

Linear Enamel Hypoplasia in Gibbons (*Hylobates lar carpenteri*)

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ABSTRACT This study describes the expression of linear enamel hypoplasia (LEH), a sensitive dental indicator of physiological stress, in Thailand gibbons (*Hylobates lar carpenteri*). Previous studies of enamel hypoplasia in hominoids have focused on great apes, with little attention given to the expression of this stress indicator in gibbons. In that gibbons differ from both monkeys and great apes in numerous life history features, LEH expression in gibbons might be expected to show significant differences from both. In this study, 92 gibbon specimens from two sites in Thailand were compared with several samples of monkeys and great apes in their expression of LEH. The intertooth distribution of LEH in gibbons was compared to that of chimpanzees and rhesus monkeys. Gibbon populations from both sites exhibit LEH frequencies intermediate between those of the monkey samples, in which LEH prevalence is usually low, and those of the great ape samples, in which LEH prevalence is high. Gibbons differ significantly from monkeys, but not great apes, in the number of individuals whose teeth record multiple stress events. Multiple episodes of stress are rarely recorded in the teeth of monkeys, while multiple stress events occur with higher frequency in gibbons and great apes. Taxonomic variation in the duration of crown formation, the prominence and spacing of perikymata on dental crowns, life history features, and/or experience of physiological stress may explain these patterns. The intertooth distribution of LEH in gibbons is, for different reasons, unlike that of either chimpanzees or rhesus monkeys. The mandibular canines of gibbons have significantly more LEH than any of their other teeth. Aspects of crown morphology, perikymata prominence/spacing, enamel thickness, and crown formation spans are potential causes of taxonomic variation in the intertooth distribution of LEH. *Am J Phys Anthropol* 112:395–410, 2000.

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Dental enamel hypoplasias have been defined as “deficiencies in enamel thickness resulting from physiological perturbations (stress) during the secretory phase of amelogenesis [the process of enamel formation]” (Goodman and Rose, 1990, p. 59). Enamel hypoplasias are manifested in a variety of ways. The defect may be a single sharp horizontal line in the crown surface, a single groove or furrow, and in some cases, “a large area of the crown surface is ridged across

with a washboard effect” (Hillson, 1986, p. 126). Some defects take the form of pits in the enamel surface (Hillson and Bond, 1997). Plane form defects (Hillson and

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Bond, 1997) are those in which large areas of enamel are missing and include localized hypoplasia of the primary canine (Skinner, 1986a) and interproximal contact hypoplasia (Lukacs, 1999a). Rare vertical enamel hypoplasias have been noted as well (Eckhardt et al., 1992).

Linear enamel defects are sensitive and nonspecific stress indicators that provide a permanent and retrospective record of systemic stresses (such as nutritional deficiency or febrile disease) encountered during crown development (Goodman and Rose, 1990). Corruccini et al. (1985) classify linear enamel defects into two groups: thin striations known as linear enamel hypoplasia (LEH), and deeper depressions known as major growth arrest lines (MGA). Goodman and Rose (1990) use the term linear enamel hypoplasia (LEH) to include both the faint and more pronounced linear defects. This latter, broader definition is adopted here.

While used extensively as a stress indicator in humans, LEH has only recently begun to receive attention in nonhuman primate studies. Colyer (1936) published initial findings on nonhuman primate enamel hypoplasia; however, extensive research on this topic did not begin until the mid 1980s (Eckhardt, 1992; Eckhardt et al., 1992; Eckhardt and Protsch von Zieten, 1993; Guatelli-Steinberg and Lukacs, 1998; Guatelli-Steinberg and Skinner, 2000; Lukacs, 1999b; Miles and Grigson, 1990; Moggi-Cecchi and Crovella, 1991, 1992; Newell, 1998; Skinner, 1986b; Skinner et al., 1995; Skinner and Guatelli-Steinberg, 1997; Stottlemire, 1998; Vitzthum and Wikander, 1988; Zhang, 1987).

The taxonomic distribution of enamel hypoplasia appears to be dichotomous. Monkeys generally exhibit little or no enamel hypoplasia (including LEH) (Colyer, 1936; Miles and Grigson, 1990; Moggi-Cecchi and Crovella, 1991; Vitzthum and Wikander, 1988) in contrast to great apes, who exhibit LEH frequencies on the order of 25–100% of individuals affected (Guatelli-Steinberg and Skinner, 2000; Moggi-Cecchi and Crovella, 1992; Skinner, 1986b; Skinner et al., 1995; Skinner and Guatelli-Steinberg, 1997; Stottlemire, 1998; Vitzthum and Wikander, 1988). Some monkey samples occasionally

exhibit high LEH frequencies (e.g., 54% in red colobus from Cameroon, $n = 24$: Guatelli-Steinberg and Skinner, 2000; Skinner and Guatelli-Steinberg, 1997). There is an apparent taxonomic influence on LEH prevalence rates potentially related to a combination of factors that include: species differences in enamel development and tooth morphology, life history features, and/or experience of physiological stress.

Monkeys and great apes also differ in the incidence of multiple defects on their tooth crowns. Great apes may have multiple defects on a tooth (particularly on the mandibular canine), whereas monkeys usually do not (Skinner et al., 1995). Skinner et al. (1995) attribute this difference in part to the prolonged period of great ape dental crown formation, which may span episodes of seasonal stress over several years.

The position of gibbons within this apparent LEH dichotomy has not been firmly established. The expression of LEH in gibbons is of interest because gibbons occupy an intermediate position to cercopithecoids and great apes in several life history features. Summarizing several studies, Dirks (1998) notes that gibbons have longer periods of gestation, later weaning ages, and later ages of first reproduction than catarrhines of similar body mass. M3 eruption in gibbons is intermediate between that of macaques and chimpanzees (Smith, 1991, after Schultz, 1960). Variation in LEH prevalence in nonhuman primate populations is potentially influenced by factors associated with life history features, including the duration of dental crown formation and exposure and susceptibility to sources of environmental stress during infancy and juvenile periods. In that life history variables might impact exposure and susceptibility to stress and/or the opportunity to record stress in developing teeth, gibbons would be expected to differ from both monkeys and great apes in their LEH expression.

