CHAPTER THREE

MACROVERTEBRATE FOSSILS

3.1 Introduction

Few studies of Quaternary large mammal faunas of Peninsula Malaysia have been done compared with other detailed studies in other South East Asia countries like southern China, Laos, Cambodia, Vietnam, Thailand, Myanmar, Java, Sumatra, and Borneo.

The particularly interesting geographical location of the Peninsular Malaysia between the Indochinese and Sundaic province enables the study of fossil vertebrate fauna to help in establishing a more detailed faunal list and provide more input on possible Pleistocene migrations routes of land mammals including prehistoric humans.

The large mammal fossil material recovered from the cave sites in this study include dissociated teeth and bones. Some of the roots of teeth and bones show traces of gnaw marks attributable to large rodents such as porcupines. This kind of taphonomy appears to be characteristic of the most fossils found in deposits of Middle Pleistocene caves in Southeast Asia (Hooijer, 1948).

In this chapter, the description for these fauna will be presented separately for two sites: Batu Caves Massif and Lenggong Valley, Perak as they are of different ages (Middle Pleistocene for Lenggong Valley and Upper Pleistocene for Batu Caves).

In the catalogue, I have included all the materials recovered from the caves studied whether they are complete or broken and the exact identification and measurements for those teeth and bones which are more or less undamaged. Each specimen has a reference number starting with letters indicative of the name of the cave as per below:

Batu Caves Massif site	
Cave name	**symbol**
Cistern Cave	CC
Swamp Cave	SC
Villa Cave	VC
Dark Cave	DC
Lenggong Valley site	
Badak Cave C	BDC
Ngaum Cave	NC

The specimens are *ex situ* when these symbols are followed by (EX). Measurements for the teeth are tabulated as: L = greatest length corresponding to the maximum mesio-distal length, W = greatest width corresponding to the maximum bucco-lingual width, (dex.) = right, (sin.) = left. All the measured dimensions relating to the large mammal's tooth or bone are in mm (± 0.1 mm).

All the specimens examined have been deposited at the Zoological Museum in the zoological collection of the Biology Department in the University of Malaya.

3.2 ORDER PRIMATES Linnaeus, 1758

3.2.1 Family Cercopithecidae Gray, 1821

The monkeys are widely distributed in the Old World from southern Europe to Africa and through central and Southeast Asia, including southern China and most of Japan. Cercopithecids are divided into two ecologically and morphologically distinct subfamilies. The more primitive subfamily Colobinae which includes the African colobus monkeys and most of the Asian genera labelled as langurs (*Presbytis, Pygathrix, Trachypithecus, Semnopithecus*) and also the proboscis monkeys *Nasalis larvatus* Wurmb, 1787, which are endemic to Borneo and *N. concolor* Miller, 1903, the Mentawai islands in Sumatra

(Corbet & Hill 1992). The subfamily Cercopithecinae, is mainly African, but includes the diverse genera of macaques which are Asian and North Africa.

There are some morphological characters of the premolars and molars of the Colobines that distinguish them from the Cercopithecines such as: the wide P_3, high molar relief, deep incised lingual notches of the lower molar, asymmetrical distal edge of the upper molar, wide spaces between the apices of the molar cusps, and short trigonid and mesial in Colobinae (Jablonski & Gu, 1991). Cercopithecids have a robust and heavily ridged skull and large upper canines separated from the incisors by a small diastema. The molars are quadrate and bilophodont and the hypoconulid is present in lower molar. Many Cercopithecids show pronounced sexual dimorphism. This may be in body size (males are up to twice the weight of females in some species), color, or in the degree of development of the canines.

The macaques have larger incisors and canines, cusps are less defined and blunt at the premolars and molars, the langurs have thinner and sharper small teeth, especially the premolars (Swindler, 1976). We attribute our fauna to the Cercopithecinae.

