THE PALAEOECOLOGICAL CONTEXT AT NIAH CAVE, SARAWAK: EVIDENCE FROM THE PRIMATE FAUNA

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ABSTRACT

There is growing evidence to support the hypothesis that ecological change, associated with global eustatic fluctuations, had a more profound impact on the diversity and distribution of the late Quaternary large mammal fauna of Borneo than did environmental disturbance by humans. A re-examination of the primate fauna from Niah Cave contributes new evidence pertinent to understanding ecological changes that occurred in Borneo during the last 40,000 years.

INTRODUCTION

Niah Cave in northern Sarawak has provided the earliest archaeological record of modern humans in Southeast Asia, possibly dating back to more than 40,000 years (Brothwell 1960; Kennedy 1977). The site was excavated by Tom Harrisson from 1954 to 1967, and then again in 1977 by a team from the Sarawak Museum (Harrisson 1957, 1958, 1959a, 1959b; Solheim 1958, 1974, 1983; Medway 1977; Majid 1982). The sites at Niah are represented by a complex of cave entrances which penetrate the Subis limestone massif. All of the six major entrances into the cave system have yielded archaeological materials, but excavations have mainly concentrated on the Main or West Mouth, with important subsidiary collections being obtained from Lobang Angus and Gan Kira (Figure 1).

GEOLOGICAL AND ARCHAEOLOGICAL CONTEXT

Unfortunately, the sequence of deposits at Niah has never been described in any detail (Majid 1982 and Solheim 1983 review this problem) and it is possible to reconstruct only a generalized stratigraphic column from the West Mouth. Radiocarbon dates on charcoal and charred bone provide a consistent series of dates for the sequence (Harrison 1959b, 1970; Medway 1977; Shutler 1977; Majid 1982). However, Spriggs (1989) has recently rejected several of the younger dates obtained from Niah because they apparently derive from other localities in Borneo.

There are over 3m of sediments, mostly comprising a uniform series of poorly-stratified detritus. One interesting feature, however, is the widespread occurrence of a "sterile pink-and-white band" at a depth of 66-72 inches which includes no artifacts or bones of large mammals, but contains abundant remains of bats and swiflets (Harrisson 1959a, 1959b; Solheim 1958, 1983). There seems to be no further information on the composition of this layer, but from its intrusive nature and its apparently rapid deposition, as well as the inclusion of cave-dwelling vertebrates only, it may represent a single major influx of volcanic ash. It is not possible to be certain without geochemical analysis of the samples, but it is intriguing that the C14 date for this level (32,630±700 BP) coincides well with published fission track dates (30±4.5 kyr and 30±0.3 kyr) for a major eruptive event from the Toba caldera complex in northern Sumatra (Stauffer *et al.* 1980; Nishimura and Stauffer 1981; however, see Chesner *et al.* 1991 for an alternative and critical review of these inferred dates).

Over two hundred human burials have been excavated at Niah (B. Harrisson 1967; Brooks *et al.* 1977). Most of these burials are found in superficial layers associated with Neolithic assemblages, and dated by C14 to younger than 6,000 BP. A number of burials are found at greater depths, down to 50 inches, and are associated with a "Mesolithic" assemblage. The oldest of these burials has been dated to 13,640±130 BP (Harrisson 1975). In addition to these burials, a skull of a subadult individual was found at a depth of 106-110 inches (the "deep skull") and an isolated talus was recovered at a depth of 102-105 inches. Radiocarbon dates on samples of charred bone and charcoal located near the deep skull, at depths of 96-100 inches and *circa* 100 inches, have yielded dates of