Colyer (1936) and Vitzthum and Wikander (1988) find that gibbons, like monkeys, have low frequencies of enamel hypoplasia (defined to include pitting, linear defects, and irregular enamel). Colyer (1936) reports a frequency of enamel hyp-

oplasia in gibbons of 4% ($n = 623$), which is more similar to the frequencies he obtained for *Papio* and *Cebus* (2% for each) than for great apes (*Gorilla*, 8%; *Pan*, 12%; *Pongo*, 17%). Vitzum and Wikander (1988, p. 284) state that "gibbon and ceboidea samples resemble cercopithecoids in frequency and severity [of enamel deformation]." Since these two studies combine different types of enamel hypoplasia in their reported frequencies, they do not indicate how gibbons compare to monkeys and great apes in the specific incidence of LEH. In addition, neither study reports on the incidence of multiple LEH defects. Recently, however, Newell (1998) (as elaborated upon below; see Discussion) reported frequencies of LEH in gibbons ranging from 19.4% in *Hylobates lar* ($N = 31$) to 79.2% in *Hylobates hoolock* ($N = 24$).

Studies of intertooth patterns in monkeys and great apes suggest that mandibular canines and maxillary incisors are the most commonly affected teeth (Moggi-Cecchi and Crovella, 1991; Skinner, 1986b). However, other teeth may also be highly affected. Moggi-Cecchi and Crovella (1991) reported that in their cercopithecoid and ceboid samples, the first tooth in the lower premolar field (P3 in cercopithecoids, P2 in ceboids) is often affected by LEH. Guatelli-Steinberg and Lukacs (1998) demonstrated that the lower P3 is preferentially affected by LEH in a large sample of rhesus monkeys.

In this study, gibbons are compared to monkeys and great apes in their LEH expression for the purpose of clarifying the distribution of LEH across anthropoid taxa. Using this comparative method, potential influences on taxonomic patterns in LEH expression can be evaluated. This study compares a large sample of wild-shot gibbons from Thailand ($n = 92$) to several great ape and monkey samples (see below) in terms of LEH prevalence, the number of individuals with multiple defects, and the intertooth distribution of LEH. Monkey and great ape samples are compared within this study because comparison across studies is complicated by interobserver differences in the scoring of LEH. While intraobserver agreement in LEH studies is usually high,

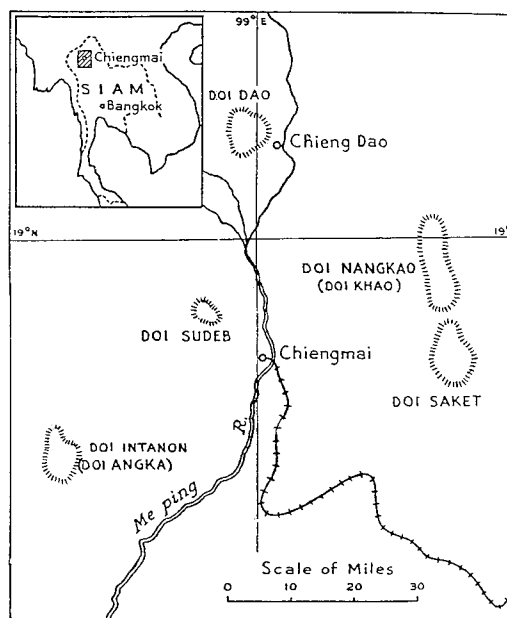


Fig. 1. Gibbon sites of Chieng Dao and Mt. Angka, Thailand. Reprinted from Carpenter (1940) with permission from Johns Hopkins University Press.

interobserver agreement is not (Danforth and Gilberti, 1992).

MATERIALS

The 92 specimens of *Hylobates lar carpenteri* (Groves, 1968) used in this study are housed at the Museum of Comparative Zoology (MCZ) at Harvard University. Specimens were collected from two sites in Thailand: Mt. Angka (35 males, 34 females) and Chieng Dao (10 males, 13 females) during the Asiatic Primate Expedition (APE) of 1937–1938 (Maria Rutzmoser, personal communication). The two sites are roughly 60 miles apart (see Fig. 1, Carpenter, 1940. Reprinted with permission from Johns Hopkins University Press.). Gibbons were collected at various elevations from Mt. Angka (from 1,500–5,700 feet; most from 4,300 feet) and from Chieng Dao (up to 1,500 feet) (Terry McFadden, personal communication).

Monkey and great ape samples used for comparison with the gibbon sample are listed in Table 1. While some of the samples are composites from several locations, all are either feral or free-ranging. A second set

TABLE 1. Monkey and great ape samples used in linear enamel hypoplasia comparisons¹

Species	Collection	Number of specimens	Number by sex: M/F/?	Provenience
<i>Cebus albifrons</i>	MVZ	17	11/4/2	Columbia; Peru
	LACMNH			
<i>Alouatta caraya</i>	UO	12	8/4/0	Argentina
<i>Saimiri sciureus</i>	MVZ	14	13/1/0	Brazil; Columbia; Peru
	LACMNH			
<i>Presbytis cristata</i>	MCZ	23	11/12/0	Borneo
<i>Nasalis larvatus</i>	MCZ	18	8/9/1	Borneo
<i>Macaca fascicularis</i>	UO	70	18/39/3	Borneo; Celebes Island
	MCZ			
<i>Macaca mulatta</i>	CPRC	360	179/181/0	Cayo Santiago
<i>Papio anubis</i>	MVZ	18	10/8/0	Niger Park; Kenya
<i>Pongo pygmaeus</i>	MCZ	14	6/7/1	Borneo; Sumatra
<i>Gorilla gorilla</i>	MCZ	23	12/11/0	Cameroon
<i>Pan troglodytes</i>	LACMNH	26	8/7/11	West Africa; Uganda
	MCZ			

¹ MVZ, Museum of Vertebrate Zoology (at University of California at Berkeley); LACMNH, Los Angeles County Museum of Natural History; UO, University of Oregon (primate collection of the Anthropology Department); MCZ, Museum of Comparative Zoology (at Harvard University); CPRC, Caribbean Primate Research Center Museum (University of Puerto Rico Medical Sciences Campus).

of comparisons involves only specimens derived from single locations so as not to obscure local influences on LEH prevalence. In addition to the collection at the Museum of Comparative Zoology, primate collections at several other institutions were employed in this study: the Caribbean Primate Research Center (University of Puerto Rico), the Museum of Vertebrate Zoology (University of California at Berkeley), the Los Angeles County Museum of Natural History, and the Department of Anthropology at the University of Oregon.