3.2.1.1 Subfamily Cercopithecinae Gray, 1821, Plate 1(A1 to B3)

As we mentioned previously this subfamily is currently represented by a single genus *Macaca* in Asia. In Southeast Asia, five species are attributed to this genus:

- Pig-tailed Macaque (Figure 3.1, A), *Macaca nemestrina* (Linnaeus, 1766) in Myanmar, Vietnam, Thailand, Sumatra, Peninsular Malaysia, and Borneo.
- Long-tailed Macaque (Figure 3.1, B), *Macaca fascicularis* (Raffles, 1821) from southern Myanmar to the islands of Java, Sumatra, Timor, Peninsular Malaysia, Borneo, Sulu Island and Southwest Mindanao in the Philippines.

- Rhesus Macaque *Macaca mulatta* (Zimmermann, 1780) in India, Bangladesh, Pakistan, Nepal, Myanmar, Thailand, Afghanistan, Vietnam, and southern China.

- Stump-tailed Macaque *Macaca arctoides* (Geoffroy, 1831) from Assam and South China to north Peninsular Malaysia.

- Assam Macaque *Macaca assamensis* McClelland, 1839, in Assam, Nepal, West Thailand, Laos, North Vietnam, and South China.

Figure 3.1 *Macaca nemestrina* (A) and *Macaca fascicularis* (B), source: animaldiversity.ummz.umich.edu

Mammalian fossils recovered from Middle Pleistocene to Holocene sites include a large collection of Southeast Asia macaques. In Sumatra, *M. nemestrina* is more common than *M. fascicularis* due to ecological differences or to human hunting strategies (Harrison, 1998). Global climate change with the fluctuating sea levels and the resulting separation between the continental land areas during the glacial period have also been enlisted to explain their distribution (Bird *et al*., 2005; Cannon *et al*., 2009; Wurster *et al*., 2010).

In Java, *Macaca* sp. from Punung and *M. fascicularis* from Bangle and Ngandong were described by Badoux (1959), Hooijer (1962b), and Aziz (1989) respectively. A single specimen of *Macaca nemestrina* has been recovered from the Middle Pleistocene of Sangiran (Aimi, 1981).

In Peninsular Malaysia, prehistoric bone remains of the Long-tailed Macaque were reported from Gua Cha by Adi Hj Taha (1981) and *Macaca* spp. teeth from Gua Gunung Runtuh (Davison, 1994). In Borneo, both *M. nemestrina* and *M. fascicularis* were reported from among primate materials from Niah Cave (Harrison, 1996).

Fossil remains of *M.* cf. *assamensis*, *M.* cf. *mulatta*, and *Macaca* sp. had also been discovered from different Middle and Upper Pleistocene sites in Vietnam (Ciochon & Olsen, 1990; de Vos & Long, 1993; Bacon *et al*., 2006 & 2008b) and of *Macaca robusta*, *Macaca mulatta*, *Macaca* cf. *andersoni* from Laos and of *Macaca* sp. (Fromaget, 1936; Bacon *et al*., 2011) and *M. nemestrina* from Thailand (Tougard, 1998). *Macaca robusta* and *Macaca* sp. from cave sediments and fissures in China was mentioned by Kahlke (1961).

Macaca fascicularis specimens had been recovered recently from Early Holocene cave sites on Palawan Island, Philippines (Reis & Garong, 2001).

In the present study, the Cercopithecinae are represented in Batu Caves by *Macaca fascicularis* and *Macaca nemestrina* and in Lenggong Valley by *Macaca nemestrina* alone (Table 3.1).

Table 3.1 Dimensions of the upper and lower teeth attributed to macaques in this study.

	Tooth Type	No.	L	W
Macaca fascicularis	M^1 (dex.)	CC 5-4	6.8	6.0
	Lower C (sin.)	SC 3-2	6.3	4.8
	M_1 (sin.)*	DC 7	5.5	5.3
	M_3 (sin.)	DC 6	7.6	5.2
Macaca nemestrina	P^3 (dex.)	BDC 5-4a	6.2	7.1
	P^4 (sin.)	VC 4-12	6.2	8.0
	M^2 (dex.)	BDC 1-7U	8.7	7.6

No. = specimens field number; L= mesio-distal length; W= bucco-lingual width. All measurements are in mm. * Incomplete sample.

