimpanzees and gorillas are affected in the same way. We did not find any published literature discussing differences in food availability or pathogens that could explain the difference in LEH prevalence between these two localities.

In orangutans, there is no difference between subspecies or between localities in the number of orangutan individuals affected. However, there are significant differences in the number of teeth affected by LEH. For orangutans in this sample, the by-teeth analysis is likely a better indicator of the degree of physiological stress in the larger population than the number of individuals affected by LEH because,

as discussed in Results, the frequencies for Bornean orangutan individuals may very well be artificially depressed by disproportionately fewer observable anterior teeth. Although there is no difference in LEH frequency between orangutans from western and southwestern Borneo, a larger sample size could provide evidence to the contrary. The same analysis by teeth was significant, with a higher frequency of LEH-affected teeth in orangutans from southwestern Borneo, and again this is likely a result of the disproportionately fewer anterior teeth in the sample of Bornean orangutan individuals.

CONCLUSIONS

This study investigates how LEH prevalence varies within the great apes. In the sample of gorillas examined here (composed of both mountain and lowland gorillas), the prevalence of LEH is low relative to that of chimpanzee and orangutan samples. This result is consistent with recent findings from similar studies. Additionally, this study examined LEH variation among subspecies of great apes, finding an extremely low prevalence in the mountain gorilla sample, whether that prevalence was calculated by individual or by teeth. Thus, the conclusion of most previous studies, that great apes have highly elevated LEH frequencies relative to monkeys, is shown not to be the case with respect to mountain gorillas. Lastly, this study found that a combined sample of gorillas and chimpanzees from Gabon had a statistically significantly higher LEH prevalence than a combined sample of gorillas and chimpanzees from Cameroon, demonstrating that, within the great apes, LEH prevalence also varies by location.

The authors considered several different possible causes for the observed patterns in the distribution of LEH prevalence within the great apes. Of the possible causes for the low prevalence of LEH in gorillas relative to chimpanzees and gorillas, the most plausible are related to diet and to the spacing of perikymata on tooth crowns. Gorillas are able to subsist on more folivorous diets than chimpanzees and orangutans, who are large-bodied frugivores and subject to fluctuation of ripe fruit availability in space and time. In addition, gorilla teeth have slightly more widely spaced perikymata, which may mean that given the same amount of stress, LEH defects on gorilla teeth will be less pronounced and therefore more difficult to detect than those on the teeth of chimpanzees. It is not yet clear (because of a lack of data bearing on this point) what the perikymata spacing of orangutans is relative to that of chimpanzees and gorillas.

The results of this study provide greater detail regarding the distribution of LEH within the great apes. It is no longer possible to argue that all great apes have high frequencies of LEH; nor is it possible to argue that they are all equally susceptible to exhibiting LEH owing to common features of their enamel, such as poor quality or long crown formation times. Thus, great apes show considerable vari-

ability in LEH prevalence, and at least part of that variability, particularly with respect to great apes living in different regions, may be related to differences among comparison groups in their experience of physiological stress.

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