METHODS

LEH was observed following methods outlined by Goodman and Rose (1990) and Lukacs (1989). Teeth were observed under conditions of diffuse lighting, with a second (incandescent) light source oriented obliquely to the specimen. Although the ambient lighting in the museums differed, the second light source and its orientation were consistently maintained. A 10× hand lens aided in the identification of defects. Following Skinner (1986b), the threshold for identifying an LEH defect was set deliberately low so that information about mild physiological stress would not be lost. Berti and Mahaney (1995, p. 313) find that there is

substantial concordance in the intertooth distribution of variously sized defects, implying that all defects, including very small ones, are "variants of the same phenomenon, LEH." Similarly, Hillson and Bond (1997, p. 98) explain that even microscopic furrows are "just as much indicators of disturbance to growth as . . . large defects." As suggested by Skinner et al. (1995), normal perikymata adjacent to the defect were identified and compared to hypoplastic lines to help reduce the chance of falsely identifying LEH. Thus the lower limits of defects observable in this study were lines or grooves that appeared accentuated compared to adjacent perikymata under 10× magnification.

It was sometimes difficult to observe perikymata on the smaller monkey and gibbon teeth. In keeping with Berti and Mahaney (1995) and Hillson and Bond (1997), it would have been useful to have taken molds of the dentition, and then made casts for examination under the scanning electron microscope (SEM) in order to see perikymata and hypoplastic furrows not visible under a magnification of 10×. However, preparing specimens for SEM examination would have restricted sample sizes and thus undermined an assessment of LEH preva-

lence, an important goal of the present study. Thus, the methods of observation adopted here make it possible to assess the taxonomic prevalence of defects within a delimited range of defect sizes: from the least conspicuous, observable under 10 \times magnification, to the more prominent lines or grooves of varying depth and width, clearly visible without magnification, and often marked by tartar pigments.

Teeth were scored as affected by LEH if one or more defects were present. Defect counts on a per tooth basis were also recorded. If one half or more of a tooth was not visible because of wear or breakage, or because the tooth was partially erupted, the tooth was not scored. Sectorial premolars were not scored if one half or more of their honing surfaces were covered by wear striations.

Individuals were scored as "positive" for LEH if matching defects (in approximately similar positions) occurred on any antimeric pair (following Goodman and Rose, 1990). This convention maximizes the possibility that the events precipitating defect formation were systemic physiological disturbances rather than cases of localized trauma to developing tooth germs (Goodman and Rose, 1990). The analyses of Berti and Mahaney (1995) and Hillson and Bond (1997) indicate that matching defects across tooth classes with known crown calcification schedules makes it possible to determine the timing of stress episodes. However, because crown calcification schedules are presently incompletely known for gibbons (Dirks, 1998) and for most monkey species (see Discussion, below), this kind of analysis is not undertaken here.

Individuals were scored as "negative" for LEH if, for the antimeric pairs present, there were no matching defects. If no antimeric pairs were present at all, the specimen was not included in the sample. Specimens were also not included if they were represented by only P4s and/or molars, since these teeth are rarely affected in any taxon. All but three specimens are represented by both maxillary and mandibular dentitions.

The number of matching pairs of defects is defined as the defect count for an antim-

eric pair. The antimeric pair with the highest defect count represents the number of stress events recorded in the teeth of an individual. An individual is considered to have recorded multiple stress events if the maximum defect count over all antimeric pairs is three or more.

To analyze differences among taxa in the incidence of LEH or in the incidence of individuals whose dentitions have recorded multiple stress events, chi-square tests and Fisher's exact tests are performed. Fisher's exact test is used when an expected cell count in a two-by-two table is less than five. To analyze the intertooth distribution of defects, generalized estimating equations (GEEs) are used (a detailed description is given in Guatelli-Steinberg and Lukacs, 1998). The GEE procedure employs a working correlation matrix approximating the average dependence among clustered observations over all subjects (Stokes et al., 1995). By taking the correlation into account, GEEs are sensitive to detecting differences in the LEH expression of different teeth within the same specimen. The GEE procedure provides an odds ratio that specifies the chances of obtaining defects on one tooth vs. another within an individual. SAS version 6.12 is used in all statistical tests.

As part of a larger study (Guatelli-Steinberg, 1998), an intraobserver error test was performed on a subsample of 30 rhesus monkeys. A period of 1 year passed between the two recording sessions. The kappa statistic was used to analyze the results of the intraobserver error test. Kappa reflects the degree of agreement between observations in excess of that expected by chance (Cohen, 1960). A formula for calculating the kappa statistic for dichotomous variables (Fleiss, 1973) was used to determine agreement between the two scoring sessions, and the guidelines of Landis and Koch (1977) for the interpretation of kappa were employed.

Teeth scored as having zero defects vs. teeth scored as having one or more defects were compared between scoring sessions (for 875 teeth). Individuals scored as LEH-positive and LEH-negative ($n = 30$) were also compared between scoring sessions. For both comparisons (at the level of the tooth as well as the level of the individual),

TABLE 2. Linear enamel hypoplasia comparisons between combined gibbon sample and samples listed in Table 1

Species	Number of LEH-positive specimens out of (N)	% of LEH-positive specimens	P-values for comparison with gibbon sample
<i>Hylobates lar</i>	33 (92)	36	—
<i>Cebus albifrons</i>	6 (17)	35	$\chi^2 = 0.002$; $P < 0.964$
<i>Alouatta caraya</i>	0 (12)	0	Fisher's exact; $P < 0.007^*$
<i>Saimiri sciureus</i>	2 (14)	14	Fisher's exact; $P < 0.094$
<i>Presbytis cristata</i>	2 (23)	9	$\chi^2 = 6.417$; $P < 0.006^*$
<i>Nasalis larvatus</i>	2 (18)	11	$\chi^2 = 4.254$; $P < 0.039^*$
<i>Macaca fascicularis</i>	8 (70)	11	$\chi^2 = 12.562$; $P < 0.001^*$
<i>Macaca mulatta</i>	61 (360)	17	$\chi^2 = 15.933$; $P < 0.001^*$
<i>Papio anubis</i>	3 (18)	17	$\chi^2 = 2.521$; $P < 0.112$
<i>Pongo pygmaeus</i>	11 (14)	79	$\chi^2 = 9.126$; $P < 0.003^*$
<i>Gorilla gorilla</i>	9 (23)	39	$\chi^2 = 0.084$; $P < 0.771$
<i>Pan troglodytes</i>	22 (26)	85	$\chi^2 = 19.356$; $P < 0.001^*$

* P-values significant at the 0.05 level.

the kappa values (0.64 and 0.70, respectively) indicate "substantial" intraobserver agreement on the scale of Landis and Koch (1977).

