

Identification of Morphological Variation in the Humeri of Bornean Primates and Its Application to Zooarchaeology

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ABSTRACT: Species of primate are physiologically and behaviorally adapted to particular environmental and ecological conditions. As a result, the presence or absence and the structure of primate communities are useful indicators of temporal and spatial variations in climate and environment. Previous zooarchaeological studies that have focused on Bornean primates have been restricted to the identification and analyses of the mandibles, maxillae, and teeth. However, adaptation to different modes of locomotion by the various species of monkeys and apes that inhabit Borneo has resulted in recognizable differences in the structure and morphology of a number of post-cranial skeletal elements. This paper focuses on just one of these elements, the humerus. It describes some of the anatomical criteria identified in modern humeri that consistently vary among the different primate genera, and demonstrates how this information can be applied to the study of primate remains recovered from archaeological contexts.

KEYWORDS: PRIMATE, LANGURS, HUMERUS, MORPHOLOGY, NIAH CAVE

RESUMEN: Las especies de primates se encuentran fisiológica y etológicamente adaptadas a condiciones ambientales específicas. Como resultado de ello la presencia o ausencia y la propia estructura de las comunidades de primates constituyen buenos indicadores de variaciones climáticas y ambientales en el espacio y en el tiempo. Los estudios zooarqueológicos que hasta la fecha se han centrado en los primates de Borneo, han quedado restringidos a la identificación y análisis de las mandíbulas, maxilares y dientes. No obstante, las adaptaciones a los distintos modos de locomoción por parte de las distintas especies de monos y antropoides que habitan en Borneo han generado diferencias reconocibles en la estructura y morfología de una serie de elementos esqueléticos post-craneales. Este trabajo se centra en uno de estos elementos, el húmero. Describe algunos de los criterios anatómicos detectados en los húmeros actuales que varían consistentemente entre los distintos géneros de primates y demuestra como esta información puede ser aplicada al estudio de los restos de primates recuperados en contextos arqueológicos.

PALABRAS CLAVE: PRIMATES, LANGURES, HÚMERO, MORFOLOGÍA, CUEVA DE NIAH

INTRODUCTION

In Borneo, the extant primate community consists of 11 species of monkey and ape, differentiated into five genera (Figure 1). Natural selective pressures have made each species of monkey or ape both physiologically and behaviorally the most successful at occupying the ecological niche within which it exists. Niche separation is evident in the different types of environments

that the various primate taxa inhabit, in their dietary preferences, and in their modes of locomotion. Thus, differences in local or regional environmental conditions will influence the presence or absence of the species, and the structure of the resident primate community. As a result, temporal and spatial variability in the suite of primates recovered from archaeological sites is a good indicator of changes in local palaeoecological conditions.

Family	Subfamily	Genus (Subgenus)	Species	Common Name
Cercopithecoidea				old world monkeys
	Colobinae			leaf monkeys
		<i>Presbytis</i>		langurs or leaf eating monkeys
			<i>melalophos</i>	banded langur
			<i>hosei</i>	Hose's langur
			<i>rubicunda</i>	maroon langur
			<i>frontata</i>	white-fronted langur
		<i>Presbytis</i> [or <i>Trachypithecus</i>]	<i>cristata</i>	silvered langur
		<i>Presbytis (presbytis)</i>		subgenus of <i>Presbytis</i> that includes all members except <i>P. cristata</i>
		<i>Nasalis</i>	<i>larvatus</i>	proboscis monkey
	Cercopithecoidea			cheek-pouched monkeys
		<i>Macaca</i>	<i>fascicularis</i>	long-tailed macaque
			<i>nemestrina</i>	pig-tailed macaque
Hominidae				apes
	Hylobatinae			gibbons and siamang
		<i>Hylobates</i>	<i>muelleri</i>	Bornean gibbon
			<i>agilis</i>	agile gibbon
	Ponginae			great apes
		<i>Pongo</i>	<i>pygmaeus</i>	orangutan

FIGURE 1

The primate species of Borneo used in this study (after Payne & Francis, 1998: 223-231; Jurmain *et al.*, 1999).

