ARCHAEOLOGICAL AND ECOLOGICAL IMPLICATIONS OF THE PRIMATE FAUNA FROM PREHISTORIC SITES IN BORNEO

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ABSTRACT

This paper presents a review of the primate faunas from four key prehistoric sites in northern Borneo – Niah, Bau and Gua Sireh in Sarawak, and Madai in Sabah. The primates are of particular interest because they represent a significant component of the modern-day fauna, they provide insights into prehistoric human hunting strategies and dietary preferences, and they offer clues to understanding paleoecological changes in Borneo during the late Quaternary. All of the genera of primates living today on Borneo are known from the archaeological record, with the exception of Nasalis and Tarsius.

A reanalysis of the dental remains of orang-utans from Niah contradict Hooijer's earlier claim that they are larger than those of their modern conspecifics and show a corresponding increase in size with increasing depth in the cave sediments. However, metrical data do indicate that the small sample of isolated teeth from Bau are larger on average than those of modern-day Bornean orang-utans. The remains of orang-utans are relatively common at Niah, implying that the human occupants may have specialized in hunting this primate. The sample of gibbons from Niah is small, but metrical evidence does support Hooijer's tentative conclusion that they are similar in size or slightly larger than extant Hylobates muelleri. The teeth of Macaca fascicularis from Niah and Bau are slightly larger than those of their modern conspecifics, while those from Madai and Gua Sireh are similar in size. This is consistent with models of ecogeographic variation in extant M. fascicularis, as well as with climatic changes in Southeast Asia during the late Quaternary. Differences in the relative frequencies of M. fascicularis and M. nemestrina at Niah and Gua Sireh probably reflect ecological distinctions. Presbytis spp. and Trachypithecus cristatus from Niah have relatively large teeth, while those from Gua Sireh are comparable in size to modern species. The larger dental size of the primates from Niah and Bau, compared with those from Madai and Gua Sireh, is probably a reflection of their greater antiquity.

The aim of this paper is to present a review of the primate faunas from prehistoric sites in Borneo. Primates are of particular interest because (1) they represent a diverse and significant component of the modern-day Bornean fauna, (2) they are generally well-represented at archaeological sites as major food species, and thus provide invaluable insights into prehistoric human hunting strategies and dietary preferences, and (3) they offer important clues to help reconstruct changes in the paleoecology of Borneo during the late Quaternary.

Remains of primates have been recovered from four key archaeological sites – Niah, Bau, and Gua Sireh in Sarawak, and Madai in Sabah (Figure 1). The most important site is Niah, which is located in northern Sarawak, about 75 km southwest of Miri. The site is represented by a complex of cave entrances that penetrate the limestone massif of Gunung Subis. Most of the faunal material has been recovered from the Main or West Mouth, but sizeable collections have also been made from Gan Kira and Lobang Angus. Niah was excavated by Tom Harrisson and his colleagues from 1954 to 1967 and subsequently, in 1977, by a team from the Sarawak Museum under the direction of Zuraina Majid (Harrisson 1957, 1958, 1970; Medway 1977; Zuraina 1982). A series of radiocarbon dates establishes that the archaeological record at Niah dates back to more than 40,000 BP (Harrisson 1958, 1959, 1967, 1975; Brooks et al. 1977).

The Bau material was collected by A.H. Everett in 1878-1879, and it was eventually sent to the Natural History Museum in London, where only part of the collection has
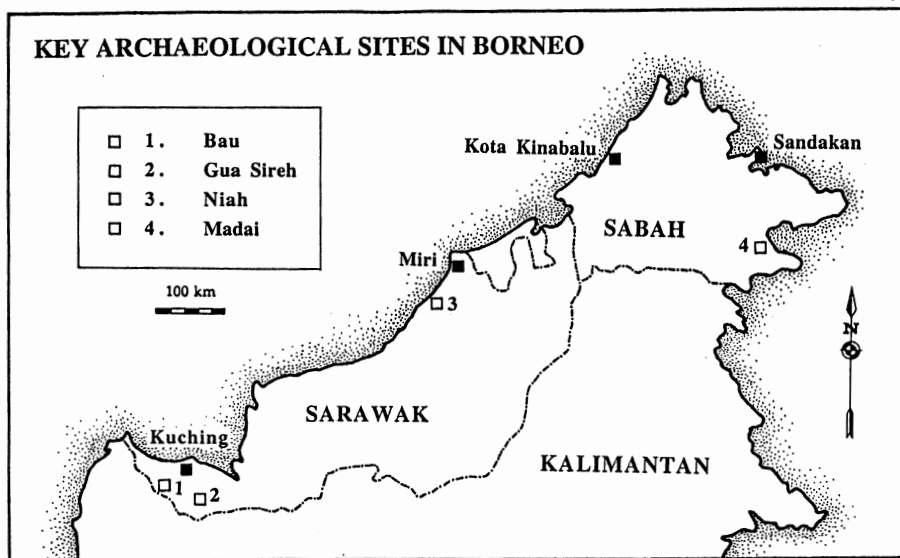
KEY ARCHAEOLOGICAL SITES IN BORNEO

□	1.	Bau
□	2.	Gua Sireh
□	3.	Niah
□	4.	Madai

100 km

Kota Kinabalu   Sandakan

SABAH

Miri

SARAWAK

KALIMANTAN

Kuching

N

Figure 1: Map of northern Borneo showing the location of the key archaeological sites discussed in this paper.

been accessioned (Everett 1880). The material appears to have been recovered from two main sources – from cave sites in Jambusan Hill and from the neigbouring Paku Flats, where they were purchased from local gold prospectors. Jambusan Hill is part of a complex of limestone hills, located just south of the mining town of Bau, about 25 km southwest of Kuching (Wilford 1964). Unfortunately, little information on the geological context of these finds was reported and their age is uncertain. However, based on faunal evidence, the sites would appear to be late Pleistocene to Holocene in age.