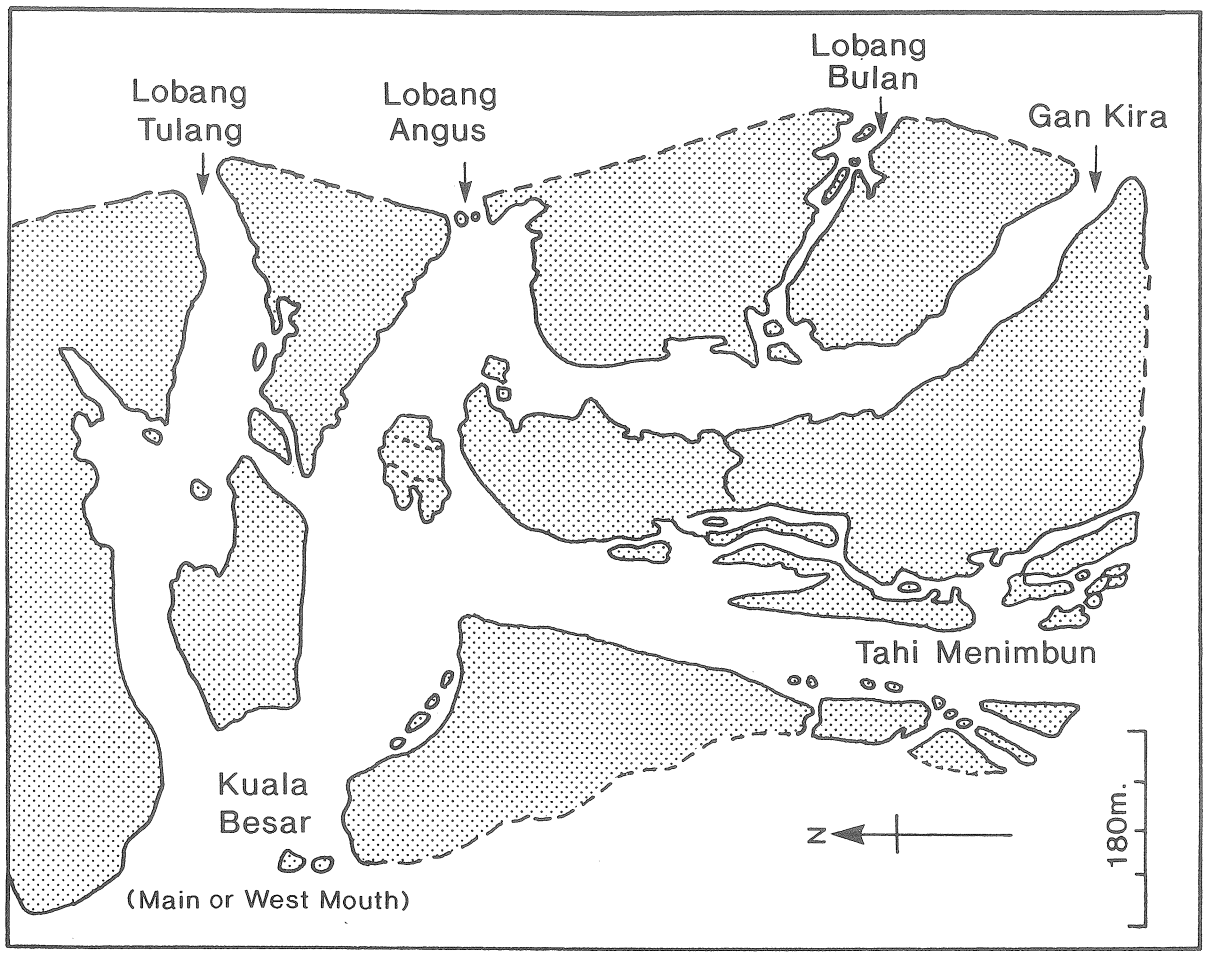

Figure 1. Plan of Niah Cave showing the location of the main entrances (adapted from Majid 1982).

39,600±1000 and 41,500±1000 BP respectively. If these dates are indicative of the age of the deep skull, then Niah provides the earliest evidence of modern humans in Southeast Asia.

EVIDENCE FOR ECOLOGICAL CHANGE

The dense accumulation of mammalian bones at Niah appears to be primarily due to human subsistence activities. There is ample evidence of bone charring in the excavated remains, but indications of bone modification and butchering marks are quite rare. The fauna is extensive, with 59 species of mammals being represented, although this includes 13 species of bats and other species of micromammals, many of which are unlikely to be present as the result of human hunting activities (Medway 1966a, 1977).