3.2.1.1.1 Teeth description (Figure 3.2)

A. *Macaca fascicularis* in Batu Caves

Upper molar

M^1: CC 5-4 (dex.), Plate 1 (A1)

This is a small molar with a rectangular shaped crown. The sharp buccal cusps (paracone and metacone) are higher than the lingual cusps (protocone and hypocone) and all are arranged in two lobes. The anterior lobe is larger than the posterior lobe and contains the larger and higher cusp (paracone). These two lobes are clearly separated by a deep groove extending downwards at the base of the crown at both the lingual and buccal sides. A contact facet is present anteriorly. Only one robust anterior fused root is preserved.

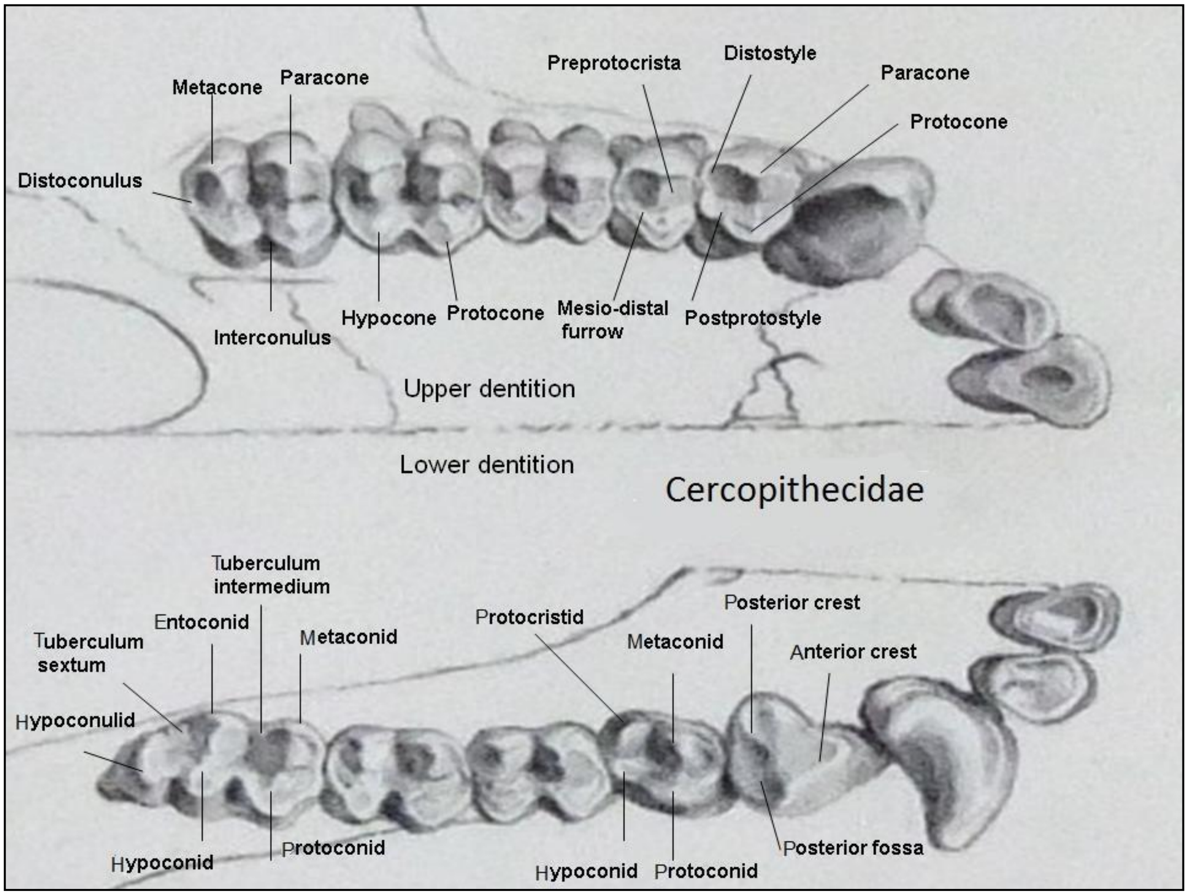


Figure 3.2 Nomenclature to describe cheek teeth structures of Cercopithecidae modified from de Blainville (1839 – 1864).