Adaptations, to different diets and locomotor behaviors in particular, have strongly influenced the development of the cranial and appendicular skeleton. The mandible, maxilla, and teeth are considered to show the greatest morphological variation, and to yield the most information on the age, sex, and numbers of species of primate represented in the archaeological record. Hooijer (1960, 1962) used cranio-dental bones recovered from Late Pleistocene and Holocene (approximately 40,000 BP onwards) deposits excavated at Niah Cave, Sarawak, Borneo, to identify changes in the density, distribution, and age structure of primate taxa. Furthermore, by using biometrical analyses of the teeth, Hooijer was able to argue that, in some species of primate, there was an evolutionary trend towards smaller tooth size in modern populations. Harrison (1996) re-evaluated the primate cranio-dental material from the Niah Cave deposits. By comparing the presence or absence and the composition of the monkeys and apes recovered from the archaeological deposits with data on modern primate community structure, he

was able to suggest that some primate taxa were either over- or under-represented in the archaeological record. Harrison (*ibid.*) argued that the differences in structure of the archaeological and modern primate communities reflected a preference for hunting particular species of monkeys by the prehistoric visitors to the cave.

However, there is the risk that, in some circumstances, the cranio-dental remains may not be representative of either the rank order or the total number of primate taxa recovered from the archaeological record. Any number of human and natural taphonomic processes could influence the presence or absence or the numbers of particular anatomical elements recovered from archaeological contexts. Therefore, more reliable and confident conclusions could be reached if the cranial data were supported by the analyses of other skeletal elements.

Bone analysts working in Southeast Asia have recognized for some time that the various genera of primates demonstrate marked differences in the

morphology of a number of post-cranial elements, and this knowledge has been used to good effect in zooarchaeological studies (Grant & Higham, 1991: 168-179). However, no one has, as yet, described the morphological criteria used to differentiate any of the appendicular bones of Southeast Asian primates, or assessed whether the analysis of different skeletal elements produces disparate results in the numbers of monkeys and apes recorded in the archaeological record.

This paper, part of an ongoing study of Bornean primates dedicated to identifying and characterizing morphological variation in the post-cranial skeleton, focuses on just one element, the humerus. It describes some of the morphological traits identified within modern comparative assemblages that are consistently characteristic of a particular primate taxon, but vary among different species of monkey and ape. The modern data are used to identify the fragmentary remains of primate humeri recovered from midden deposits investigated during recent excavations at Niah Cave, Sarawak, Borneo. The paper compares the results with the cranio-dental material from the same sequence of sediments, and discusses differences in the compositions of the primate community, identified using either cranial material or humeri.

METHODS

The modern primate humeri used in this study are part of the reference collection held at the Natural History Museum (NHM), London. The analysis includes the leaf monkeys (Colobinae) including the langurs (*Presbytis* spp.), macaques (*Macaca* sp.), gibbons (*Hylobates* sp.), and orangutan (*Pongo pygmaeus*), but not the slow loris (*Nycticebus coucang*) or the western tarsier (*Tarsius bucanus*). The siamang (*Symphalangus syndactylus*) lives today only in Sumatra and the Malay Peninsula; it is one of those animals, like the tiger, the panther, and the Malay tapir, that are absent from the recent fauna of Borneo (Hooijer, 1962). Excavations at Niah and other cave sites in Borneo have produced evidence of the tiger and tapir (Medway, 1959, 1960; Harrison, 1998) but, as yet, no remains of the siamang. Therefore the siamang is not regarded as a past inhabitant of Borneo and is not included in this study.

The left and right humeri of each specimen of Bornean primate in the reference collection were

examined, and every possible surface of the bone was studied and compared with the humeri from each of the other taxa. Each morphological characteristic typical of, and consistent within, each taxon was recorded. When both males and females of the same species were present in the NHM collection, they were compared closely, to establish whether an identified morphological trait was not determined by the sex of the individual.