Harrisson (1961) suggested that human hunting during the late Pleistocene had a profound effect on the fauna of Borneo. He used the following evidence from Niah to support his argument:

1. At least one species of mammal found at Niah, the giant pangolin (*Manis palaeojavanica*) has become entirely extinct (Hooijer 1960a; Harrisson *et al.* 1961) (Table 1)
2. Several species of large mammals found at Niah and present in other parts of southeast Asia today are now extinct in Borneo (i.e., *Panthera tigris* and *Tapirus indicus*[1])(Medway 1959a, 1960, 1964a, 1977) (Table 1)
3. Some species found at Niah are rare or absent in the local area today (i.e., *Dicerorhinus sumatrensis*, *Elephas maximus*, and *Pongo pygmaeus*)

Table 1. List of large mammal species (excluding domesticates) from Niah[a]

Species represented at Niah		Status in Borneo today
Primates		
Pongo pygmaeus	Orang-utan	Present
Hylobates muelleri	Gibbon	Present
Trachypithecus cristatus	Silvered leaf monkey	Present
Presbytis spp. (?*P. rubicunda*)	Leaf monkey	Present
Macaca fascicularis	Long-tailed macaque	Present
Macaca nemestrina	Pig-tailed macaque	Present
Nycticebus coucang	Slow loris	Present
Pholidota		
Manis palaeojavanica	Giant pangolin	Extinct
Manis javanica	Malay pangolin	Present
Carnivora		
Ursus malayanus	Sun bear	Present
Panthera tigris	Tiger	Absent
Pardofelis nebulosa	Clouded leopard	Present
Mustela nudipes	Malayan weasel	Present
Melogale everetti	Bornean ferret-badger	Mt. Kinabalu only
Lutra sumatrana	Hairy-nosed otter	Present
Viverra tangalunga	Malay civet	Present
Arctictis binturong	Bearcat	Present
Hemigalus derbyanus	Banded palm civet	Present
Herpestes sp.	Mongoose	Present
Perissodactyla		
Tapirus indicus	Malayan tapir	Absent
Dicerorhinus sumatrensis	Sumatran rhinoceros	Present, but rare
Artiodactyla		
Sus barbatus	Bearded pig	Present
Tragulus napu	Large Malay mouse-deer	Present
Tragulus javanicus	Lesser Malay mouse-deer	Present
Muntiacus muntjak	Barking deer	Present
Cervus unicolor	Sambar	Present
Bos javanicus	Banteng	Present
Proboscidea		
Elephas maximus	Asian elephant	Present in Sabah only

[a] Sources: Medway (1959a, 1959b, 1960, 1964a, 1966b, 1977); Harrison (unpublished); Corbet & Hill (1992).

4. Several forms are larger in size, especially at deeper levels in the cave deposits.

By contrast, Medway (1977; Cranbrook 1988) has argued that the impact of hunting on the fauna was insignificant, and that variations in the mammalian community structure during the late Quaternary were due to ecological changes. Increasing evidence from a number of inter-related lines of research tend to support this latter view:

1. The most common mammal remains from Niah (presumably the most commonly hunted mammals) are the orang-utan, several species of monkeys, and the bearded pig, which are still frequent in Borneo at present, while the large mammals that are now rare or

Table 2. Frequency of large mammal species at Niah

Very common > 200 specimens	**Quite common** >20 specimens	**Rare** < 20 specimens	
Pongo pygmaeus	*Trachypithecus cristatus*	*Hylobates muelleri*	*Viverra tangalunga*
Presbytis spp.	*Bos javanicus*	*Macaca nemestrina*	*Arctictis binturong*
Macaca fascicularis		*Manis palaeojavanica*	*Hemigalus derbyanus*
Sus barbatus		*Manis javanica*	*Herpestes* sp.
		Ursus malayanus	*Muntiacus muntjak*
		Panthera tigris	*Cervus unicolor*
		Pardofelis nebulosa	*Tragulus napu*
		Mustela nudipes	*Tragulus javanicus*
		Melogale everetti	*Tapirus indicus*
		Lutra sumatrana	*Dicerorhinus sumatrensis*
			Elephas maximus

absent locally are also very scarce in the collections (Table 2). This is hardly the pattern to be expected if humans on Borneo were responsible for exterminating species through over-hunting.