Lower canine

SC 3-2 (sin.)

This is a small complete canine of a female. It is triangular in cross section. The crown is narrow at the anterior face and sub-concave at the internal face. Both these faces have a shallow longitudinal groove running from the crown and along the robust curved root. A distinct cingulid is present at the base of the posterior enamel. A large contact facet is located at the tip of the posterior apex.

Lower molars

M_1: DC 7 (sin.)

This is a small incomplete tooth with the posterior lobe broken off so that not many features can be seen. The anterior lobe includes the lingual cusp (metaconid) and buccal cusp (protoconid). The lingual cusp is sharp, pointed, and higher than the buccal cusp. The broken posterior lobe has only a small part of the lingual cusp, the hypoconid with an incomplete single root. A wide root stock is still preserved at the base of the anterior lobe. A contact facet is preserved at the anterior side with traces of cingulid.

$M_{3:}$ DC 6 (sin.), Plate 1 (A2)

This tooth is has a rectangular crown with sharp pointed cusps forming three distinct lobes. The first lobe with metaconid and protoconid is larger than the second lobe with entoconid and hypoconid. A small accessory tubercle (tuberculum sextum) is present between the entoconid and the third small lobe (hypoconulid) with all surrounded by a small talonid. The lingual cusps are higher than the buccal cusps. Traces of an anterior contact facet is preserved with three broken roots.

B. *Macaca nemestrina* in Batu Caves

Upper premolar

P^4: VC 4-12 (sin.), Plate 1 (B1)

The occlusal view of the tooth is semi-squarish and swollen at the lingual side. The tooth is badly worn so that the dentine is exposed at the apex of the buccal and lingual cusps or paracone and protocone respectively. A small third dentine (hypocone) is present distally to the protocone. The posterior fossa is bigger and deeper and extends more posteriorly than the anterior fossa. It ends mesialy in an elongated preprotocrista. The anterior and posterior contact facets are present on both sides to give some indication of the correct position. Three roots, one lingual and two buccal are present with the anterio- buccal root semi square at broken out.

C. *Macaca nemestrina* in Lenggong Valley

Upper premolar

P^3: BDC 5-4a (dex.), Plate 1 (B2)

This is a slightly worn bicuspid tooth. The crown is sub-triangular in shape, swollen at the lingual surface, with antero-labial angle extending forward. The buccal cusp (paracone) is higher and bigger than the lingual cusp (protocone). The posterior fossa is larger than the anterior fossa and the preprotocrista is located nearer the mesial side. The mesio-distal furrow is visible at the occlusal view. The occlusal contact facet covers all the buccao-posterior area with a small interproximal facet appearing on the same side giving the correct serial position. Three complete well preserved roots, one buccaly and two lingual, are present.

Upper molar

M^2: BDC 1-7U (dex.), Plate 1 (B3)

This sample has similar morphological characters to M^1 *Macaca fascicularis* but is larger in size.

The crown is semi- rectangular in outline and swollen lingually. The tooth has four unworn cusps arranged in two lobes. The anterior lobe is larger than the posterior lobe and both are separated by a deep groove running buccally and lingually until the base of the crown. The buccal cusps (paracone and metacone) are higher than the lingual cusps (protocone and hypocone).The mesio-distal furrow is extended to both lobes. A small anterior contact facet is present at the tip of the lingual cusp. Three fragmented roots are present.

3.2.1.1.2 Remarks

It is very difficult to differentiate the various species of macaque when the materials recovered are only isolated teeth like in this study as the structural details for comparative study between living and fossil *Macaca* are insufficient. So size measurements had to be resorted to despite that some species have more or less similar dimensions such as *Macaca assamensis, M. arctoides,* and *M. nemestrina*.