To aid in future identification the bones were photographed using a Nikon F55 camera and black and white film. The images were scanned using an Afga Snapscan e20 scanner, and digitally drawn using Macromedia FreeHand 10 and Adobe Photoshop Version 6 to highlight the most important morphological characteristics of the bones.

The fragments of humeri and crania recovered from the Area D excavations (see below) at Niah Cave were identified using the comparative skeletons and skulls held in the NHM. In addition, the morphological characteristics of the archaeological humeri were checked against the criteria recorded for the modern comparatives.

Unfortunately, the NHM holds only a small number of primate skeletons from Borneo. For example, there was only one proboscis monkey (*Nasalis lavartus*) and one Hose's langur (*Presbytis hosei*), and no white-fronted langur (*P. frontata*) or agile gibbon (*Hylobates agilis*) skeletons. Therefore, in many cases, it was not possible to identify whether some morphological characteristics observed in the humeri of a single individual were consistent traits found within that taxon, or potentially varied within a population, or whether subtle differences existed between closely related species. Thus, most distinctions described in this paper refer to gross morphological variations in the structure of the humerus that can be confidently used to differentiate between the primate taxa. However, the NHM did contain several silvered langurs (*Presbytis cristata*), and clear, confident differences in the morphology of the humerus could be identified between the silvered langur and the other leaf monkeys resident in Borneo.

FUNCTION AND VARIATION IN THE MORPHOLOGY OF PRIMATE HUMERI

Figures 2a-e show the locations of the anatomical structures of the humerus in different orientations of the bone. The shape of the distal end of the

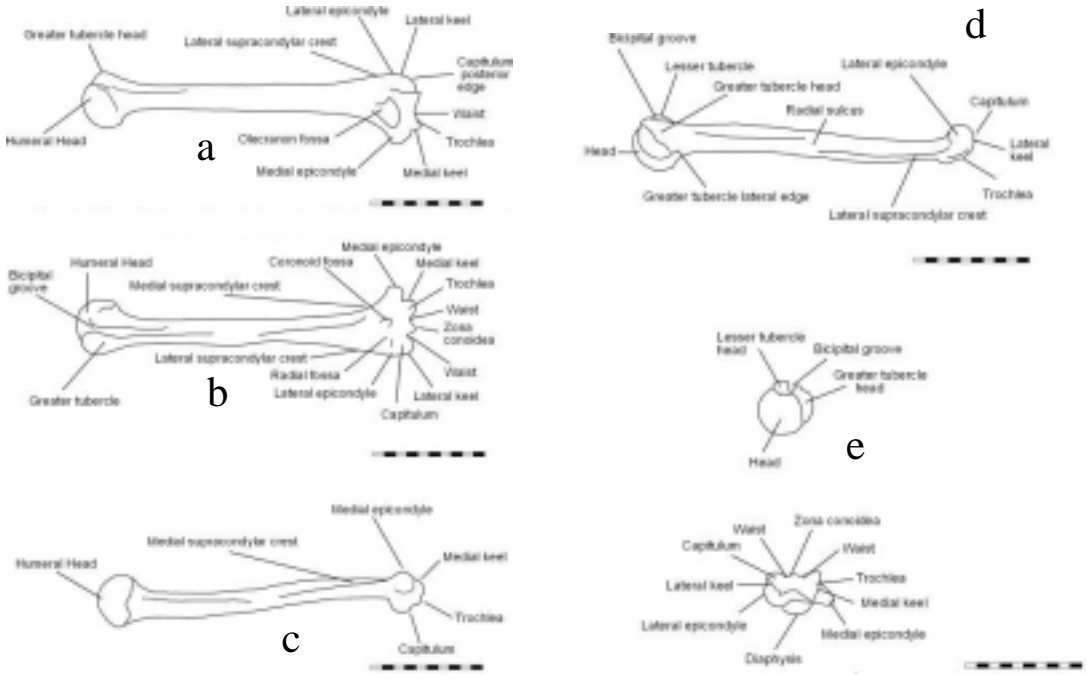


FIGURE 2

a. The posterior surface of a humerus showing the different anatomical structures; b. The anterior surface of a humerus showing the different anatomical structures; c. The medial surface of a humerus showing the different anatomical structures; d. The lateral surface of a humerus showing the different anatomical structures; e. The proximal and distal ends of a humerus showing the different anatomical structures.