The cave site of Gua Sireh is located about 55 km southeast of Kuching in an isolated limestone outcrop, Gunung Nambi, located near the town of Serian in Sarawak. Excavation were first conducted by Harrisson and Solheim in 1959, and more recently by Zuraina Majid in 1977, and Ipoi Datan and Bellwood in 1989 (Ipoi 1993; Bellwood 1997). The site appears to have been occupied sporadically from about 20,000 BP, but most of the archaeological material, including all of the primate fauna, is younger than 6,000 BP (Ipoi 1993). Madai Cave represents a network of tunnels that penetrates the Madai limestone massif, located about 7 km inland from Lahad Datu Bay in eastern Sabah (Bellwood 1988). The primate fauna discussed here was recovered from the site of Agop Atas (MAD 1/28 trench) in 1980 (Bellwood 1988; Harrison 1998). Radiocarbon dates indicate that human occupation occurred intermittently from 10,500-7000 BP, and again shortly after 3000 BP Primate remains, including those of orang-utans, macaques and colobines, have also been reported from Agop Sarapad (MAD 2) (Cranbrook 1988), dated to 10,000-9000 BP (Bellwood 1988), but these have

not yet been analysed in detail and are not included in the present review.

Of the eight genera of primates currently found on Borneo, six of them are represented in the archaeological record (only *Tarsius* and *Nasalis* are not recorded) (Table 1). Each of these primates is discussed below, except for *Nycticebus coucang* – the slow loris, which is known only from a few fragmentary specimens from Niah Cave.

PONGO

The geographic range of the orang-utan (*Pongo pygmaeus*) is today limited to northern Sumatra and to Borneo (von Koenigswald 1982; Röhrer-Ertl 1988; Groves 1989), but evidence from the palaeontological and archaeological record has shown that the species was much more widely distributed throughout southeast Asia during the middle to late Pleistocene and Holocene. Fossil and subfossil orang-utan material has been recovered from a number of sites in southern China, Vietnam, Laos, Cambodia, Thailand, Sumatra, Java and Borneo (Pei 1935; Hooijer 1948a, 1948b; Kahlke 1972; Delson 1977; Aigner 1978; Han and Xu 1985; Gu *et al.* 1987; Olsen and Ciochon 1990; Cuong 1992; Nisbett and Ciochon 1993; Schwartz *et al.* 1994, 1995). On mainland southeast Asia, the remains of orang-utans have been found at sites in southern China that possibly date back to the early Pleistocene, and it appears that the species survived until the latest Pleistocene in cave sites in Vietnam (Nisbett and Ciochon 1993; Schwartz *et al.*

Table 1: List of extant non-human primates on Borneo

Lorisidae	
Nycticebus coucang	Slow loris
Tarsiidae	
Tarsius bancanus	Western tarsier
Cercopithecidae	
Presbytis femoralis	Banded leaf-monkey
Presbytis hosei	Hose's leaf-monkey
Presbytis rubicunda	Maroon leaf-monkey
Presbytis frontata	White-fronted leaf-monkey
Trachypithecus cristatus	Silvered langur
Nasalis larvatus	Proboscis monkey
Macaca fascicularis	Long-tailed macaque
Macaca nemestrina	Pig-tailed macaque
Hylobatidae	
Hylobates muelleri	Bornean gibbon
Hominidae	
Pongo pygmaeus	Orang-utan

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1995). However, the fossil record documenting the early evolutionary history of orang-utans in the islands of southeast Asia is much more scanty, and is restricted to occurrences on Java (the late Pleistocene or early Holocene Punung fissures of Gunung Kidul, and possibly also the Middle Pleistocene of Sangiran and Trinil – but see De Vos and Sondaar 1982 and De Vos 1983, 1984, for an alternative view of the assignment of these latter specimens), Sumatra (early Holocene cave sites of Lida Ajer, Sibrambang and Djamboe in the Padang Highlands) and Borneo (late Pleistocene to Holocene of Niah Cave, Sarawak). This present contribution records further occurrences of sub-fossil orang-utans from Quaternary sites in Sarawak and Sabah, and discusses the material in the context of a reinterpretation of orang-utan zoogeography and systematics.

As a basis for comparison with the subfossil material, I have used Hooijer's (1948a) metrical data on the dentition of extant orang-utans and combined it with my own data (Table 2). Two subspecies of orang-utans are generally distinguished – *Pongo pygmaeus pygmaeus* and *Pongo pygmaeus abelii*, from Borneo and Sumatra respectively (von Koenigswald 1982; Courtenay *et al.* 1988; Groves 1989). Recently, there has been some discussion concerning the possibility of recognizing additional subspecies or even separating the Sumatran and Bornean populations at the species level (Courtenay *et al.* 1988; Groves *et al.* 1992), but the more widely accepted taxonomy is followed here. Individuals from Sumatra, especial males, are on average slightly smaller in overall size than their counterparts from Borneo (Groves *et al* 1992; Smith and Jungers 1997), and although the same tendency can be recognized in the dental measurements of the samples included in this study, the differences are minor and are not statistically significant. As a consequence, the metrical data from Sumatran and Bornean orang-utan populations are combined. The means, ranges and standard deviations for the occlusal areas (mesiodistal length x buccolingual breadth) of each of the permanent teeth are summarized in Table 3, and the distribution of the areas of individual teeth in relation to their deviation from their respective means is presented in Table 4. The use of occlusal areas instead of linear measurements for the dental data serves to facilitate comparisons based on overall size, and the use of ranges of variation based on standard deviation from the mean allows comparisons to be made using data that combines teeth from the entire dental series. The latter technique is extremely useful when one is attempting to make generalizations about overall dental size based on relatively small samples, such as the collections from Borneo.

Between 1888 and 1890 Eugene Dubois made a major collection of subfossil mammals from a number of early

Table 2: Summary of geographical distribution and sex of the extant orang-utan (*Pongo pygmaeus*) sample used in this study

	Borneo	Sumatra	Unknown	Total
Female	23	5	8	36
Male	17	12	9	38
Unknown	5	0	3	8
Total	45	17	20	82

Table 3: Mean, range and standard deviation of occlusal areas (length x breadth) of permanent teeth of extant orang-utan (*Pongo pygmaeus*)[a, b]

	N	Mean	Range	S.D.
I^1	22	161.6	129.3 - 219.6	24.67
I^2	39	74.0	52.5 - 104.5	14.44
C^1	25	256.8	177.1 - 368.4	44.65
C^1	31	136.1	107.1 - 184.0	20.78
P^3	56	130.0	90.2 - 184.2	22.25
P^4	54	122.6	74.5 - 165.6	19.26
M^1	75	160.8	117.7 - 211.6	23.91
M^2	62	170.0	99.4 - 242.7	30.97
M^3	53	151.8	83.9 - 218.4	32.14
I_1	27	88.1	63.9 - 122.0	15.22
I_2	33	91.7	66.4 - 128.0	15.97
C_1	23	205.1	150.7 - 280.9	31.46
C_1	29	111.7	73.8 - 174.3	20.17
P_3	60	148.8	92.3 - 240.7	32.60
P_4	61	131.9	79.5 - 197.5	22.87
M_1	67	155.1	112.9 - 207.7	22.95
M_2	61	173.9	112.4 - 257.3	32.05
M_3	44	168.0	119.7 - 246.0	34.27

[a]Data from Hooijer (1948) and Harrison (unpublished).
[b]Excludes teeth with obvious pathologies and supernumery molars.