Based on the reference material on *Macaca fascicularis* and *M. nemestrina* available to me and published literature, the following observations are listed below:

- The upper premolars can be distinguish generally by their shape and size besides few other features like; 1) the small third cusp (hypocone) exposed in P^4 teeth from my personal observation and Aimi (1981), who assigned the presence of this cusp to *M. nemestrina* fossils from Java, 2) the posterior fossa is often larger than the anterior fossa except in *M. mulatta* (Tougard, 1998) or they are almost identical, and 3) the preprotocrista is normally mesial, or very mesial in *M. assamensis* Tougard (1998). These characters are clearer in *M. nemestrina* than in *M. fascicularis* allowing our premolar fossil teeth (VC 4-12 and BDC 5-4a) to be identified as *M. nemestrina*.

- There is a marked sexual dimorphism in the canines of the Cercopithecids being smaller sized in the female and larger in the male. Although Hooijer (1962b) and Tougard (1998) stated that the lower premolars of those sexes can be differentiated, no lower premolars were found in this study. *Macaca fascicularis* has smaller canines than those of *M. nemestrina* (Table 3.2).

- The posterior lobe of the upper molars are reduced in size compared to the anterior lobe. This character is present in BDC 1-7U and in CC 5-4. Tougard (1998) noted the reduction or absence of the posterior lobe in *M. nemestrina*. This reduction is most marked at the level of M^3.

- The third lower molar with the talonid is preserved in our specimen. This talonid varies in development even in the same individual and may be reduced in size or absent in the M_3 of the living *Macaca fascicularis.*

- The accessory tubercle like a tuberculum sextum which is located distally to the entoconid as in DC 6 is noted in both *Macaca fascicularis* and *M. nemestrina* by Tougard (1998) and less frequently for other species. Another accessory tubercle, the tuberculum intermedium between the metaconid and the entoconid, is not seen in my collection. Hooijer (1962b) mentioned that the accessory internal tubercle to the talonid is a variable character occurring more often in larger rather than smaller $M_{3.}$

- *M. nemestrina* is represented in this study by two upper premolars and one upper molar All appearing somewhat swollen at the lingual surface more than in *Macaca fascicularis*. Jablonski and Gu (1991) listed this character among other characters as shared between *Megamacaca lantianensis* (latter re-allocated to the genus *Rhinopithecus*) with other *Rhinopithecus*. My specimens resemble those reported by Jablonski and Gu (1991) only in their swollenness. This character cannot be conclusively determined because of the small number of specimens for comparison between my specimens with others (e.g., Jablonski and Gu, 1991).

For the comparative measurements in (Table 3.2), teeth of *M. nemestrina* are larger in size than *M. fascicularis* with an overlap between the modern dimensions of *M. fascicularis* teeth with those of the modern and fossil *M. nemestrina* of both sexes.

The molars of *M. fascicularis* from Batu Caves are near or outside the upper end of the range of variation in size of the modern Sumatra and Borneo material and within the range of the modern Java material except for M_3 which is rather variable in the development but usually easily distinguishable from the other teeth. They are at the lower limit of the male variation range of the modern Sumatra and Borneo material.

It is more likely that the solitary lower canine that I have is a female as it conforms to the general morphological shape as mentioned above and by its measurements especially the length.

Three maxillary specimens (P^3, P^4, M^2) are identified as *M. nemestrina* with the largest range of dimensions specially the width when compared with recent *M. nemestrina*. They fall outside the upper variation limits in females and are near to the upper range of the males and within the length variation of the Vietnam material but fit better with those from Laos.

Table 3.2 Comparative measurements of well-preserved macaque teeth in this study with other modern and prehistoric material.