2. The impact that human hunting has on local faunas is related to the extent to which the fauna has co-evolved with hominid predation in the past. Where humans have come into contact for the first time with highly endemic faunas, such as in the New World, Australia or Madagascar, hunting has led to major extinctions. In contrast, where communities have co-evolved with hominids for a long time, as in Eurasia and Africa during the Pleistocene, levels of extinction are much lower. The mammal fauna on Borneo in the late Pleistocene was typically Indo-Malayan, apparently with few endemic species, and one with a long evolutionary history of association with hominids. In addition, archaeological and historical evidence suggests that human populations on Borneo may have been quite sparse (Bellwood 1990, 1993), in which case hunting may have had little impact on the fauna.
3. Evidence from other parts of Southeast Asia suggest that eustatic fluctuations had a pronounced effect on the ecology and climate of northern Borneo during the late Pleistocene. The mean annual temperature on Borneo at the time of the last glacial maximum, around 18,000 BP, might have been 5-6^{o}C lower than present (20-22^{o}C), and precipitation was reduced and more seasonally distributed (Peterson 1969; Haile 1971; Biswas 1973; Verstappen 1975; Medway 1977). With a sea level probably as much as 120 m below that at present, Niah would have been more than 200 km inland from its present position, which is now only 16 km from the coast. The drier, more seasonal, forest would have provided a more suitable biome for large herbivorous mammals, along with their dependent predators (Medway 1977). With the establishment of the present climatic regime during the Holocene, and the development of ever-wet tropical rainforest, suitable habitats for these large mammals diminished, leading to declining numbers and extinction.
4. The Niah Cave fauna itself indicates ecological changes. Larger dental or inferred body size of the subfossil specimens relative to extant conspecifics has been reported in the orang-utan, macaques, leaf monkeys, murids, Sumatran rhinoceros and barking deer (Hooijer 1961, 1962; Medway 1959b, 1964b, 1966a, 1966b; Cranbrook 1986). This is presumably associated with a purportedly cooler early Quaternary climate. The presence of two exclusively montane forest species, the lesser gymnure (*Hylomys suillus*) and ferret badger (*Melogale everetti*), also supports this view (Medway 1964a, 1977).
5. Heaney (1986) has shown that the rate of extinction of mammals by attrition on the islands of southeast Asia following inundation of the Sunda shelf to be correlated with island size. Such extinctions would have had a minor impact on an island the size of Borneo, but may have been sufficient to account for the low level of impoverishment indicated by the archaeological record at Niah and other prehistoric cave sites in Borneo.

Table 3. The percentage of primates (cranio-dental specimens) by level from the West Mouth at Niah

Depth	N	*Presbytis* spp.	*Macaca fascicularis*	*Macaca nemestrina*	*Trachypith. cristatus*	*Pongo pygmaeus*	*Hylobates muelleri*
Unknown	27	18.5	18.5	7.4	18.5	37.0	0.0
0-12"	23	26.1	8.7	4.3	21.7	39.1	0.0
12-24"	37	24.3	13.5	2.7	8.1	51.4	0.0
24-36"	50	18.0	24.0	4.0	28.0	24.0	2.0
36-48"	28	35.7	10.7	0.0	0.0	53.6	0.0
48-60"	17	11.8	23.5	0.0	11.8	52.9	0.0
+ 60"	35	34.3	11.4	2.9	0.0	51.4	0.0
Total	100.0%	24.4%	16.1%	3.2%	13.4%	42.4%	0.5%
N	217	53	35	7	29	92	1

Table 4. The density of extant primates in Borneo compared with the frequency of subfossil primates from West Mouth, Niah

	Kutai Nature Reserve, Borneo[a]		**Niah, West Mouth**
	Individuals per km^2	Frequency	Frequency
Pongo pygmaeus	4.0	7.9%	42.4%
Hylobates muelleri	14.6	29.0%	0.5%
Leaf monkeys	20.4	40.6%	37.8%
Macaca nemestrina	5.8	11.5%	3.2%
Macaca fascicularis	5.5	10.9%	16.1%

[a] Data from Rodman (1978), Waser (1987).

PRIMATE MATERIAL FROM NIAH CAVE

My preliminary research on the subfossil primates from Niah contributes new information that is pertinent to understanding the nature of the ecological changes that took place in Borneo during the late Quaternary. Along with pigs and squirrels, primates are the most common mammals at Niah. Eight species of primates are represented, including all genera currently living on Borneo, with the exception of *Tarsius* and *Nasalis*.