Table 4. Occlusal area (length x breadth) of permanent teeth of extant orang-utan (*Pongo pygmaeus*) showing distribution by standard deviation from their respective means (using data from Table 3)

N	-4SD	-3SD	-2SD	-1SD	1SD	2SD	3SD	4SD
822	0	4	136	304	235	113	29	1
%	0	0.5	16.5	37.0	28.6	13.7	3.5	0.1

Holocene cave sites in the Padang Highlands of central Sumatra (Dubois 1891). The collection includes over 3000 specimens of orang-utans, almost entirely consisting of isolated teeth. Just under half of the specimens come from Sibrambang Cave, and about one-third comes from Lida Ajer, while the remainder are from Djamboe and other cave sites in the Padang Highlands. These have been described and analyzed in detail by Hooijer (1948a). On the basis of their larger overall size, greater degree of canine sexual dimorphism, and differences in the relative sizes of the

incisors, premolars and molars, he was able to distinguish the Sumatran collection from extant populations of orang-utans. As a consequence, Hooijer (1948a) recognized a new subspecies, *Pongo pygmaeus palaeosumatrensis*, based on an isolated left M_3 from Sibrambang Cave, and included all of the material from the Padang Highlands. Badoux (1959) and Kahlke (1972) have suggested that the differences between the subfossil samples and extant subspecies are insufficient to justify the recognition of a taxonomic distinction.

A comparison of the data on subfossil orang-utans from Sumatra presented by Hooijer (1948a) with data on extant orang-utans (Table 5), shows that the subfossils are consistently larger than those of the living subspecies. In extant orang-utans 54% of individual teeth fall below their respective mean values, with 0.6% of the sample falling three standard deviations above or below the mean value. Although the range of the subfossil sample overlaps substantially with that of the extant orang-utan sample, only 24.9% falls below the mean values for modern orang-utan teeth, with no teeth falling three standard deviations below the mean, while 4.3% exceed the known upper size range of modern orang-utans (Table 5). The permanent teeth of the subfossil orang-utans from Sumatra are on average 15% larger (by area) than those of the living orang-utan (with every tooth being larger on average than its homologue and the difference between them ranging from 2.6% to 24.6%). It is worth noting that this average difference would

be somewhat greater if the subfossil forms were compared only with modern populations from Sumatra. This size difference in the dentition between the subfossil sample and the living orang-utan is significant, providing further support for Hooijer's contention that the sample from the Padang Highlands represents a separate, slightly larger subspecies of orang-utan.

Making the assumption that *P. p. palaeosumatrensis* belonged to a population that was ancestral to the modern subspecies, Hooijer (1948a) concluded that there had been, along with other changes in the dentition, a general diminution in the size of the teeth of the orang-utan lineage through time. Further support for this proposition comes from isolated teeth of orang-utans from early and middle Pleistocene cave deposits in South China, assigned by Hooijer (1948a) to a distinct subspecies, *P. p. weidenreichi*. These teeth are larger still, being 18.5% larger on average than living orang-utans (using data from Gu *et al.* 1987). Similarly, isolated teeth of orang-utans from Middle to Late Pleistocene sites in Vietnam (i.e., Tham Khuyen, Tham Om, and Lang Trang) are 22.3% larger than their modern counterpart, while those from the terminal Pleistocene cave site of Hang Hum are only 6.0% larger (data from Schwartz *et al.* 1995).[1] As noted by Hooijer (1946a, 1946b, 1947, 1948a, 1949, 1960, 1962a) and Medway (1964), a comparable reduction in size occurs in other mammals (i.e., cercopithecids, siamangs, rhinoceroses, tapirs, forest rats, and porcupines) in Southeast Asia during the Pleistocene,

Table 5: The distribution by occlusal areas (length x breadth) of the permanent teeth of the subfossil orang-utan sample from the Padang Highlands in relation to the mean values and standard deviation intervals of the respective teeth of extant orang-utans as presented in Table 3

	Standard deviation intervals from the mean of extant orang-utans								
	-3	-2	-1	+1	+2	+3	+4	+5	+6
I^1	0	0	1	7	3	4	2	0	0
I^2	0	0	0	16	7	3	1	1	0
C^1	0	1	15	24	21	8	3	2	1
P^3	0	5	39	59	35	16	6	2	2
P^4	0	11	61	79	68	35	7	3	1
M^1	0	11	112	115	64	25	2	0	0
M^2	0	1	34	100	118	55	25	2	1
M^3	0	16	73	85	40	10	3	0	1
I_1	0	0	1	5	2	1	0	0	0
I_2	0	3	16	32	25	15	4	1	0
C_1	0	0	10	13	6	10	2	2	0
P_3	0	11	60	83	48	22	8	1	0
P_4	0	8	50	96	60	37	9	1	0
M_1	0	1	43	64	51	27	4	0	0
M_2	0	0	18	69	71	40	8	2	1
M_3	0	4	69	70	36	15	3	1	1
Total	0	72	592	917	655	323	87	18	8
%	0.0	2.7	22.2	34.3	24.5	12.1	3.3	0.7	0.3

and Hooijer (1950, 1952) has even suggested that this trend may be apparent in prehistoric human populations.

Nevertheless, this recognizable trend in *Pongo* to reduce the size of its dentition over time is evidently not a simple one. For example, the few isolated teeth of fossil orang-utans known from middle Pleistocene sites on Java (i.e., Trinil and Sangiran) are apparently morphologically indistinct and no larger than modern orang-utans, and are smaller than their mainland contemporaries and the later subfossil populations from the Padang Highlands. Hooijer (1952) has suggested that the fossil orang-utans fit well with evidence from other mammalian groups to suggest that the fauna from Java had undergone an accelerated rate of diminution in relation to faunas from neighboring islands. The current evidence would suggest that dental size in orang-utan populations may be of some potential as an aid to biochronological correlation, but that a simple model of diminution through time may not be the most appropriate given the geographical and temporal variation of orang-utan populations during the Pleistocene.