humerus is dictated by the muscles that originate or insert into it and control part of most of the forelimb functions. The forelimb needs some flexibility of function, but has developed varied typical orientations and strain responses depending on the type of locomotion to which particular primate taxa are adapted (Schwarz *et al.*, 1989; Demes *et al.*, 1998). As a result, the movement and function of the whole forelimb have influenced the shape and morphology of the humerus and produced a structure that is characteristic of each species (Anderson, 1978).

Arboreal quadrupedal primates have a highly generalized bone structure as a result of spending a large proportion of their time using secondary modes of locomotion, such as terrestrial quadrupedalism, clinging, leaping, and suspensory movement (Senturia, 1995). Leaf monkeys, the proboscis monkey, and the long-tailed macaque are all arboreal quadrupeds to some degree. The pig-tailed macaque is classed as a terrestrial quadruped, spending much more time on the ground than the other monkeys (Rodman, 1979, 1990).

MACAQUES

The long-tailed and pig-tailed macaques have humeri with similar morphological characteristics. In general, the humerus appears robust, with marked muscle attachment regions on the shaft (Figure 3). Like all the monkeys, the macaques have an oval-shaped humeral head that is slightly wider mediolaterally than proximodistally. However, the greater tubercle extends above the head of the humerus. In the pig-tailed macaque, the bicipital groove is wider, shallower, and more U-shaped than that observed in the leaf monkeys (except the silvered langur), when viewed from the proximal end. The long-tailed macaque has a narrower, deeper, and more sharply U-shaped bicipital groove. Both the macaque species have a distinctive mediolateral curvature in the humerus, approximately a third of the way down the shaft from the proximal end. The curvature is accentuated by a pronounced medial margin to the bicipital groove that starts at the medial surface of the greater tubercle. The deltoid tuberosity-



FIGURE 3

Pig-tailed macaque (*Macaca nemestrina*: Natural History Museum Accession No. (NHM A^{cen}. No.) 82.11.18.5) male left humerus: Lateral, anterior, medial and posterior views, and Proximal and distal ends (Scale 10 cm: Image by K. Ki-Kydd).

ty is always visible and often pronounced, and strong muscle attachment regions can be observed on the medial and lateral supracondylar crests. Both the medial and lateral epicondyles protrude posteriorly, giving the distal articulation a U-shaped appearance when viewed from the distal end. The medial surface of the trochlea is concave, unlike that of the other primates, and the articular surface of the trochlea extends into the lateral margins of the olecranon fossa. The zona conoidea (the lateral margin of the trochlea) appears to be variable in shape and size, but is not pronounced. There is considerable variation in the overall proportions of the distal articular surface in all the primates examined. However, while there is a trend for the anteroposterior dimension to become relatively longer as absolute size in primates increases, the cercopithecines do appear to have a distal articular surface that is relatively

deep anteroposteriorly, and proximodistally wide (Rose, 1988).

Although not a morphological trait, the humerus of the long-tailed macaque can be easily differentiated from that of the pig-tailed macaque by size. Even taking into consideration sexual dimorphism, the long-tailed macaque is much smaller and more gracile than the pig-tailed macaque, a difference that is reflected in the size and robusticity of the post-cranial skeleton.