RESULTS

LEH incidence in gibbon, monkey, and great ape samples

Composite samples. In the combined sample of 92 *Hylobates lar* specimens, 33 (or 36%) were LEH-positive. Table 2 compares the frequency of LEH-positive individuals in the combined gibbon samples to the frequencies obtained for monkey and great ape samples. The red colobus data (Guatelli-Steinberg and Skinner, 2000; Skinner and Guatelli-Steinberg, 1997) is not included because it was not collected by the present author. The gibbon sample displays a significantly higher incidence of LEH than 5 of the 8 monkey samples. In comparison to the remaining three monkey samples, gibbons display a higher incidence of LEH, but the difference is nonsignificant. All three of the great ape samples exhibit higher frequencies of LEH than the gibbon samples, but only the *Pongo* and *Pan* samples show significantly higher frequencies.

The frequency of LEH exhibited by the combined gibbon sample therefore overlaps with the highest frequencies obtained for monkeys and the lowest frequencies obtained for great apes. Figure 2 is a histogram of these frequencies.

Comparisons for primates collected from single sites.

The frequency of LEH-positive individuals from the Mt Angka region was 36% (25 out of 69 individuals affected) and 35% from the Chieng Dao region (8 of 23 individuals affected). Table 3 lists the species sampled from single sites which are compared in their LEH frequencies to the gibbons from Chieng Dao (column A) and then the gibbons from Mt. Angka (column B). As in the composite comparison, gibbons from both sites exhibit intermediate frequencies to those obtained for monkey samples and for *Pongo*.

The Chieng Dao gibbon sample has a higher frequency of LEH than do any of the monkey samples; the difference is significant for 4 of the 7 samples. The small sample of *Pongo* specimens from the Kinabatangan River site has a frequency of LEH that is significantly higher than the Chieng Dao gibbon sample.

The Mt. Angka gibbon sample has a significantly higher frequency of LEH than 5 of the 7 monkey samples. The remaining two monkey samples have lower LEH frequencies than does the Mt. Angka gibbon sample, but the difference is nonsignificant.

The frequency of LEH in the Kinabatangan River *Pongo* specimens is significantly higher than that of the Mt. Angka gibbon sample.

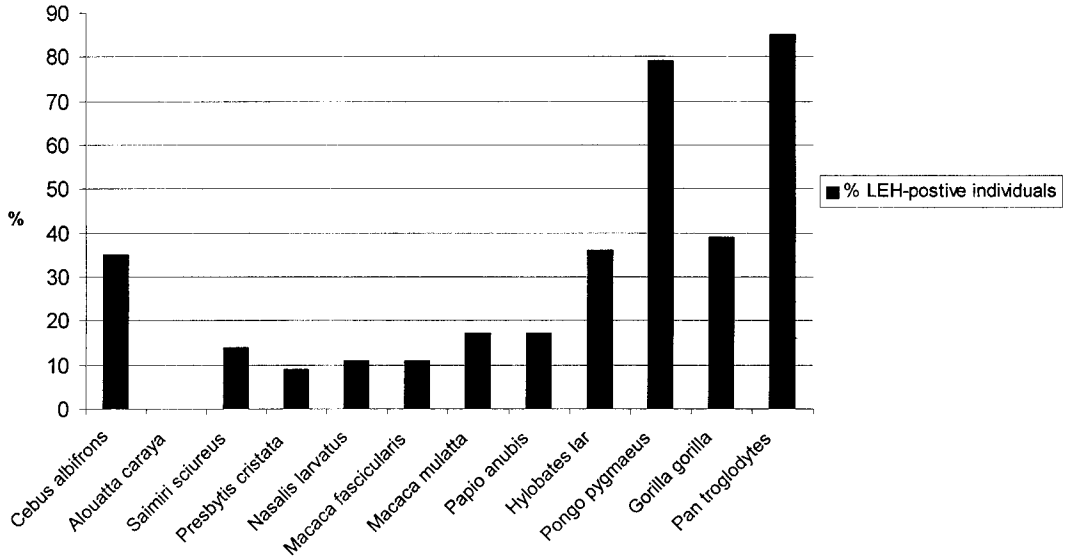


Fig. 2. Histogram of frequencies (given in Table 2) of LEH-positive individuals.

Frequency of individuals recording multiple stress events: gibbons compared to monkeys and great apes

Because the number of individuals recording multiple stress events is low, the combined gibbon sample (n = 92) is compared to the entire monkey sample (n = 532) and the entire great ape sample (n = 63). The data are presented in Table 4.

In 532 monkeys sampled over eight species, both suborders, and numerous locations, only four specimens had three or more defects on a pair of antimeres. The highest number of multiple stress events recorded in the teeth of these four monkeys (one specimen of *Cebus albifrons* and three *Macaca mulatta* specimens) was three. The multiple defects occur on the lower canines of the *Cebus* specimen and on the lower P3s of the *Macaca* specimens.

In the sample of 92 gibbons, nine individuals had three or more defects on a pair of antimeres. Four specimens exhibited four defects on a pair of antimeres; five specimens had three defects on an antimeric pair. The antimeric pair was in each case the right and left lower canines. Some examples of multiple defects on gibbon canines are show in Figure 3.

In the sample of 63 great apes, 11 individuals had three or more defects on a pair of antimeres. The highest number of multiple stress events recorded in the teeth of these great ape specimens was eight (exhibited by one gorilla specimen's lower canines; one orangutan had seven pairs of defects on its lower canines). Seven of the 11 specimens exhibited their highest defect count on their lower canines. The other four specimens had their highest defect counts (counts of 3–5) on their lower first and second incisors, lower P3s, upper canines and lower second incisors, and upper incisors, respectively. Each of these four specimens was missing one or more lower canine teeth, so it is possible that had these teeth been present, these specimens might have displayed higher defect counts. For instance, in one specimen, both the upper canines and lower second incisors have three pairs of defects, while the lower right canine has seven defects and the lower left canine is missing.