A small, but significant collection of subfossil orang-utan specimens was recovered from the site of Niah Cave in Sarawak by Tom Harrisson during the late 1950s. The collection, consisting primarily of isolated teeth, has been described briefly by Hooijer (1961). In addition, several undescribed specimens from Niah Cave are included in this analysis (see Table 6 for details). Orang-utans are found throughout the sequence at Niah Cave, ranging from the most superficial layers down to a depth of $99''$-$114''$ (Von Koenigswald 1958; Hooijer 1961, 1963), and their remains are common, being second in importance only to the bearded pig, *Sus barbatus* (Medway 1959; Harrisson 1972). From his analysis of the *Pongo* teeth, Hooijer (1961) concluded that the Niah Cave material conforms to the general tendency in southeast Asian Pleistocene mammals to a decrease in size through time. However, I have reanalysed the data and can find no strong justification to support this contention.

The sample from Niah Cave comprises 105 permanent teeth, of which only 65 specimens are complete enough to provide length and breadth measurements. Of these, the majority (n=56; 86.2%) were recovered from the main cave entrance or the West Mouth, while the remainder were recovered from the smaller entrances of Gan Kira (n=4) and Lobang Angus (n=5). A comparison of the size of the teeth

Table 6: A list of previously undescribed orang-utan cranio-dental specimens from Niah cave

Location	Specimen	Measurements[1]
West Mouth X/V1 24″-36″	Almost complete frontal.	
West Mouth L/3 18″-24″	(a) Left parietal fragment.	
	(b) Left parietal fragment.	
	(c) Left mandibular corpus (edentulous).	
West Mouth L/5 36″-42″	Left M_2. Heavily worn.	13.7 x 12.8
West Mouth HO/17 97″-99″	(a) Right upper canine.	
	Root and base of crown only.	20.2 x 15.0
	(b) Right M^2. Slightly worn.	14.0 x 14.0
Lobang Angus US/22 42″-48″	Left I_2. Abraded apex.	8.9(-) x 11.1
Lobang Angus US/21a 36″-42″	Right M_3. Slightly worn.	14.6 x 12.3
Lobang Angus US/17a. 12″-18″	Left M^2 (or M^1). Slightly worn.	14.8 x 12.5
Lobang Angus US/21a 30″-36″	Right maxilla with P^3-M^2 and alveolus of canine. Dentition badly abraded.	
Lobang Angus US/13 0″-6″	Left dP_4.	11.5 x 9.2
Lobang Angus US/17a 30″-36″	(a) Left dP_4.	11.3 x 9.0
	(b) M^1 or M^2.	12.6 x 13.2
	(c) M_1 or M_2.	13.9 x 12.2
Lobang Angus US/13 18″-24″	Right I^1.	15.0 x 11.4
Lobang Angus US/13 12″-18″	Right M_2 (or M_1). Abraded.	12.1(-) x 10.8 (-)

[1]The two measurements correspond to mesiodistal length and buccolingual breadth respectively. Measurements followed by (-) are minimum values.

shows that the entire sample fits well within the range of variation for modern orang-utans (Table 7). There is no indication, contrary to Hooijer's claim, that the orang-utans from Niah Cave are larger in dental size. Furthermore, Hooijer's suggestion that larger teeth are mostly from deeper levels is not supported by a reanalysis of the data (Harrison 1996).

Comparisons of the small sample of isolated teeth of subfossil orang-utans from the limestone caves in the vicinity of Bau have proved quite interesting (Table 8). Although the occlusal areas of the permanent teeth do not exceed the maximum size limits of modern-day orang-utans, they do tend to be relatively large. Of the 13 permanent teeth from Jambusan and Paku Flats, only two fall below the corresponding mean values of modern orang-utans, while five have an occlusal area that is greater than one standard deviation from the mean. The teeth are on average 14.3% larger than those of the corresponding teeth in modern orang-utans. It is difficult to know how to interpret this size difference given the small sample available, but the strongly skewed distribution of the teeth towards the large end of the size range of modern orang-utans may prove to be significant. After all, only 8 of the 65 measurable specimens from Niah (12.3% of the sample) exceed one standard deviation from the mean, compared with 5 of the 13 specimens (38.5%) from Jambusan and Paku Flats. Clearly

Table 7. A comparison of the occlusal areas (length x breadth) of the permanent teeth of the subfossil orang-utans from Niah Cave, Sarawak with those of modern orang-utans[1]

| | | Standard deviation interval from the mean values for extant orang-utans | | | | | | |
	N	-3	-2	-1	+1	+2	+3	+4
Modern	822	4	136	304	235	113	29	1
Pongo	100%	0.5%	16.5%	37.0%	28.6%	13.7%	3.5%	0.1%
Niah Cave	65	0	3	24	30	7	1	0
Pongo	100%	0%	4.6%	36.9%	46.2%	10.8%	1.5%	0%

[1]Data from Hooijer (1948) and Harrison (1996).

more material will need to be collected to confirm these results, but it does indicate that the orang-utans from Bau may have been relatively larger, perhaps more comparable in size to those of *P. p. palaeosumatrensis*.

Orang-utans remains have also been recovered from excavations at Madai Caves (MAD 1/28) (Harrison 1998) and Gua Sireh (Ipoi Datan 1993), but they are relatively much rarer than at Niah. Only 5 specimens have been recovered from MAD 1/28 (a distal metapodial, three phalanges, and a distal calcaneum). From Gua Sireh, a shaft of an isolated proximal phalanx of an orang-utan (O13 6″-12″) was obtained by Tom Harrisson during the course of his excavation at the site in 1959. By comparison with Niah, where orang-utan specimens comprise more than 30% of non-human primate specimens (Harrison 1996), those from MAD 1/28 and Gua Sireh represent only 8.5% and 2.7% respectively (Harrison 1998, unpublished data). It is possible that these important differences reflect major ecological distinctions, perhaps caused by human hunting pressure or disturbance, which affected the distribution and density of local populations of orang-utans (Harrison 1996). However, the abundance of orang-utans at Niah seems extraordinarily high, especially when compared with other mammals at the site, and its relative frequency far exceeds that found in modern-day faunal communities (e.g., *Pongo* represents only 7.9% of the primate fauna at Kutai Nature Reserve; Rodman 1978, Waser 1987).