	P^3	**P^4**	**M^1**	**M^2**	**Lower C**	**M_1**	**M_3**
Macaca fascicularis							
Modern Zoological Museum (University of Malaya)							
N	10	10	10	10	9	9	11
L	3.9 - 5.5	4.5 - 6.1	5.7 - 8.0	6.3 - 8.4	4.4 - 6.8	6.0 - 7.5	7.4 -9.5
W	4.6 - 6.5	5.0 - 7.1	5.6 - 7.0	6.2 - 8.0	3.6 - 6.4	4.8 - 6.4	5.2 -7.3
National Museum of Natural History (Leiden)							
Java[1]							
L					7.7 - 11.3♂		8.7-12.5♂
					5.3 - 7.0♀		9.0-10.7♀
W	5.1 - 6.4♂	5.5- 6.9♂	6.0 - 7.2♂	7.0 - 8.6♂	4.7 - 6.2♂	4.8 - 6.3♂	5.7-7.9♂
	5.0 - 6.5♀	5.5- 6.9♀	6.0 - 7.5♀	6.7 - 8.2♀	2.9 - 3.7♀	5.2 - 5.8♀	6.0-7.0♀
Sumatra &Borneo[1]							
L					7.2 - 9.5♂		7.6 -10.5♂
					4.8 - 6.5♀		7.4 -5.8♀
W	4.7 - 6.0♂	5.1- 6.3♂	5.7 - 6.7♂	6 0 - 7.8♂	4.6 - 5.5♂	4.5 - 5.5♂	5.3 -6.8♂
	4.6 - 5.7♀	5.2- 5.9♀	5.2 - 6.3♀	5.6 - 7.2♀	2.7 - 3.6♀	4.3 - 5.2♀	4.9 -5.8♀
In this study							
Batu Caves^							
N			1		1	1	1
L			6.8		6.3	5.5	7.6
W			6.0		4.8	5.3	5.2
Macaca nemestrina							
Modern Zoological Museum University of Malaya							
N	1	1	1	1	1	1	1
L	6.4	6.3	7.3	9.3	7.7	7.4	8.8
W	6.6	6.6	6.6	8.3	7.4	5.8	7.1

Table 3.2,continued

	P^3	P^4	M^1	M^2	Lower C	M_1	M_2
Macaca nemestrina Modern National Museum of Natural History (Leiden) Sumatra &Borneo[1]							
L					9.8 - 12.5♂ 5.9 - 8.4♀		10.0-13.8♂ 9.8-11.8♀
W	5.8 - 8.5♂ 5.5 - 6.7♀	6.5 - 7.9♂ 6.3 - 7.0♀	6.9 - 7.8♂ 6.5 - 7.3♀	7.6 - 9.3♂ 7.6 - 8.7♀	5.7 - 7.8♂ 4.0 - 4.9♀	5.5 -7.4♂ 5.4 - 6.3♀	7.4 -9.5♂ 6.4 -8.6♀
Prehistoric							
Sangiran (Java)[2]							
N	1	1	1	1	2	2	2
L	5.9	6.3	8.4	9.0	9.6 - 9.7	8.4 - 8.6	12.6
W	6.6	7.8	8.4	10.3	6.8 - 6.9	7.4 - 7.8	7.7 -9.2
Niah Cave[3]							
N					1	1	2
L					10.2♂	7.4	11.5 -12.0
W					6.3♂		8.0 -8.4
Thum Wiman Nakin (Thailand)[4]							
N	1	1	1	3			3
L	5.8	5.4	6.6	8.0 - 9.6			10.2-10.7
W	6.3		7.1	7.1 - 9.8			5.7-8.0 (N=4)
In this study Lenggong Valley^							
N	1			1			
L	6.2			8.7			
W	7.1			7.6			
Batu Caves^							
N		1					
L		6.2					
W		8.0					