The most common primate at Niah West Mouth is *Pongo pygmaeus*, which comprises 42.4% of the total from the site. This is followed in importance by *Presbytis* spp. (24.4%), *Macaca fascicularis* (16.1%) and *Trachypithecus cristatus* (13.4%). *Macaca nemestrina* and *Hylobates muelleri* are, by contrast, quite rare. The distribution of these species with increasing depth in the cave does not appear to change significantly, but it should be noted that the sample sizes are relatively small (Table 3). Medway (1959b) has suggested that there was an abrupt increase in the relative frequency of arboreal animals, such as monkeys and squirrels, above the 48 inch level, which he associates with the advent of a more sophisticated technology, including greater use of bone as a raw material, especially in the manufacture of projectile tips.

However, raw data on the absolute numbers of primate specimens provides no real clues to how intensively these primates were being exploited for food. Density information for living primates gives us some indication of the relative abundance of different primates in a modern setting (Table 5). If these frequencies are representative of primate communities on Borneo in the past, then we can gain some idea of hunting preference from them. The data seem to suggest that orang-utans and leaf monkeys are over-represented in the collections from Niah, while the macaques, and especially the gibbons, are dramatically under-represented. This different representation may reflect either food preferences by prehistoric human populations or more likely that orang-utans and leaf monkeys are easier prey to catch.

Table 5. Percentage of primates (cranio-dental specimens) from the major sites at Niah.

Site	N	*Presbytis* spp.	*Macaca fascicularis*	*Macaca nemestrina*	*Trachypith. cristatus*	*Pongo pygmaeus*	*Hylobates muelleri*
West Mouth	217	24.4	16.1	3.2	13.4	42.4	0.5
Lobang Angus	114	20.2	50.9	0.9	14.9	12.3	0.9
Gan Kira	38	26.3	28.9	2.6	7.9	31.6	2.6

Table 6. Comparison of occlusal area (mesiodistal length x buccolingual breadth) of upper and lower cheek teeth combined in modern and subfossil orang-utans from Borneo and Sumatra[a]

Standard deviation intervals from the mean values for extant orang-utans

	N	-3	-2	-1	+1	+2	+3	+4	+5
Extant	822	4	136	304	235	113	29	1	0
Pongo	100%	0.5%	16.5%	37.0%	28.6%	13.7%	3.5%	0.1%	0%
Padang	2672	0	72	592	917	655	323	87	26
Pongo[b]	100%	0%	2.7%	22.2%	34.3%	24.5%	12.1%	3.3%	1.0%
Niah Cave	65	0	3	24	30	7	1	0	0
Pongo	100%	0%	4.6%	36.9%	46.2%	10.8%	1.5%	0%	0%

[a] Data obtained from Hooijer (1948) and Harrison (unpublished).

[b] The subfossil orang-utans from late Quaternary sites in the Padang Highlands of Sumatra have been descibed by Hooijer (1948). The results presented here confirm Hooijer's contention that the dental remains from the Padang Highlands are significantly larger than the teeth of extant orang-utan.

Aside from this, the distribution of different primate species in the collections from the various cave mouths at Niah differ significantly from each other: orang-utans represent 42.4% of all primates at the West Mouth, but only 12.3% at Lobang Angus, while the long-tailed macaque (*Macaca fascicularis*) represents 16.1% and 50.9% respectively (Table 6). A simple explanation is not possible. The composition of the forest around Lobang Angus, which opens onto the eastern side of Subis, may have been somewhat distinct from that surrounding the west facing Main Mouth, thereby allowing human hunters access to subtly different mammalian communities. However, this suggestion needs to be tested further with comparisons of the remaining fauna.

The suggestion that several species of primates have undergone size reduction in Borneo during the Quaternary, presumably as a response to increased ambient temperatures (Hooijer 1961, 1962), is an important piece of evidence used in support of changed ecological conditions. The orang-utans and the long-tailed macaques provide the best samples from Niah to test this inference. Orang-utans have a quite limited distribution in Sarawak today and are not found in the vicinity of Niah (Figure 2). This is probably as a result of recent hunting pressure and disturbance (Medway 1977). When the dental size of extant orang-utans is compared with those from Niah, the latter are not significantly different. A re-examination of the dental size of orang-utans from Niah show that the teeth tend to be slightly larger on average than those of modern animals, but all specimens fall well within the range for extant orang-utans (Tables 6 and 7). This finding contradicts the conclusion of Hooijer (1961) that the subfossil orang-utans from Borneo were relatively larger than their modern counterparts.