LEAF MONKEYS (INCLUDING LANGURS)

All the leaf monkeys have an oval-shaped humeral head that is slightly wider mediolaterally than proximodistally (Figure 4). With the exception of the silvered langur, the bicipital groove is generally narrow and U- or V-shaped. The medial margin of the bicipital groove of the greater tubercle extends distally, for approximately a quarter of the length of the shaft. There is generally a slight mediolateral curvature halfway down



FIGURE 4

Maroon langur (*Presbytis rubicunda*: NHM A^{cen}. No. 1894.6.12.12) male left humerus: Lateral, anterior, medial and posterior views, and proximal and distal ends (Scale 10 cm: Image by K. Ki-Kydd).

the shaft. However, the curvature is not as pronounced as it is in the macaques; it is located further down the shaft. And when viewed from the posterior, the medial margin of the bicipital groove is not as prominent, and does not protrude posteriorly to the same extent. In all of the leaf monkeys the medial and lateral epicondyles protrude slightly posteriorly when viewed from the distal end, but do not produce the distinctive U-shape observed in the macaques. The colobines have a thinner, more elongate and gracile medial epicondyle than do the cercopithecines.

Within the small comparative assemblage of leaf monkeys available for study in the NHM there were no consistent morphological characteristics that could be used to differentiate the banded langur (*Presbytis melalophos*), Hose's langur (*P. hosei*), and maroon langur (*P. rubicunda*) from one another. Only with future studies of large sample size will it be possible to reach any conclusions on whether the leaf monkeys can be differentiated on skeletal morphology alone.

However, there were some marked and consistent differences in the morphology of the humeri of the silvered langur (*Presbytis cristata*) and other

langur species (*Presbytis* spp.; Figure 5). The humerus of the silvered langur is generally larger and more robust than those of the other leaf monkeys. The bicipital groove is much wider and shallower and is U-shaped. The medial margin of the bicipital groove of the greater tubercle extends distally, up to a third of the way down the humeral shaft, and the deltoid process is much more pronounced. As in the other langurs, the trochlea has a noticeable waist (concavity of the articular surface), but a greater proportion of the articular surface extends into the lateral margins of the olecranon fossa. The olecranon fossa itself is wider, deeper, and more U-shaped.

The suggestion that the humeri of the silvered langur and other leaf monkeys show some marked morphological variation is supported by studies of the crania. Hooijer (1962) noted some striking differences in the morphology of the crania of the silvered langur and the other langurs that made it easy to spot the former in a selection of *Presbytis* (*presbytis*) sp. skulls. As a result, Hooijer decided to revive the genus *Trachypithecus* and to separate the silvered langurs from the other langurs at the generic level. Some primatologists also place *cristata* in the genus *Trachypithecus* (Rowe, 1996: 187).



FIGURE 5

Silvered langur (*Presbytis cristata*: NHM A^{cm}. No. 1855.12.17.22) female left humerus: Lateral, anterior, medial and posterior views, and proximal and distal ends (Scale 10 cm: image by K. Ki-Kydd).

PROBOSCIS MONKEY

The proboscis monkey humerus is larger than those of the leaf monkeys, long and straight but similarly gracile, with indistinct muscle attachment regions on the shaft (Figure 6). The shaft is proportionately longer in comparison with the size of the articular ends than the shafts of either the macaque or leaf monkey humeri. The humeral head is more rounded than in the other monkeys, but is still slightly wider mediolaterally than proximodistally. The greater tubercle is wide in an anterolateral-posteromedial direction, has a straight anteromedial surface, and projects above the humeral head. The bicipital groove is shallow, wide, and U-shaped, and the medial margin extends distally for approximately a third of the length of the shaft. The medial and lateral epicondyles do not protrude to any great extent medially or laterally, giving the distal articular end a narrow, compact appearance. As a result there is no medial and lateral "flaring" of the supracondylar ridges. The articular surface of the trochlea has only a shallow waist, and a straight medial surface.



FIGURE 6

Proboscis monkey (*Nasalis larvatus*: NHM A^{cm}. No. 1855.12.26.242) female left humerus: Lateral, anterior, medial and posterior views, and proximal and distal ends (Scale 10 cm: Image by K. Ki-Kydd).