Table 4 also gives the results of statistical tests comparing the frequency of individuals displaying multiple stress events for gibbons vs. monkeys and gibbons vs. great apes. Note that gibbons have a significantly higher frequency than monkeys. Gibbons

TABLE 3. Linear enamel hypoplasia comparisons between gibbons and primates collected from single sites

Species	Site location	No. of LEH-positive specimens out of (N)	% LEH-positive specimens	Column A: P-values for comparison with Chieng Dao gibbons	Column B: P-values for comparison with Mt. Angka gibbons
<i>Hylobates lar</i>	Chieng Dao	8 (23)	35	—	—
<i>Hylobates lar</i>	Mt. Angka	25 (69)	36	—	—
<i>Alouatta caraya</i>	Rio Parana Islands	0 (12)	0	Fisher's exact; $P < 0.021^*$	Fisher's exact; $P < 0.007^*$
<i>Presbytis cristata</i>	Kinabatangan River	2 (23)	9	$\chi^2 = 4.600$; $P < 0.032^*$	$\chi^2 = 6.308$; $P < 0.012^*$
<i>Nasalis larvatus</i>	Kinabatangan River	2 (18)	11	Fisher's exact; $P < 0.081$	$\chi^2 = 4.209$; $P < 0.040^*$
<i>Maccaca fascicularis</i>	Kinabatangan River	6 (29)	21	$\chi^2 = 1.295$; $P < 0.255$	$\chi^2 = 2.281$; $P < 0.131$
<i>Maccaca fascicularis</i>	Celebes Island	2 (41)	5	Fisher's exact; $P < 0.003^*$	$\chi^2 = 13.651$; $P < 0.001^*$
<i>Maccaca mulatta</i>	Cayo Santiago	61 (360)	17	Fisher's exact; $P < 0.037^*$	$\chi^2 = 13.439$; $P < 0.001^*$
<i>Papio anubis</i>	Niger Park	2 (15)	13	Fisher's exact; $P < 0.137$	Fisher's exact; $P < 0.074$
<i>Pongo pygmaeus</i>	Kinabatangan River	6 (7)	86	Fisher's exact; $P < 0.025^*$	Fisher's exact; $P < 0.008^*$

* P-values significant at the 0.05 level.

have a lower frequency than great apes, but the difference is not statistically significant. As in the comparisons of overall incidence, gibbons again appear to occupy a position intermediate between monkeys and great apes in their LEH expression.

Intertooth distribution of LEH in gibbons in relation to that of rhesus monkeys and chimpanzees

In gibbons, the lower canine tooth is most often affected by LEH. Table 5 shows, for the combined gibbon sample, the percentage of teeth with LEH for each tooth type in individuals scoring positive for the defect. Figure 4a is a histogram of these frequencies. GEE analysis of presence/absence is conducted on the lower canine, lower incisors, and lower P3 (all other teeth had too few defects to be included in the analysis). Relative to these teeth, the lower canines shows a significantly greater occurrence of LEH. Table 6 gives the results of the GEE analysis.

The chimpanzee and rhesus samples are the only samples with sufficient numbers of LEH-positive individuals (>20) to be used in GEE analyses. Table 7 shows the percentage of teeth affected by LEH in 22 LEH-positive chimpanzees. Figure 4b is a histogram of these frequencies. A GEE analysis (Table 8) compares the incidence of LEH on the lower canine to all teeth except molars (molars had too few defects to be included). The analysis shows that the lower incisors, lower P3, and upper canine do not differ significantly from the lower canine in the presence of LEH. Unlike the gibbon sample, in the chimpanzee sample, when the lower canine is affected by LEH, the lower incisors, lower P3 and upper canine are generally affected as well.

The intertooth distribution of the Cayo Santiago rhesus monkey sample is the subject of a previous paper (Guatelli-Steinberg and Lukacs, 1998), in which a pattern of preferential expression on the lower P3 was established. For comparison, the histogram of LEH presence/absence from this paper is included in Figure 4c.

TABLE 4. Comparison between gibbon and monkey samples and gibbon and great ape samples in the frequency of individuals recording multiple stress events (three or more defects on an antimeric pair)

Taxonomic group sampled	Number of specimens with multiple stress events (N)	% of specimens with multiple stress events	P-values for comparison with gibbon sample
<i>Hylobates lar</i>	9 (92)	10	—
<i>Ceboidea and Cercopithecoidea</i>	4 (532)	1	Fisher's exact; $P < 0.001^*$
<i>Pongidae</i>	11 (63)	18	$\chi^2 = 1.961; P < 0.161$

* P-values significant at the 0.05 level.

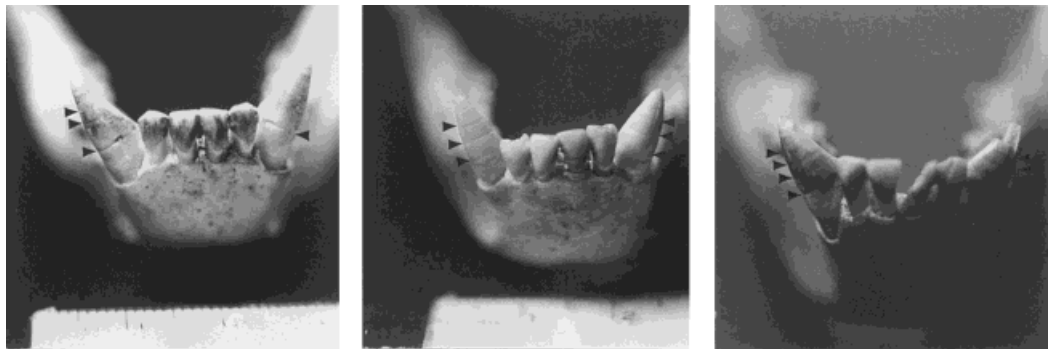


Fig. 3. Gibbons specimens in which the lower canines exhibit three or four matching pairs of defects. Arrowheads indicate LEH grooves. **Left:** Male specimen with three pairs of defects on the lower canines. Two of the three defects on the left lower canine are not visible. **Center:** Female specimen with three pairs of defects on the lower canines. **Right:** Specimen with four pairs of defects on the lower canines (two defects on the lower left canine are not visible).

TABLE 5. Presence of linear enamel hypoplasia (LEH) on the lower canine relative to other teeth: gibbons (33 individuals scoring positive for LEH)

Tooth type	Total teeth in lower jaw sample	Percent of teeth affected in lower jaw	Total teeth in upper jaw sample	Percent of teeth affected in upper jaw
I1	66	9.1	64	3.1
I2	65	7.7	64	0.0
C	62	94.0	56	19.6
P3	56	30.4	66	4.8
P4	64	4.7	66	4.8
M1	65	0.0	64	0.0
M2	65	1.5	64	0.0
M3	56	0.0	55	0.0

DISCUSSION

LEH prevalence and multiple stress events: observed patterns

This study provides evidence that gibbon samples from two neighboring sites in Thailand exhibit LEH frequencies that are intermediate between those of monkey and great ape samples (whether the samples are composite or derived from single sites). The ad-

vantage of comparing the gibbon samples to monkey and great ape samples within the same study is that interobserver differences in LEH scoring can be ruled out as factors contributing to LEH frequency variation across taxa.