The long-tailed macaques provide a more convincing case for significant size reduction: the cheek teeth of the subfossil forms are on average 13% larger (based on occlusal area) than those of their modern conspecifics from Borneo (Table 8). In addition, there appears to have been a gradual reduction in overall size of the dentition through time (Figure 3). A recent study of skull length (used as a measure of overall size) in *Macaca fascicularis* has shown a gradual increase with distance from the Equator (Fooden and Albrecht 1993). They explain this

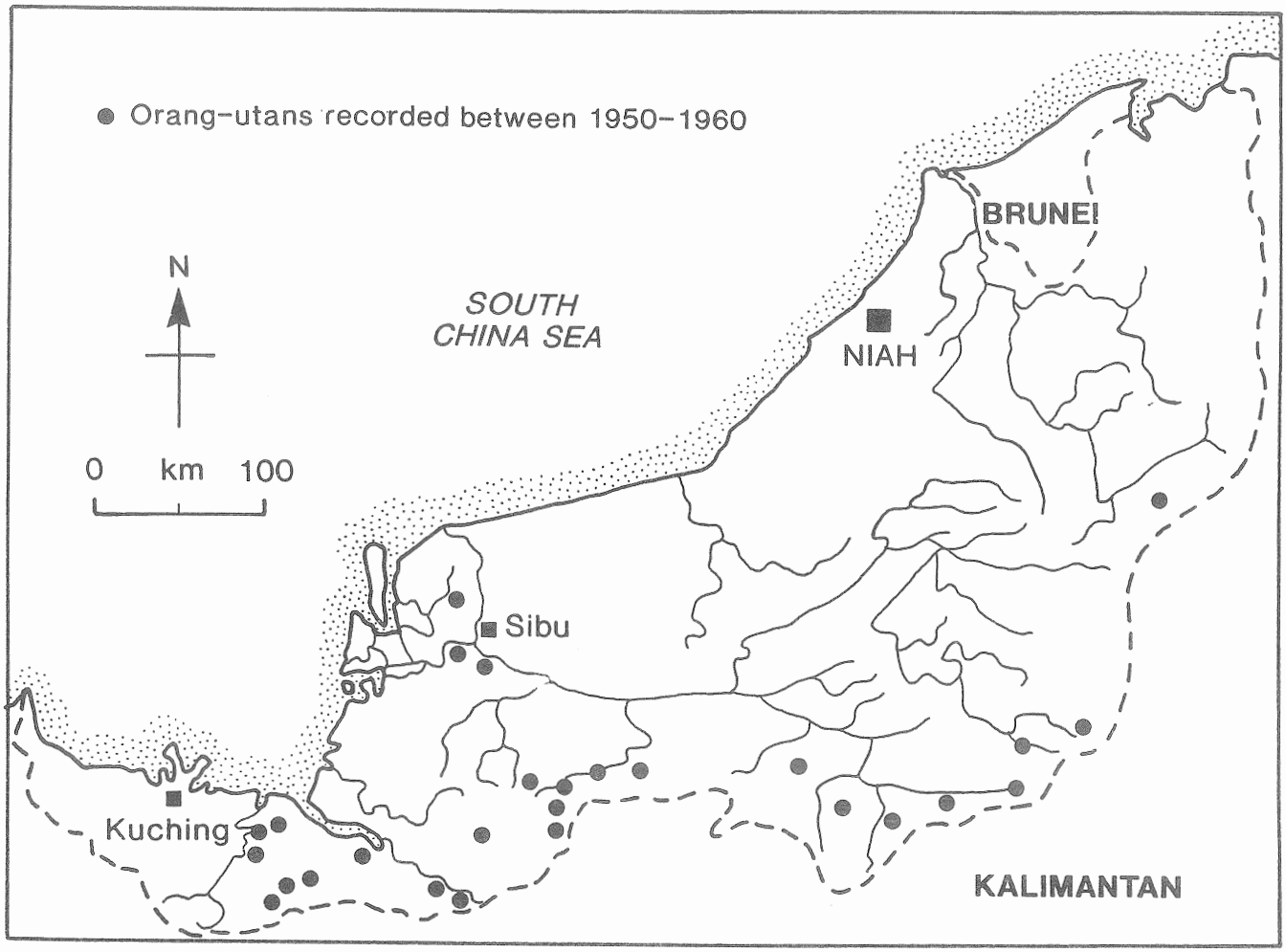

Figure 2. The recent distribution of orang-utans in Sarawak in relation to Niah Cave (adapted from Reynolds 1967).

as a consequence of Bergmann's rule, in which increased body size occurs as an adaptive response to cooler climates. It should be noted that the subfossil macaques from Niah correspond in dental size with those that inhabit regions of Thailand today which have mean annual temperatures similar to that inferred for northern Borneo during the last glacial maximum.