It is possible, therefore, that the human occupants at Niah were orang-utan specialists. However, closer scrutiny of the data permits a fuller explanation. While cranio-dental specimens of orang-utans are well-represented in the collections from Niah, limb bones are dramatically under-represented (a single proximal femur has been recovered). This is quite different from the preservational pattern seen in cercopithecids, where limb bones are relatively common (Table 9). The distribution of anatomical elements and the nature of their preservation suggest that monkeys were brought back to the site and roasted whole, as is typical of

Table 8: Subfossil orang-utan material from Jambusan and Paku Flats, Bau, Sarawak

Accession Number	Locality	Specimen	Measurements[a]
M.19579	Paku Flats	Right M^3	13.4 x 14.6
		Left M^3	13.6 x 15.6
		Left M^{2b}	12.9 x 15.3
M.20554	Fissure near Jambusan III	Right M^1	11.7 x 13.4
		Right M^3	11.1 x 12.6
		Right I_1	9.5 x 10.7
		Right dC^1	10.9 x 8.5
M.20559	Jambusan XVIII	Left P^4	10.2 x 14.1
M.20562	Jambusan	Right M^{2b}	13.4 x 15.6
		Right M_{1c}	13.4 x 12.5
		Right M_{2c}	15.4 x 13.5
		Right M_{3c}	14.0 x 12.7
		Left M_2	15.4 x 13.3
M.20563	Paku Flats	Right M^3	11.6 x 13.7

[a]The two measurements correspond to mesiodistal length and buccolingual breadth respectively.
[b]These specimens, purportedly from different sites, appear to be antimeres.
[c]These three teeth are almost certainly an associated dental row.

Table 9: Comparisons of the frequency of cranial and postcranial elements of orang-utans and cercopithecid monkeys from Niah Cave

| Element[1] | *Pongo* | | Cercopithecids | |
	N	%	N	%
Cranio-dental	118	77.1	248	46.8
Limbs	1	0.7	147	27.7
Cheiridia	34	22.2	135	25.5
Total	153	100.0	530	100.0

[1]Categories of element defined as follows:
Craniodental - total isolated teeth, mandibular and cranial fragments
Limbs - total entire or fragmentary scapulae, clavicles, humeri, ulnae, radii, pelves, femora, tibiae and fibulae
Cheiridia - total entire or fragmentary tarsals, carpals, metapodials and phalanges

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present-day Bornean hunter-gatherers, such as the Punan (Hose 1929). The rarity of orang-utan limb bones at Niah can best be explained as a consequence of human selectivity, rather than due to preservational factors. The combination of large body size and relatively dispersed distribution of orang-utans (with an average density of 0.7 individuals per km^2; Tilson et al. 1993) makes transportation of entire carcasses a difficult enterprise. The evidence indicates that orang-utans were butchered elsewhere, presumably at the kill-site, and only certain parts were transported back. Given the distribution of anatomical elements at the site (Table 9), it would seem that, in addition to orang-utan meat, hunters returned with heads, hands and feet, possibly as trophies. It is common for orang-utan skulls to be hung on display in longhouses in Borneo today. Similar practices in the past could account for the high frequency of orang-utan specimens represented at Niah, especially given the abundance of isolated teeth which tend to be easily lost from dry skulls.

HYLOBATES

A number of authorities recognize distinct species of gibbons on Borneo, but Groves (1984) has argued that they can all be subsumed into a single species, *Hylobates muelleri*. This latter taxonomic scheme is followed here.

The remains of gibbons are rare at archaeological sites in Borneo. At the West Mouth of Niah, for example, gibbons comprise only 0.5% of the total primate fauna (Harrison 1996). Only five mandibular fragments and one cranial fragment are known, all referable to *H. muelleri*. In addition to the specimens referred to by Medway (1959, 1966) and Hooijer (1962b), one further specimen has been found in the collections: US/27 24"-30" (Lobang Angus), an edentulous left mandibular fragment. Although the sample is small, the evidence does support Hooijer's (1960, 1962b) suggestion that the prehistoric gibbons from Niah are similar in size or slightly larger than extant *H. muelleri* from Borneo. All of the lower cheek teeth from Niah exceed the mean values of corresponding teeth from extant populations, but, with one exception, all fall within the 95% confidence limits. It may be of some significance that this exception, a mandibular fragment with M_2, which is 6.2% larger than the largest specimen from the extant sample, is from a relatively deep level (E/G3 60"-66").

Gibbons are also rare at Gua Sireh and Madai Caves. They are represented only by a lower canine and a calcaneum from Gua Sireh, and by a distal humerus and proximal radius from MAD 1/28. These specimens are identical in size and morphology to those of extant *H. muelleri*.

MACACA

There are presently two species of macaques on Borneo: the long-tailed macaque (*Macaca fascicularis*), which is common and widely distributed throughout lowland areas, while the larger pig-tailed macaque (*Macaca nemestrina*) is somewhat less common and prefers hill forests and adjacent lowlands (Medway 1970; Payne et al. 1985). Both species are recorded at archaeological sites in Borneo. The two species can be readily distinguished on the basis of overall size (*M. fascicularis*, average body mass of males, 5.4 kg and females, 3.6 kg; *M. nemestrina*, average body mass of males, 11.2 kg and females, 6.5 kg [Fooden 1975, 1995]) and dental morphology (relatively broader cheek teeth and a relatively larger M_3, with a more strongly developed hypoconulid in *M. nemestrina*).

At Niah Cave, *M. fascicularis* is much more common (n=118) than *M. nemestrina* (n=11) and is second in abundance only to *Pongo pygmaeus* among the primates (Hooijer 1962b; Harrison 1996). Harrison (1996) has noted, however, that there are marked differences in the composition of the primate faunas at different sites in the Niah Cave complex. For example, *M. fascicularis* comprises 50.9% of the primate fauna at Lobang Angus and only 16.1% at the West Mouth (Harrison 1996). It is possible that the composition of the forest around Lobang Angus, which opens on the eastern side of Gunung Subis, may have been somewhat different from that adjacent to the West Mouth, affording hunters access to different mammalian communities (Harrison 1996).