GIBBONS AND ORANGUTAN

Suspensory primates (gibbons and orangutan) have a relatively larger surface area of the humeral head and trochlea in comparison with members of the Family Cercopithecidae (the monkeys), providing a greater range of circumduction, but they also have a stable hinge joint at the distal end for weight transferral through the ulna (Senturia, 1995). The greater range of motion required for brachiation has produced a circular humeral head that protrudes in a posteroproximal direction above the greater and lesser tubercles. In the monkeys the medial epicondyle and trochlea are relatively small in comparison with the overall size of the distal articular end of the humerus, producing a less stable joint for the hinge motion. However, the capitulum is larger for greater weight transferral between the humerus and radius, providing even weight distribution between fore- and hind-

limbs during locomotion (Senturia, 1995). Unlike the compressive nature of the forces involved in quadrupedal locomotion, there are more tensile and torsional forces produced during suspensory movement, requiring a more stable hinge joint with the lower arm. The medial epicondyle is large, providing a greater surface area for muscle attachment, as required for a species relying mainly on the forelimbs for locomotion (Senturia, 1995). In the suspensory primates the medial keel of the trochlea extends posteriorly around the medial epicondyle and up to the margins of the olecranon fossa. Thus, when the distal articular end is viewed from the medial side, it appears that the medial epicondyle is centrally located, anteroposteriorly, within the medial surface of the trochlea. In contrast, the medial epicondyle in the monkeys is wide anteroposteriorly and, as a result, there is no clear distinction between the posterior aspect of the medial keel of the trochlea and the medial epicondyle; instead the medial epicondyle appears to extend posteriorly. In addition, there is a tendency among the monkeys for the capitulum to be longer proximodistally than anteroposteriorly. The anterior aspect of the trochlea is often extended in a proximolateral direction to varying degrees to form a developed tail (Rose, 1988). This last feature is most marked in the macaques, but was absent in the proboscis monkey specimen examined in this study.

Gibbons have a very rounded, almost ball-shaped humeral head, and the bicipital groove is narrow, sharply U-shaped, and deep (Figure 7). The shaft of the humerus is long and slender with two slight, but distinctive, anteroposterior curvatures close to the proximal and distal ends. On the shaft are visible a few indistinct muscle attachment regions. The surface of the trochlea is convex, with a deep waist between the medial keel and zona conoidea, providing a large surface for articulation with the ulna. There is a deep waist between the trochlea and the capitulum. The zona conoidea is thin but markedly pronounced.

The orangutan humerus can be differentiated from the other non-hominoid primates on size alone. In fact, fragments of orangutan humeri are more likely to be confused with human humeri than with those of other Bornean primates. Being a suspensory primate (though they are also good quadrumanous climbers), the orangutan has a humerus similar in morphology to that of the gibbon. The humerus has a round ball-shaped head and the bicipital groove is wide, shallow, and U-shaped (Figure 8). The shaft is long, slender, and straight,

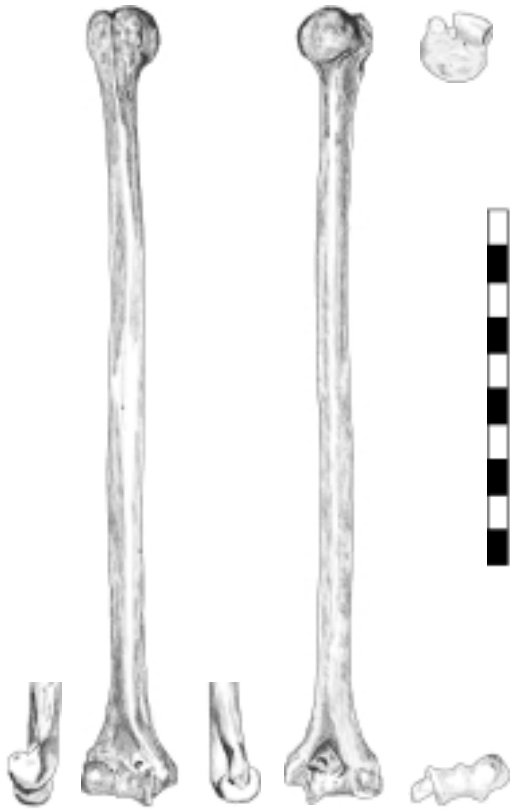


FIGURE 7

Bornean gibbon (*Hylobates muelleri*: NHM A^{cn}. No. 1879.8.30.1) left humerus (No sex): right, lateral, anterior, medial and posterior views, proximal and distal ends (Scale 10 cm).