CONCLUSIONS

There is growing evidence to support the hypothesis that ecological change, associated with global eustatic fluctuations, had a more profound impact on the diversity and distribution of the late Quaternary large mammal fauna of Borneo than did environmental disturbance by humans. A re-examination of the primate fauna from Niah Cave contributes new evidence pertinent to understanding ecological changes that occurred in Borneo during the last 40,000 years. The major findings of this study can be summarized as follows:

1. The orang-utan, leaf monkeys and macaques represent significant components of the modern fauna of Borneo, despite what appears from the archaeological evidence at Niah to have been a pattern of preferential hunting of these species by humans throughout the late Quaternary;
2. *Pongo pygmaeus* and *Presbytis* spp. appear to be over-represented in the collections at Niah, at least when compared with modern patterns of abundance, and this may reflect either food preferences or limitations in the hunting capabilities of prehistoric humans;

Table 7. Comparison of the occlusal area (mesiodistal length x buccolingual breadth) of the permanent teeth of the orang utan sample from West Mouth, Niah, compared with the standard deviation intervals from the means of the corresponding teeth of extant orang-utans, arranged by their depth in the cave.

	Depth at Niah	N	Minimum S.D. interval	Maximum S.D. interval	Mean S.D. interval
Extant orang-utans		822	-2.50	+3.50	0.0
Subfossil orang-utans	0"-12"	5	-0.87	+0.34	-0.12
	12"-24"	13	-0.96	+0.95	-0.27
	24"-36"	8	-0.96	+1.42	+0.15
	36"-48"	12	-0.34	+1.62	+0.65
	48"-60"	2	+0.47	+0.77	+0.62
	60"-72"	7	-0.26	+2.00	+0.79
	72"-84"	1	-0.27	-0.27	-0.27
	Below 84"	2	+0.84	+1.03	+0.94
	All levels	57	-1.29	+2.00	+0.19

Data from Hooijer (1948) and Harrison (unpublished)

Table 8. Relative difference in occlusal areas (mesiodistal length x buccolingual breadth) of cheek teeth in extant *Macaca fascicularis* from Borneo and subfossil *M. fascicularis* from Niah.

	Mean area in extant form	Mean area in subfossils	% Difference
Upper P4	23.8	26.7	+12.2%
Upper M1	35.7	38.8	+8.7%
Upper M2	44.5	50.5	+13.5%
Upper M3	41.6	47.2	13.5%
Lower P4	19.9	23.6	+18.6%
Lower M1	27.8	32.0	+15.1%
Lower M2	39.5	44.2	+11.9%
Lower M3	45.7	51.1	+11.8%
Mean Difference			+13.2%

3. Differences in the proportions of primates from the various cave mouths at Niah may reflect subtle ecological variations in the forest surrounding the Subis limestone massif, thereby allowing human hunters access to different resources;
4. The subfossil orang-utans from Niah do not differ significantly in dental size from their extant counterpart, contrary to Hooijer (1960b);
5. The long-tailed macaques (*Macaca fascicularis*) from Niah are significantly larger in dental size than their modern conspecifics from Borneo, but they apparently decrease in size through time; and
6. The subfossil macaques from Niah have teeth similar in size to those of *Macaca fascicularis* populations living today in Thailand where the mean annual temperatures correspond to those inferred for northern Borneo during the last glacial maximum, at about 18,000 BP.