Previous analyses (Harrison 1996) have shown that the dental remains of long-tailed macaques from Niah are on average 13% larger (based on occlusal area) than their modern conspecifics from Borneo. Moreover, the evidence points to a gradual diminution in size of the dentition through time. A possible explanation is provided by the ecogeographic relationship between climatic conditions during the late Pleistocene and Bergmann's rule (Harrison 1996). Data on modern populations of *M. fascicularis* indicate that there is a clinal increase in size with distance from the Equator that represents an adaptive response to cooler climates (Fooden and Albrecht 1993). The long-tailed macaques from Niah correspond in dental size with those living in Thailand today, where annual temperatures are similar to those inferred for northern Borneo during the last glacial maximum, around 20,000-18,000 B P (i.e., ~5-6 °C lower than today) (Petersen 1969; Fooden 1976; Medway 1977; Harrison 1996).

As noted above, *M. nemestrina* is quite rare at Niah; the remains are ten times less common than those of their smaller congeners. All of the dental specimens fall within the range of modern pig-tailed macaques from Borneo and Sumatra (see also Hooijer 1962b).

The primate fauna from Gua Sireh also includes both species of macaques. Although the sample of cranio-dental specimens is small (n=12), some significance can probably be attached to the fact that five (42%) of the specimens belong to *M. nemestrina*. Relative to Niah, pig-tailed macaques were either more common in the area or at least more extensively hunted by the human occupants of Gua Sireh. Since the two species have quite distinct ecological preferences, with *M. nemestrina* being confined mainly to inland primary forests (Medway 1970), the higher incidence of *M. nemestrina* at Gua Sireh could be of some ecological significance. All of the macaques fall within the ranges of the modern species, with no indication of a size difference. An isolated upper canine of an aged male pig-tailed macaque from Gua Sireh (N/8 12-18″) exhibits a crude perforation through the root (2 mm in diameter), evidently for use as a pendant. Similar artifacts are known from Niah (Harrisson and Medway 1962) and Madai (Harrison 1998).

Only six isolated teeth of cercopithecids are represented in the collections from MAD 1/28, and all are referable to *M. fascicularis*. They are indistinguishable in size from modern long-tailed macaques. The isolated postcranial bones of monkeys from the site have not yet been identified taxonomically, but they are concordant in size either with *M. fascicularis* or *Presbytis* spp.

At least eight isolated teeth from Bau can be identified as belonging to *Macaca*. An upper central incisor, a P_4 and lower molar are referred to *M. fascicularis*. Just as at Niah, the specimens appear to be relatively large, falling in the uppermost extreme of the range for their modern counterparts. *M. nemestrina* is represented at Bau by at least five isolated teeth (two incisors, two canines and an M_3). All fall within the range of the modern species.

COLOBINES

Six species of colobines are recognized today on Borneo – four species of *Presbytis* (*P. femoralis*, *P. frontata*, *P. hosei* and *P. rubicunda*), as well as *Trachypithecus cristatus* and *Nasalis larvatus*. Taxonomic identification of these colobines at the generic level is relatively easy, using a combination of size and morphological criteria, but distinguishing the species of *Presbytis* is much more problematic, especially with fragmentary material. The four species are similar in size (5-7 kg), and are closely comparable in morphology. However, a few minor features of the dentition do serve to distinguish them. For example, the molars of *P. femoralis* differ from those of *P. rubicunda* and *P. hosei* in having smaller and slightly narrower upper and lower molars, less of a size differential between M1 and M2, a relatively smaller last molar, and a more reduced hypoconulid on M_3. In these respects, *P. frontata* is more

like *P. rubicunda* and *P. hosei*, except that the hypoconulid on M_3 tends to be vestigial to absent.

A relatively large sample of cranio-dental remains of *Presbytis* (n=86) has been recovered from Niah Cave. The genus comprises 23.1% of the primate fauna from the site, being only slightly less common than *Macaca*. As discussed above, it is exceedingly difficult to assign these specimens to a particular species. Of the four extant species on Borneo today, all but *P. frontata* occur in the local environs of Niah (Figure 2). *P. rubicunda*, the maroon leaf-monkey, is the most common in the surrounding forests (Medway 1959), but *P. hosei* and *P. femoralis* occur in the general area. Morphologically, the material from Niah is easily distinguished from *P. femoralis* in being larger in size, having broader molars, a more marked size differential between M1 and M2, and a relatively much larger M_3 in which the hypoconulid usually forms a distinct cusp.

P. frontata   P. rubicunda

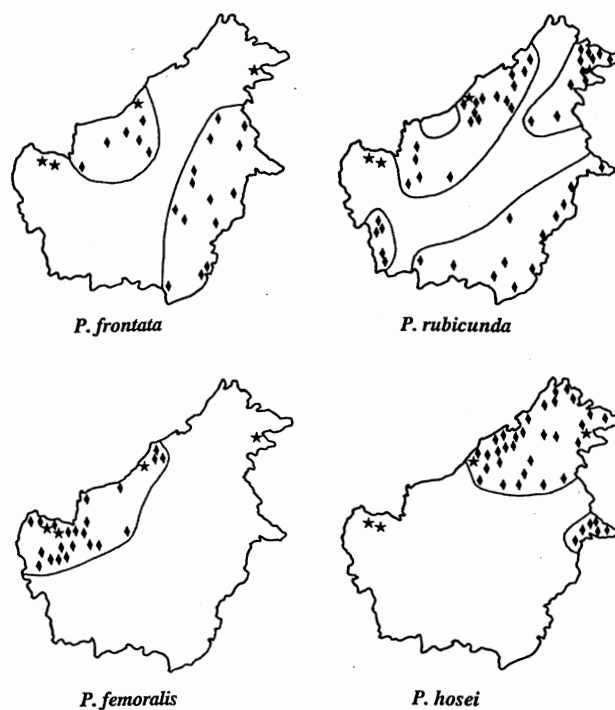P. femoralis   P. hosei

Figure 2. The distribution of Presbytis *spp. in Borneo. The stars represent the location of the archaeological sites of Bau, Gua Sireh, Niah and Madai (see Figure 1 for details). The diamonds represent collecting localities of extant* Presbytis *specimens (data derived from Medway, 1970; Payne* et al.*, 1985; Napier, 1985; Harrison, unpublished museum records).*

Comparisons show that the material is most similar in dental morphology to *P. rubicunda* and *P. hosei*, particularly the former. The current distribution of these two species and the relatively large size of the teeth from Niah would tend to favor their attribution to *P. rubicunda*, although it is likely that the sample contains some specimens belonging to *P. hosei*. Comparisons of dental size (using occlusal area) show that the Niah material is larger on average than all modern-day *Presbytis* species from Borneo (Table 10). The upper and lower cheek teeth are on average 17.3% larger than those of *P. femoralis*, 11.8% larger than *P. hosei*, and 5.6% larger than *P. rubicunda*. A significant proportion of the individual cheek teeth from Niah (11.7%) exceed the range of *P. rubicunda*, which is dentally the largest of the four species of *Presbytis* living on Borneo today. These results provide confirmation of Hooijer's (1962b) preliminary observation that the *Presbytis* material from Niah is somewhat larger in dental size than the modern species. It would seem that *Presbytis*, like *M. fascicularis* (and possibly also *H. muelleri*) has undergone a diminution in size during the late Pleistocene.