FIGURE 8

Orangutan (*Pongo pygmaeus*: NHM A^{cn}. No. 1992.156) male left humerus: Anterior and posterior views (Scale 10 cm: Image by K. Ki-Kydd).

with distinct, but not pronounced, muscle attachment regions, radial groove and deltoid tuberosity. The coronoid fossa is deeper than the radial fossa, unlike in the other Bornean primates. The medial surface of the trochlea is convex, and there is a deep waist between the medial keel and the zona conoidea. There is also a deep waist between the trochlea and the capitulum, and both the keels of the capitulum and trochlea are pronounced.

THE PRIMATE HUMERI FROM NIAH CAVE

The Niah Caves are a complex of enormous caverns in a limestone outcrop forming the northern outlier of the Gunung Subis massif on the

coastal plain of northern Sarawak, Borneo. Excavations conducted by Tom and Barbara Harrisson in the 1950s and 1960s brought the Niah Caves to world attention with the discovery in the West Mouth of the so-called Deep Skull, at c. 40,000 BP the oldest modern human in Southeast Asia (Barker *et al.*, 2002a).

In 2001 and 2002, as part of a project undertaken by an interdisciplinary team of researchers reinvestigating the stratigraphic sequences and chronology in the West Mouth, at Niah Cave, a trench (Trench 1) 2 m long north to south and 1 m wide east to west was dug behind the area excavated by the Harrissons towards the interior of the cave, defined by the project as Area D (Barker *et al.*, 2002a, 2002b, 2003). The purpose of the test trench was to evaluate whether any archaeological

deposits still existed in situ beyond those investigated in the 1950s and 1960s. The northern half of the trench consisted of a series of inter-cutting channels that had carried water dripping from an overhang in the cave roof. These channels had become infilled with the sediments that they had truncated. In the south of the trench, the sediments (0.5 m deep) consisted primarily of a series of guano build-ups, separated by a sequence of strata indicating stabilization events (Barker *et al.*, 2002b, 2003). The deposits contained substantial amounts of human food refuse, including bones, shells, and plant remains. The completeness of some fragile skeletal elements and the lack of sedimentary compaction suggest that the trench was excavated through an area towards the interior of the cave that was reserved for the dumping of waste by prehistoric hunters and foragers to the cave (Barker *et al.*, 2003). Recently obtained C¹⁴ dates indicate that the sequence of deposits had accumulated between c. 10,000 BP and c. 8,000 BP (Barker, personal communication).

The bone assemblage contained 10 fragments of primate humeri from seven different contexts (Table 1). The two species of macaque, leaf monkeys including the silvered langur, and the gibbon were all represented. The same sequence of deposits produced 14 fragments of primate cranio-dental material (Table 2). However, only the long-tailed macaque and the other leaf monkeys (but not the silvered langur) could be identified. The results of the study suggest that, in this example,

the analysis of the cranio-dental material in isolation would have underestimated the number of primate taxa represented in the archaeological record. As a result, the evidence could have led to the misinterpretation of, for example, human hunting strategies by implying that, for one reason or another, the prehistoric hunters visiting the cave preyed on only the long-tailed macaque and leaf monkeys (other than the silvered langur). In addition some important environmental indicators provided by those parts of the primate community not represented in the cranial material would have been missed. For example, the identification of the silvered langur complements the presence of the long-tailed macaque by emphasizing the close proximity of coastal, riverine, and swamp forests to the cave entrance during the early Holocene (Payne & Francis, 1998: 227). The gibbon is the only completely arboreal taxon and is found only in high canopy dipterocarp rainforest (Payne & Francis, 1998: 229-230). Unfortunately, the fragment of gibbon humerus was recovered from a redeposited channel fill and cannot be used in the palaeoecological reconstruction, but other gibbon post-cranial elements have recently been recovered from the midden sequence.