Although interobserver differences complicate the comparability of studies, enamel hypoplasia frequencies previously reported

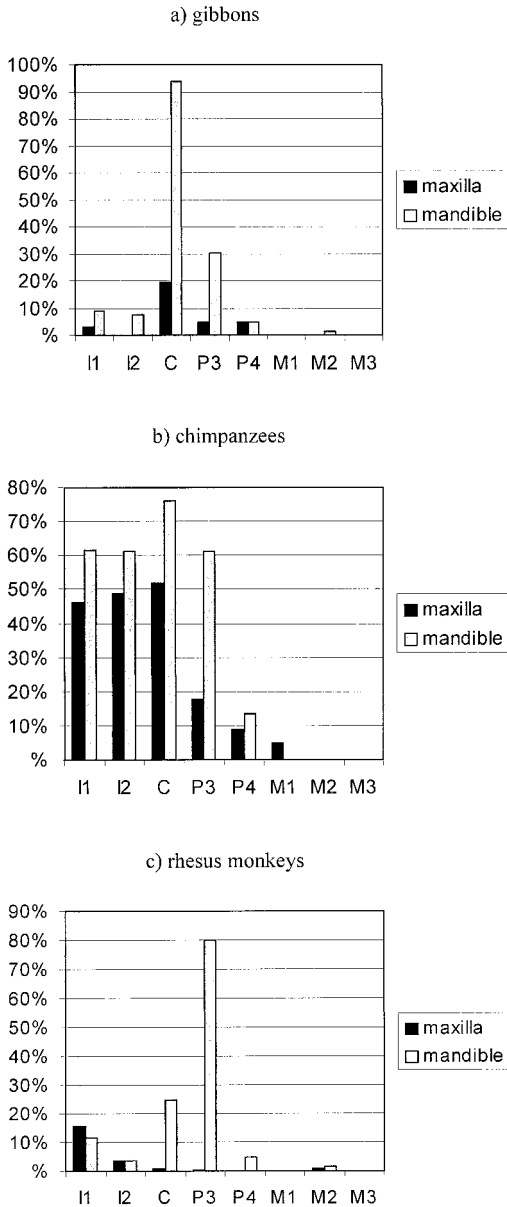


Fig. 4. Intertooth distribution of defects in 33 LEH-positive gibbons (a), 22 LEH-positive chimpanzees (b), and 61 LEH-positive rhesus monkeys (c).

for monkeys (Colyer, 1936; Schuman and Sognnaes, 1956; Swindler and Beynon, 1993; Vitzthum and Wikander, 1988) are lower than the LEH frequencies of both the Chieng Dao (n = 23) and the Mt. Angka gibbons (n = 69). The high frequency of LEH in red colobus from Cameroon is an

exception (Skinner and Guatelli-Steinberg, 1997), as are the relatively high frequencies of LEH reported in some monkey samples of Newell (1998). Most previously reported frequencies of LEH in modern great apes are higher than those of the Chieng Dao and Mt. Angka gibbons. Eckhardt (1992) found an incidence of LEH of 69.7% (on the mandibular canines of 280 individuals) in *Pan troglodytes verus* from Liberia. Skinner (1986b) reports frequencies of 58% for *Pan* (n = 110) and 76% for *Gorilla* (n = 119) from Cameroon. Stottlemire (1998) reports LEH frequencies of 80.6% in *Pan* (n = 98) and 27.5% in *Gorilla* (n = 143) from Cameroon.

Both Colyer (1936) and Vitzthum and Wikander (1988) found low frequencies of enamel hypoplasia (of all types) in gibbons. All enamel hypoplasia frequencies of Colyer (1936) are depressed (even for the great apes), strongly suggesting that his scoring methods differ in some significant way from those of subsequent researchers. The comment by Vitzthum and Wikander (1988) that enamel hypoplasia occurs at a low rate in gibbons that is comparable to that in monkeys is more difficult to understand, since these researchers report high frequencies of enamel hypoplasia in the African apes. Vitzthum and Wikander (1988) also view gibbon enamel hypoplasia as comparable to monkey enamel hypoplasia in severity. However, some of the specimens in this study exhibited pronounced defects (Fig. 3) that subjectively appear more similar to the groove defects of great apes than to the milder linear defects seen in most monkeys.

Unlike Colyer (1936) and Vitzthum and Wikander (1988), Newell (1988) provides a description of her methodology. She considers individuals to be affected by LEH if just one tooth exhibits a defect, and she records mild, shallow linear defects as enamel hypoplasia. In that she records mild expressions of LEH, her methods are closer to those employed in this paper than are the methods of Colyer (1936) and Vitzthum and Wikander (1988). Thus, her range of gibbon LEH prevalence, 19.4% in *Hylobates lar* (N = 31) to 79.2% in *Hylobates hoolock* (N = 24), is more similar to the frequencies given here than to those of Colyer (1936) and Vitzthum and Wikander (1988). However, New-

TABLE 6. Presence of linear enamel hypoplasia (LEH) on the lower canine relative to other teeth in gibbons (33 individuals scoring positive for LEH)

Tooth	Rate at which LEH is more likely to occur on lower canine relative to tooth listed at left	df	Standard error	Chi-square value	P value
Lower I1	145.00	1	0.6712	55.0	0.0001
Lower I2	174.00	1	0.6956	55.00	0.0001
Lower P3	33.27	1	0.5930	34.92	0.0001

TABLE 7. Presence of linear enamel hypoplasia (LEH) on the lower canine relative to other teeth: chimpanzees (22 individuals scoring positive for LEH)

Tooth type	Total teeth in lower jaw sample	Percent of teeth affected in lower jaw	Total teeth in upper jaw sample	Percent of teeth affected in upper jaw
I1	39	61.5	39	46.2
I2	36	61.1	37	48.6
C	25	76.0	27	51.9
P3	36	61.1	34	17.7
P4	37	13.5	34	8.8
M1	42	0.0	41	4.9
M2	42	0.0	38	0.0
M3	29	0.0	27	0.0

TABLE 8. Presence of linear enamel hypoplasia (LEH) on the lower canine relative to other teeth in chimpanzees (22 individuals scoring positive for LEH)

Tooth	Rate at which LEH is more likely to occur on lower canine relative to tooth listed at left	df	Standard error	Chi-square value	P value
Upper I1	3.69	1	0.5679	5.3	0.0214
Upper I2	3.34	1	0.5726	4.5	0.0350
Upper C	2.94	1	0.6063	3.2	0.0753
Upper P3	14.78	1	0.6494	17.2	0.0001
Upper P4	32.72	1	0.7648	20.8	0.0001
Lower I1	1.98	1	0.5724	1.4	0.2330
Lower I2	2.02	1	0.5798	1.5	0.2269
Lower P3	2.02	1	0.5798	1.5	0.2269
Lower P4	20.27	1	0.6712	20.1	0.0001

ell's scoring criteria, by including individuals with just one defect, may have resulted in elevated LEH prevalence data with respect to those reported in this paper.