Trachypithecus is represented on Borneo by a single species – *Trachypithecus cristatus*.

Trachypithecus specimens are well-represented in the collections from Niah (n=49; 13.3% of the primate fauna), but, as noted by Hooijer (1962b), they are not found uniformly throughout the deposits. *Trachypithecus* is absent from depths greater than 60", whereas 14.0% of *Presbytis* is found at depths from 60 to 108". As suggested by Hooijer (1962b) this could indicate a change in hunting strategies or dietary preferences. However, this period of sedimentation coincides approximately with the Last Glacial

Maximum, a time period when Niah was located about 200 km inland (presently, it is only 17 km from the coast). Since *T. cristatus* prefers riverine forests, peat swamps and mangrove, it is found mainly on the coastal plain of Borneo (Medway 1970; Payne *et al.* 1985; Bennett and Davies 1994; Figure 3). It is likely, therefore, that during the Last Glacial Maximum, the human inhabitants of Niah were beyond the immediate range of *Trachypithecus*, but as sea levels rose again at the end of the Pleistocene it became increasingly possible for hunters to obtain this species in close proximity to Niah.

Trachypithecus is similar in dental size to *Presbytis*, but it can be distinguished in the following features:

1. Greater size differential between M1 and M2 (M_1 is 81% of the area of M_2; M^1 is 84% of the area of M^2 – corresponding values for *Presbytis* are: *P. rubicunda*, 95% and 94%; *P. femoralis*, 96% and 96%; *P. frontata*, 89% and 94%; *P. hosei*, 89% and 90%) ;

2. Relatively larger M_3 (M_3 is 114% of the area of M_2 – corresponding values for *Presbytis* are: *P. rubicunda*, 103%; *P. femoralis*, 93%; *P. frontata*, 100%; *P. hosei*, 110%); and

3. M_3 has a longer talonid, with a well developed hypoconulid.

Comparisons show that the occlusal areas of the cheek teeth of *Trachypithecus* from Niah are considerably larger (on average 14% larger) than those of extant *T. cristatus* from Borneo (Table 11). As for the other primate from Niah, this provides evidence of a significant reduction in the size of the dentition over time in this species (Hooijer 1962a, 1962b). Nevertheless, the material from Niah is distinctly smaller than the fossil *Trachypithecus* material from Tegoean

Table 10: Comparison of occlusal areas (mesiodistal length x buccolingual breadth) of cheek teeth in extant *Presbytis* from Borneo and subfossil *Presbytis* from Niah

	P. femoralis (n = 15)	*P. hosei* (n = 8)	*P. frontata* (n = 4)	*P. rubicunda* (n = 10)	Niah	% Difference from *P. rubicunda*
			Mean areas of cheek teeth			
Upper P3	20.1	19.3	21.0	21.8	23.2	+ 6.4
Upper P4	21.6	20.5	23.1	23.4	25.8	+ 10.3
Upper M1	31.9	32.1	31.3	33.2	35.4	+ 6.6
Upper M2	33.3	35.6	35.3	35.4	37.7	+ 6.5
Upper M3	26.4	32.4	28.9	33.1	35.1	+ 6.0
Lower P3	23.0	24.8	24.8	27.7	27.8	+ 0.4
Lower P4	18.9	17.8	19.9	19.8	21.9	+ 10.6
Lower M1	27.2	27.0	27.1	29.0	29.2	+ 0.7
Lower M2	28.5	30.5	28.9	30.7	31.4	+ 2.3
Lower M3	26.7	33.4	29.0	31.7	33.7	+ 6.3
Mean	25.8	27.3	26.9	28.6	30.1	+ 5.6

Trachypithecus cristatus

Figure 3. The distribution of Trachypithecus cristatus *in Borneo. The stars represent the location of the archaeological sites of Bau, Gua Sireh, Niah and Madai (see Figure 1 for details). The diamonds represent collecting localities of extant* Trachypithecus *specimens (data derived from Payne et al. 1985; Napier, 1985; Harrison, unpublished museum records).*

in Java, which Hooijer (1962a) has attributed to a separate subspecies, *T. cristatus robustus*.

The colobines from Gua Sireh comprise 35% of the primate fauna, and all of them appear to be assignable to a single species of *Presbytis*. Since the teeth fall into the size range of all of the modern Bornean species, and no diagnostic material has yet been recovered, the taxonomic identification of this species is uncertain. However, the only species of leaf-monkey living today in the extreme western portion of Sarawak is *P. femoralis* (Figure 2). The material from Gua Sireh is identical in size and morphology to this species, and there is no reason to exclude it from this particular taxon.

No cranio-dental specimens of colobines are known from MAD 1/ 28, although this is likely to be a consequence of inadequate sampling. Both *P. hosei* and *P. rubicunda* occur in the general area today (Figure 2). There is a sizeable collection of postcranial bones belonging to cercopithecids (n=46) in the size range of *Presbytis* spp. and *M. fascicularis*, some of which might eventually

prove to be assignable to *Presbytis*. Few cranio-dental specimens of colobines are known from Bau, although a number of well-preserved postcranial elements are represented in the collections. The isolated teeth clearly belong to *Presbytis*.

Reference should also be made a left mandibular fragment with P_4-M_2 (BMNH.M1971) of a fossil colobine monkey from Borneo that was presented to the British Museum of Natural History by P.L. Sclater in 1884 (Lydekker 1887; Hooijer 1962b; Napier, 1985). The only available provenience information is that it was recovered from gravels in Sarawak, Borneo. Its heavy mineralization indicates that the specimen was not originally recovered from a cave site, but it could possibly be derived from Paku Flats. Based on its size and morphology the specimen can be attributed to *Presbytis*, but it is not possible to assign it to a particular species.