DISCUSSION

The study of modern comparative primate humeri suggests that the suspensory apes can be

Context	Taxa	Side	Proximal/Distal/Complete
2041	<i>Macaca cf. fascicularis</i>	Right	Complete
2474	<i>Macaca cf. fascicularis</i>	Left	Distal
3014	<i>Presbytis cf. cristata</i>	Right	Proximal
3014	<i>Presbytis sp.</i>	Right	Distal
3021	<i>Presbytis cf. cristata</i>	Left	Proximal
3021	<i>Presbytis sp.</i>	Left	Distal
3021	<i>Macaca cf. nemestrina</i>	Left	Proximal
3025	<i>Hylobates sp.</i>	Right	Distal
3030	<i>Presbytis sp.</i>	Right	Distal
3223	<i>Macaca cf. fascicularis</i>	Right	Proximal

TABLE 1

Niah Cave, Trench 1, Area D: The primate taxa identified from the archaeological humeri, recorded by context.

Context	Taxa	Description
3014	<i>Macaca cf. fascicularis</i>	Fronto-nasal junction
3014	<i>Macaca cf. fascicularis</i>	Fronto-nasal junction
3014	<i>Macaca cf. fascicularis</i>	Upper right M1
3014	Primate	Skull fragment
3021	Cercopithecidae	Skull fragment
3021	<i>Presbytis</i> sp.	Auditory meatus region
3021	<i>Presbytis</i> sp.	Frag. of occipital
3021	<i>Presbytis</i> sp.	Occipital foramen
3021	<i>Presbytis</i> sp.	Frag. of frontal bone
3021	Primate	Maxillary fragment
3021	Primate	Molar fragment
3024	Cercopithecidae	Skull fragment
3025	Primate	Skull fragment
3017	<i>Macaca cf. fascicularis</i>	Maxilla (M1 and M2)

TABLE 2

Niah Cave, Trench 1, Area D: The primate taxa identified from the cranio-dental material, recorded by context.

easily differentiated from the monkey family, and the orangutan from the gibbons. Furthermore, there are distinctive morphological characteristics that permit the confident separation of the proboscis monkey, macaques, and leaf monkeys. Morphological differences in the humerus can also be used to distinguish the silvered langur from the other leaf monkeys, and the two species of macaque can be separated primarily by size and robustness or gracility. In addition the study demonstrates that the morphological criteria used to distinguish between the humeri of modern primate taxa can be used to identify the fragmentary remains of Bornean monkey and ape humeri recovered from the archaeological record.

However, the small number of comparative skeletons held within the Natural History Museum, London, has so far constrained our attempts to identify the more subtle morphological differences in the humerus that might exist between some closely related species. This is unfortunate because at present some species of primate (especially the leaf monkeys) have fragmented and restricted distributions on the island of Borneo. Therefore, the identification of different species of monkey and ape in the archaeological record not only is important for the interpretation of past human subsis-

tence strategies and palaeoecological reconstruction, but also can have an impact on contemporary biological conservation issues such as establishing the former distributions of the primates on the island.

The preliminary study undertaken on the primate humeri and cranio-dental remains recovered from Trench 1, Area D in the West Mouth of Niah Cave demonstrates how the identifications of only a small number of anatomical elements can lead to an underestimation of the number of taxa represented in a faunal assemblage. To produce reliable and confident interpretations of the structure and composition of primate assemblages, cranio-dental analyses should be supported by the identification of as many post-cranial elements as possible, to as low a taxonomic level as possible.

Future studies of the primates recovered from other areas of the site during the recent and earlier excavations will test whether previous interpretations of community composition, human hunting strategies, and palaeoecological reconstructions were accurate using just the cranio-dental remains, or when both post-cranial and cranial elements are used as complementary sources of evidence.

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