The present data challenge the earlier studies of Colyer (1936) and Vitzthum and Wikander (1988), who report low enamel hypoplasia frequencies in gibbons. The frequencies given here are more comparable to those by Newell (1998), most likely because of similarities in scoring criteria. It is argued here, however, that scoring as affected only those individuals with bilateral LEH provides a retrospective indication of systematic metabolic disruption. In addition, because of the potential sensitivity of LEH

frequencies to local environmental conditions, the most useful data are those derived from population rather than from composite samples. These data show that samples of gibbons from two nearby sites exhibit LEH frequencies best described as "intermediate" between those of monkeys and great apes. Whether this observation can be generalized to samples from other gibbon populations is a question that needs to be settled by additional research.

In this study, the maximum number of matched defects over all antimeric pairs defines the number of stress events recorded in the teeth of an individual. The data indicate that gibbons are significantly more

likely than monkeys to record multiple stress events. In 9 out of 9 gibbon specimens recording multiple stress events, the antimeric pair with the highest number of paired defects is the lower canine pair. Although the incidence of individuals with multiple defects is lower in the gibbon sample than it is in the great ape samples, the difference is not statistically significant. Most of the great ape specimens also record their highest number of matched defects on their lower canines (with the exception of specimens missing these teeth). Great apes show up to eight paired defects, while gibbons show up to four pairs of defects on their lower canines. As with LEH prevalence, the expression of multiple stress events in gibbons also appears to be intermediate between monkeys and great apes.

LEH prevalence and multiple stress events: potential causes of observed patterns

A combination of aspects of dental development and morphology, life history features, and environmental factors are likely to be involved in the taxonomic patterns observed; however, the relative contribution of these variables is not currently known. These variables, and their expected impact on variation in LEH expression across taxa, are discussed here.

Skinner et al. (1995) also note that monkeys, in contrast to great apes, rarely show multiple defects on their teeth, a difference the authors attribute to the short period of crown formation in monkeys relative to the great apes. Thus, great ape mandibular canines form over several seasons and have a greater opportunity to record seasonal stress.

Unfortunately, data on gibbon lower canine crown formation do not yet exist in the published literature; however, Dirks (personal communication) recently used histological techniques to reconstruct the crown formation time of a single siamang mandibular canine as 3.5 years. Monkey canines may take as little as 0.57 years to form (*Callithrix jacchus*; Johnston et al., 1970). The mandibular canines of *Macaca nemestrina* males form in 3.1 years (Siriani and Swindler, 1985), and those of *Theropithecus*

gelada in 5.2 years (Swindler and Beynon, 1993). Aside from these, other monkey species' canine crown formation times have not been published. Great apes appear to have extended mandibular canine crown formation times relative to gibbons and monkeys: 5.65 years in chimpanzees (average for male and female; Kuykendall, 1996), 8.6 years in a single orangutan specimen (Beynon et al., 1991), and greater than 5.2 years in a single gorilla specimen whose crown had not completed formation at the time it was examined (Beynon et al., 1991). Because data on canine crown formation times from a wide variety of species do not yet exist, it is not currently possible to determine if crown formation spans are exerting a strong influence on the distribution of LEH across primate taxa.

At present, the data suggest an influence of crown formation time on the number of multiple stress events recorded: in gibbons, whose mandibular canines appear to have shorter crown formation spans than those of great apes, fewer episodes of stress are recorded (4 at most as opposed to 8 at most in great apes). However, it seems likely (based on crown formation times in *T. gelada* and *M. nemestrina*) that some of the monkey species examined in this study might have mandibular canine crown formation times comparable to those of gibbons, yet these monkey species rarely exhibit multiple defects. Thus, factors other than crown formation span alone must be influencing differences in LEH expression across taxa.

Other intrinsic tooth attributes, such as the morphology of the canine tooth and the prominence and spacing of perikymata, may be affecting the taxonomic distribution of LEH. Moggi-Cecchi and Crovella (1991) suggest that crown height differences between great apes and monkeys may be related to their difference in LEH incidence. Data from this study do not strongly support this interpretation, since the incidence of LEH in *Papio anubis* specimens is low, while mandibular canine crown heights may be higher than those of gibbons and great apes (Guatelli-Steinberg, 1998).

Species differences in the prominence of perikymata and their spacing along the tooth crown may help to explain why LEH is

more easily observed on the teeth of great apes (and gibbons) than it is on monkeys. LEH defects result when a perturbation during development causes a wider band of ameloblasts (than is normal for the formation of perikymata) to switch over to maturation (Hillson, 1986). Thus, if perikymata are more prominent, LEH defects would be expected to be more easily visible. Hillson and Bond (1997) also showed that perikymata spacing on different parts of a tooth crown affects the dimensions of linear defects. Where perikymata are less closely spaced, defects are wider and shallower. Perikymata subjectively appear more visible on the canines of great apes (and gibbons to a lesser extent) and are less closely spaced than they are on monkey canines. This observation may mean that, given the same level of stress, great ape and gibbon LEH defects will be both more easily observed and wider than those of monkeys.

Another possible influence on taxonomic patterns in the distribution of LEH is maturation length. Newell (1998) found that in 20 nonhuman primate species, age at M1 eruption was highly correlated with LEH frequency ($r = 0.87$) and explained 74.3% of the taxonomic variation in LEH. Newell (1998) also found that other variables associated with maturation length, specifically adult brain mass and neonate body mass, are highly correlated with LEH expression across taxa. Newell (1998) explained that protracted periods of maturation provide greater opportunity for episodes of stress to affect the developing dentition. While this explanation is plausible, what remains to be determined is the relationship between the duration of crown formation and LEH expression across species: it is the length of crown formation that directly determines the amount of time available to record episodes of stress. However, variation in maturation length may affect LEH expression in a different manner, also considered by Newell (1998). The longer a primate lives as an infant or immature, the more vulnerable it may be to nutritional stress. Infants may be affected by food shortages as a result of reduced maternal milk production (Richard, 1985). After weaning, juvenile primates may be more susceptible to malnutrition

during periods of food scarcity than are adults (e.g., Dunbar, 1988; Richard, 1985). Enamel formed during infancy and juvenile periods might therefore be especially prone to disruption.