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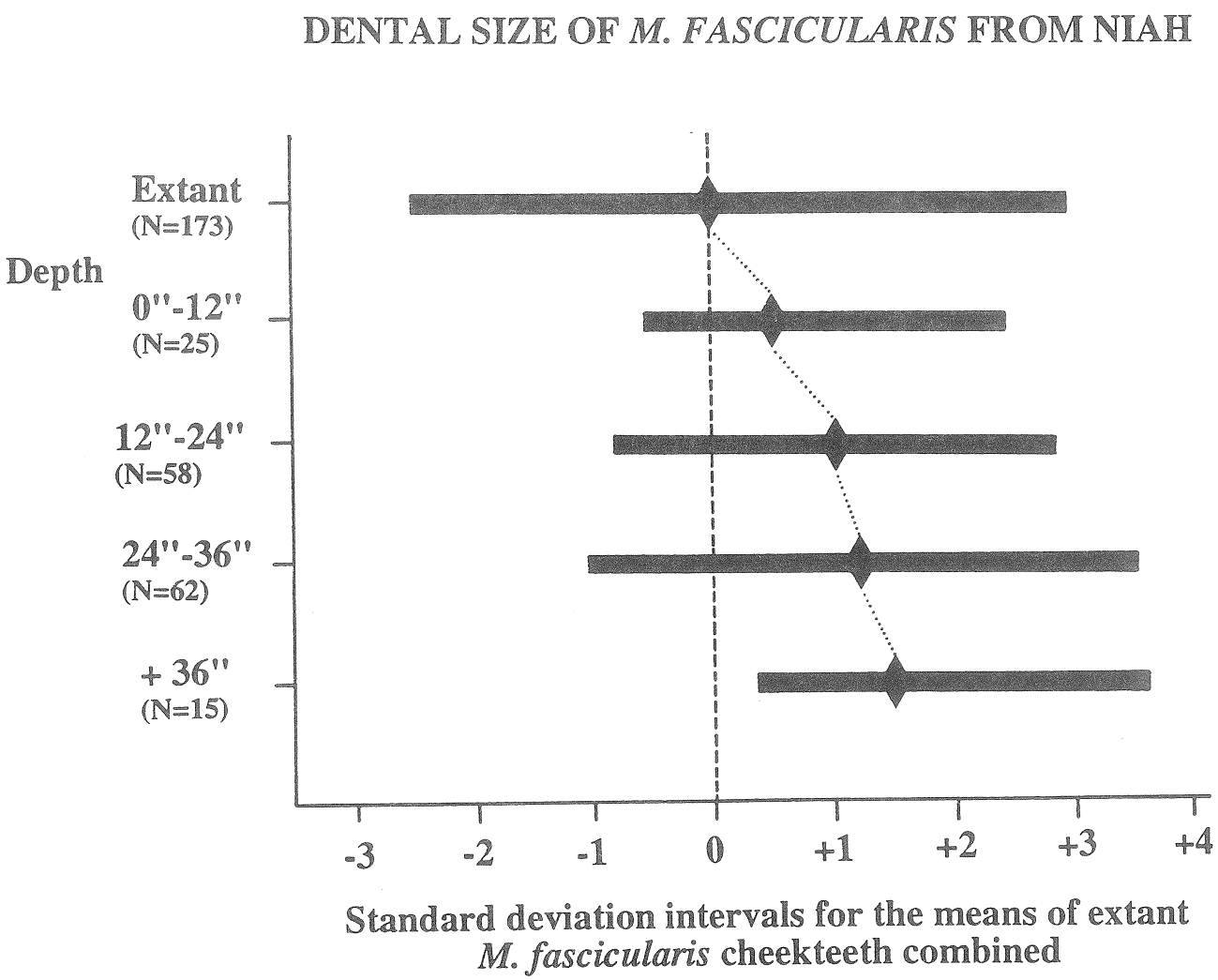

Figure 3. The dental size of subfossil Macaca fascicularis *from Niah compared with that of extant conspecifics from Borneo. The samples are arranged according to their depth in the cave; sample sizes are given in parentheses. The x-axis represents the standard deviation intervals from the mean values of the occlusal areas (mesiodistal length x buccolingual breadth) of all upper and lower cheek teeth in extant* M. fascicularis. *Solid bars are ranges; diamonds are mean values. Note that the cheek teeth of subfossil macaques from Niah are larger at deeper levels in the cave deposits, and that they gradually decreases through time to the present.*

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NOTE

1. Evidence from archaeological sites in Sabah demonstrate that the Javan rhinoceros (*Rhinoceros sondaicus*) and the dhole (*Cuon alpinus*) have also become extinct on Borneo since the late Quaternary (Cranbrook 1986, 1988).

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