CONCLUSIONS

This paper presents a review of the primate faunas from key prehistoric sites in Borneo – Niah, Bau and Gua Sireh in Sarawak, and Madai in Sabah. The primates are of particular interest because they represent a significant component of the modern-day fauna, they provide invaluable insights into prehistoric human hunting strategies and dietary preferences, and they offer clues to understanding paleoecological changes during the late Quaternary. All of the genera of primates living today on Borneo are known from the archaeological record, with the exception of *Nasalis* and *Tarsius*.

The main findings of this study can be summarized as follows:

Table 11: Comparison of size of cheek teeth in extant *Trachypithecus* from Borneo and subfossil *Trachypithecus* from Niah and Java.

	Mean areas of cheek teeth			Maximum breadth of cheek teeth		
	Modern (n = 12)	Niah	% Difference	Modern (n = 12)	Niah	Tegoean, Java[1] (*T. c.robustus*)
Upper P3	21.3	24.3	+ 14.1	5.8	5.9	6.7
Upper P4	22.1	26.7	+ 20.8	5.6	6.5	7.2
Upper M1	32.7	34.5	+ 5.5	6.2	6.5	7.1
Upper M2	38.8	43.2	+ 11.3	6.5	7.2	7.6
Upper M3	35.6	42.6	+ 19.7	6.6	7.0	
Lower P3	25.8	32.7	+ 26.7	4.5	4.8	
Lower P4	19.2	23.0	+ 19.8	4.4	4.8	
Lower M1	29.1	31.7	+ 8.9	5.1	5.6	
Lower M2	35.9	39.1	+ 8.9	6.1	6.2	
Lower M3	40.9	42.8	+ 4.6	5.8	5.8	
Mean	30.1	34.1	+ 14.0	5.7	6.0	7.2

[1]Data from Hooijer (1962a)

1. A reanalysis of the dental remains of orang-utans from Niah contradict Hooijer's (1961) claim that they are larger than their modern conspecifics and show a corresponding increase in size with increasing depth in the cave sediments (Harrison 1996). However, metrical data do indicate that the small sample of isolated teeth from Bau are somewhat larger on average than those of modern-day Bornean orang-utans.

2. The remains of orang-utans are relatively more common at Niah than at the other archaeological sites included in this study. This might imply, perhaps, that the human occupants at Niah specialized in hunting orang-utans (a proclivity that may have contributed to the absence of orang-utans in the immediate environs of Niah during recent times – see Harrison 1996 for further details). The frequency of different anatomical elements recovered at Niah indicates that orang-utan carcasses were butchered elsewhere, probably at the kill site, and that heads, hands and feet were preferentially transported back to Niah, possibly as trophies.

3. The remains of gibbons are rare at archaeological sites in Borneo. Although the sample from Niah is small, the evidence does support Hooijer's (1960, 1962b) tentative conclusion that they are similar in size or slightly larger than extant *H. muelleri*.

4. The teeth of long-tailed macaques (*M. fascicularis*) from Niah and Bau are slightly larger than those of their modern conspecifics from Borneo, while those from Madai and Gua Sireh are comparable in size. Reduction of the size of the dentition through time is consistent with models of ecogeographic variation in extant populations of *M. fascicularis*, as well as with climatic change in Southeast Asia during the late Quaternary. It is worthwhile noting that there appears to have been no corresponding change in the size of the dentition of contemporary populations of *M. nemestrina*.

5. Differences in the relative frequencies of *M. fascicularis* and *M. nemestrina* at Niah and Gua Sireh, and also at the different cave entrances at Niah, may reflect ecological distinctions.

6. Material from Niah suggests that *Presbytis* spp. and *T. cristatus*, like *M. fascularis* (and possibly also *H. muelleri*), have undergone a significant reduction in dental size during the late Pleistocene. *Presbytis* specimens from Gua Sireh, by contrast, are comparable in size to their modern congeners.

7. The larger size of the teeth of primates from Niah, in comparison to those from Gua Sireh and Madai, is almost certainly reflective of the greater time span and antiquity of the sedimentary sequence at Niah, which extends back beyond the Last Glacial Maximum into the Late Pleistocene. The primate samples from Gua Sireh and Madai are derived from a more restricted time period in which warmer, more humid post-glacial conditions prevailed, and under which natural selection favored a reduction in overall body mass. It is interesting that the material from Bau, which is of unknown age, has samples of *M. fascicularis* and *P. pygmaeus* that are larger on average than their living counterparts. This suggests that at least a portion of the material antedates the Last Glacial Maximum, and, given the larger size of the orang-utan teeth, that the samples from Bau might be older than those from Niah.

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NOTE

1. Schwartz *et al.* (1995) have proposed that the collections of isolated teeth of fossil hominoids from cave sites in Vietnam represent a diversity of taxa. In addition to *Homo* and *Gigantopithecus*, they recognize *Langsonia liquidens* (from Tham Khuyen), *Pongo hooijeri* (from Tham Khuyen), *P. pygmaeus ciochoni* (from Lang Trang), *P. p. devosi* (from Hang Hum), *Pongo p. kahlkei* (from Tham Khuyen), and *P. p. fromageti* (from Tham Om). The view that multiple hominoid taxa are represented at these sites has recently received additional support from Walters *et al.* (1998). Unfortunately, I have not had the opportunity to study the collections in Vietnam, but my preliminary assessment of the published evidence makes me skeptical of the validity of this taxonomic scheme. The remarkable degree of dental variability seen in extant orang-utans, the problems of correctly identifying the serial position of isolated teeth (made especially difficult by the occurrence of appreciable numbers of orang-utans with supernumerary molars; 7.0% with M^4 and 4.3% with M_4, according to Hooijer 1948a), and the overall greater size range of extinct orang-utans, may all contribute to creating an impression

of taxonomic diversity among the fossil collections. Taking these factors into account, and making comparisons of the published photographs of the type specimens and referred material, it seems most likely to me that all of the material assigned by Schwartz *et al.* (1995) to *Langsonia and Pongo* can be accommodated in *P. pygmaeus*. I would tentatively assign the relative large Middle and Late Pleistocene material (from Tham Khuyen, Keo Leng, Lang Trang, and Tham Om) to *P. p. weidenreichi*, while the material from Hang Hum, which is comparable in overall dental size to modern orang-utans, should be classified as *Pongo pygmaeus* subsp.

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