Finally, it is possible that many monkey populations may be more resistant to environmental stress, or are simply exposed to less frequent or severe stress, than are gibbon and great ape populations. The sample of Preuss's red colobus of Skinner and Guatelli-Steinberg (1997) stands out as a departure from this possible explanation. Lee et al. (1988) list the subspecies *Procolobus [badius] pennanti preussi* as endangered. According to Lee et al. (1988, p. 87), because of a dependence on high-canopy trees, Preuss's red colobus is "particularly vulnerable to logging or activity disrupting the canopy."

In this study, the two gibbon samples exhibit nearly equivalent LEH prevalence. Contributing to the similar frequencies is the fact that both samples derive from populations of *Hylobates lar carpenteri*, possessing shared life history features, aspects of dental morphology, and inhabiting similar habitats. Carpenter (1940) provides information on gibbon diet from both locations, based on feeding observations and analysis of stomach contents, collected during the months of March through June 1937. Most of the dietary data were gathered from the Chieng Dao area, where rice field clearings provided better visibility than the dense forests of the slopes of Mt. Angka. However, data gathered from both sites indicate reliance on the same primary food sources during March–June: figs, the fruit of bamboo trees, a blue plum-like fruit (*Polyalthia*), and grapes.

Of the nine gibbon specimens recording multiple stress events, five had defects that appeared to be regularly spaced. Skinner et al. (1995) suggest that such regular repetition in LEH reflects seasonal stress. Seasonal stress in gibbons seems unlikely to be related to food availability. Chivers (1984, p. 215) states that gibbons inhabit "diverse and less seasonal forests where toxic effects can be reduced by frequently changing foods." He adds that the "structurally complex environment buffers the effect of sea-

sonality," allowing gibbons to maintain a year-round intake of ripe fruit. Skinner et al. (1995) suggest that malarial outbreaks following seasonal rains may cause the regularly repeating defects observed in African apes. Malaria might be involved in gibbon LEH, as infection by *Plasmodium youngi* in gibbons is accompanied by fever (Keeling and McClure, 1972). However, there might be seasonal peaks in any number of parasites (including a variety of nematodes, cestodes, and protozoans) known to cause morbidity in gibbons (Keeling and McClure, 1972).

A point of interest in these data is the low frequency of LEH in gorillas relative to the other great ape samples, and the similarity in gorilla LEH prevalence to that of the gibbon samples. Stottlemire (1998) found that gorillas had significantly lower LEH frequencies than chimpanzees: 27.5% (n = 229) vs. 80.6% (n = 98). Likewise, Newell (1998) found that gorillas had relatively lower LEH frequencies than orangutans and chimpanzees: 32.9% (n = 146) compared to 62.5% (n = 48) and 51.9% (n = 79), respectively. (But see Skinner (1986b) for a case in which gorillas from Cameroon have significantly higher LEH prevalence than sympatric chimpanzees.) The distributional pattern of LEH in great apes may be related to dietary differences associated with degrees of frugivory and folivory. However, a simplistic dietary explanation requires a more fine-grained analysis on subpopulations, with special attention to LEH in bonobos, who include more leaves in their diets than common chimpanzees (Kano, 1979). and to lowland gorillas, whose diets are composed of fruit to a large percentage (Rogers et al., 1990).

Intertooth distribution of defects

The gibbon sample exhibits an intertooth distribution of LEH with similarities to, and differences from, both the rhesus and chimpanzee samples. Like the rhesus sample, the gibbon sample exhibits significantly greater expression of LEH on one tooth type; however, this tooth is the mandibular P3 in rhesus and the mandibular canine in gibbons. In both the gibbon and great ape samples, the mandibular canine is the tooth

most likely to be affected by LEH; however, in chimpanzees, LEH on the mandibular canine is accompanied by LEH on other teeth (the lower incisors, lower P3, and upper canine).

The causes of these patterns are not known. In chimpanzees, maxillary canines and mandibular P3s, canines, and incisors have overlapping periods of crown calcification (Anemone et al., 1991). Thus, these teeth may record some of the same stress events. Gibbon lower incisors may show little LEH because these teeth form over a short period of time: 1.43 years for the lower I1, and 1.79 years for the lower I2 (Dirks, 1998). Although Dirks (1998) has data on the crown formation span of a siamang mandibular canine (3.5 years), the amount of temporal overlap in the calcification schedules of gibbon mandibular canines relative to their other teeth is not yet known. Another possible reason that LEH is significantly more frequent on gibbon mandibular canines than on other gibbon teeth is that perikymata appear more prominent on these teeth than they do on others.

The intertooth distribution of the rhesus sample is discussed in Guatelli-Steinberg and Lukacs (1998). The authors argue that factors specific to the sectorial premolars of rhesus monkeys and perhaps other cercopithecines (such as an angled morphology and a thick enamel layer) may explain why LEH is preferentially expressed on this tooth.

CONCLUSIONS

Contrary to early reports of low enamel hypoplasia frequencies in gibbons (Colyer, 1936; Vitzthum and Wikander, 1988), this study demonstrates that the incidence of LEH in a sample of 92 gibbons falls between the LEH frequencies obtained for various monkey and great ape samples. The frequency of gibbon individuals recording multiple stress events is closer to great ape than to monkey frequencies. However, the maximum number of stress events recorded in the teeth of great apes (eight) is higher than that exhibited by gibbons (four). The intertooth distribution of LEH in gibbons is characterized by significantly greater expression on the mandibular canine relative to other

teeth. This intertooth pattern diverges from those of both the rhesus monkey and chimpanzee samples (for different reasons). Further study of LEH in other gibbon samples can help clarify how widespread these patterns are. By studying gibbons from a variety of locations, the range of variation in gibbon LEH expression can be established.

Taxonomic patterns in LEH expression may reflect a combination of factors, including species differences in intrinsic tooth attributes (such as crown formation spans and the prominence and spacing of perikymata), variation in life history features (especially those related to extended periods of infant and juvenile dependency), and differences in the degree of physiological stress experienced across habitats. Assessing the contribution of intrinsic influences on the taxonomic distribution of LEH will require detailed information on species differences in dental development, morphology, and histology. Determining the contribution of environmental factors requires documentation of stresses encountered during the period of dental crown formation in a variety of species from diverse habitats. When the impact of these influences is more clearly understood, researchers will be in a better position to use LEH as a stress indicator in nonhuman primates.

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