Table 3.2,continued

	P^3	**P^4**	**M^1**	**M^2**	**Lower C**	**M_1**	**M_3**
***Macaca* sp.**							
Niah Cave[3]							
N	5	8	5	6	4	18	19
L					8.6 - 9.8♂		6.8-10.0
W	4.8 - 5.7	5.2 - 6.1	5.5 - 6.4	6.5 -7.5	5.0 - 5.7♂	4.6 - 5.6	5.2-6.8
Sumatran Cave[1]							
N					29		32
L					8.2 - 13.7♂		9.0 -13.5
W					5.1 - 7.7♂		5.7 -9.4
N					4		
L					6.9 - 8.7♀		
Punung (Java)[5]							
N		1			5		
L		5.0			5.7 - 6.9		
W		7.0			3.5 - 4.9		
Lang Trang Caves (Vietnam)[6]							
N			94			23	10
L			7.1-13.6 $M^1/M^2/M^3$*			7.5-10.6 M_1/M_2*	10.2 -13.2
W			6.9-10.3 $M^1/M^2/M^3$*			6.0-8.6 M_1/M_2*	7.0 -8.7
Duoi U'Oi Cave (Vietnam)[7]							
N	43		69			16	15
L	4.4-11.8 P^3/P^4*		7.6-10.2 $M^1/M^2/M^3$*			7.3-9.7 M_1/M_2*	10.2 - 12.4
W	4.1-6.8 P^3/P^4*		7.1-10.2 $M^1/M^2/M^3$*			5.7-7.4 M_1/M_2*	6.4 -7.5
Ma U'Oi Cave (Vietnam)[8]							
N	1	2	1		1	1	2
L	5.1	5.3 - 6.4	9.1 M^1/M^2*		5.3	8.5 M_1/M_2*	10.2 - 1.0
W	5.7	4.4 - 6.0	8.2 M^1/M^2*		6.5	6.3 M_1/M_2*	6.2
N	1						
L	4.8 P^3/P^4*						
W	5.8 P^3/P^4*						

Table 3.2, continued

	P^3	**P^4**	**M^1**	**M^2**	**Lower C**	**M_1**	**M_3**
Tam Hang (Laos)[9]							
N	11	7	41			12	7
L	5.4 - 7.0	5.6 - 6.6	8.0-10.2 $M^1/M^2/M^3$*			7.6-10.0 M_1/M_2*	10.1 -13. 7
W	5.6 - 8.0	6.0 - 8.0	7.1-9.8 $M^1/M^2/M^3$*			5.8-8.9 M_1/M_2*	7.0 – 9.0

N= number of samples, L= mesio-distal length; W= bucco-lingual width.
All measurements in mm after:
[1]Hooijer (1962b); *Macaca fascicularis* in Java identified as *Macaca fascicularis mordax*
[2]Aimi (1981)
[3]Hooijer (1962c)
[4] Tougard (1998)
[5] Badoux (1959)
[6] De Vos & Long (1993)
[7] Bacon *et al*. (2008b)
[8] Bacon *et al*. (2004 & 2006)
[9] Bacon *et al*. (2011)
*The measurements are for the unclassified group
^Refer to (Table 3.1) for more details

3.2.2 Family Hominidae Gray, 1825

The hominids are the members of the biological family Hominidae (the great apes, humans and their fossil relatives), the classification of the great apes changed over time as new evidence from fossil discoveries and comparisons of anatomy and DNA analysis have changed the understanding of the relationships between hominid members.

Commonly, this family includes four living genera The three grouped within the subfamily Homininae are the chimpanzees and bonobo (*Pan*), gorillas (*Gorilla*), humans (*Homo*) while Orangutans (*Pongo*) belong to the Ponginae subfamily.

The dental fossils recovered in the current study are attributed to the Ponginae. These are the first fossil *Pongo* recorded in Peninsula Malaysia.

3.2.2.1 Subfamily Ponginae Elliot, 1913, Plate 1(C1 to C10)

This subfamily has one living genus *Pongo* with two species; *P. abelii* Lesson, 1827, that is confined to the island of Sumatra and *P. pygmaeus* (Linnaeus, 1760) (Figure 3.3) in Borneo (Groves, 2001a; Brandon-Jones *et al.*, 2004). The Bornean Orangutan has at least three subspecies:

- Northwest Bornean Orangutan *P. p. pygmaeus* in Sarawak (Malaysia) and northern West Kalimantan (Indonesia)

- Central Bornean Orangutan *P. p. wurmbii* in southern West Kalimantan and Central Kalimantan (Indonesia)- Northeast Bornean Oangutan *P. p. morio* in Sabah (Malaysia) and East Kalimantan (Indonesia), (Figure 3.4) show the distribution map of Bornean Orangutan.

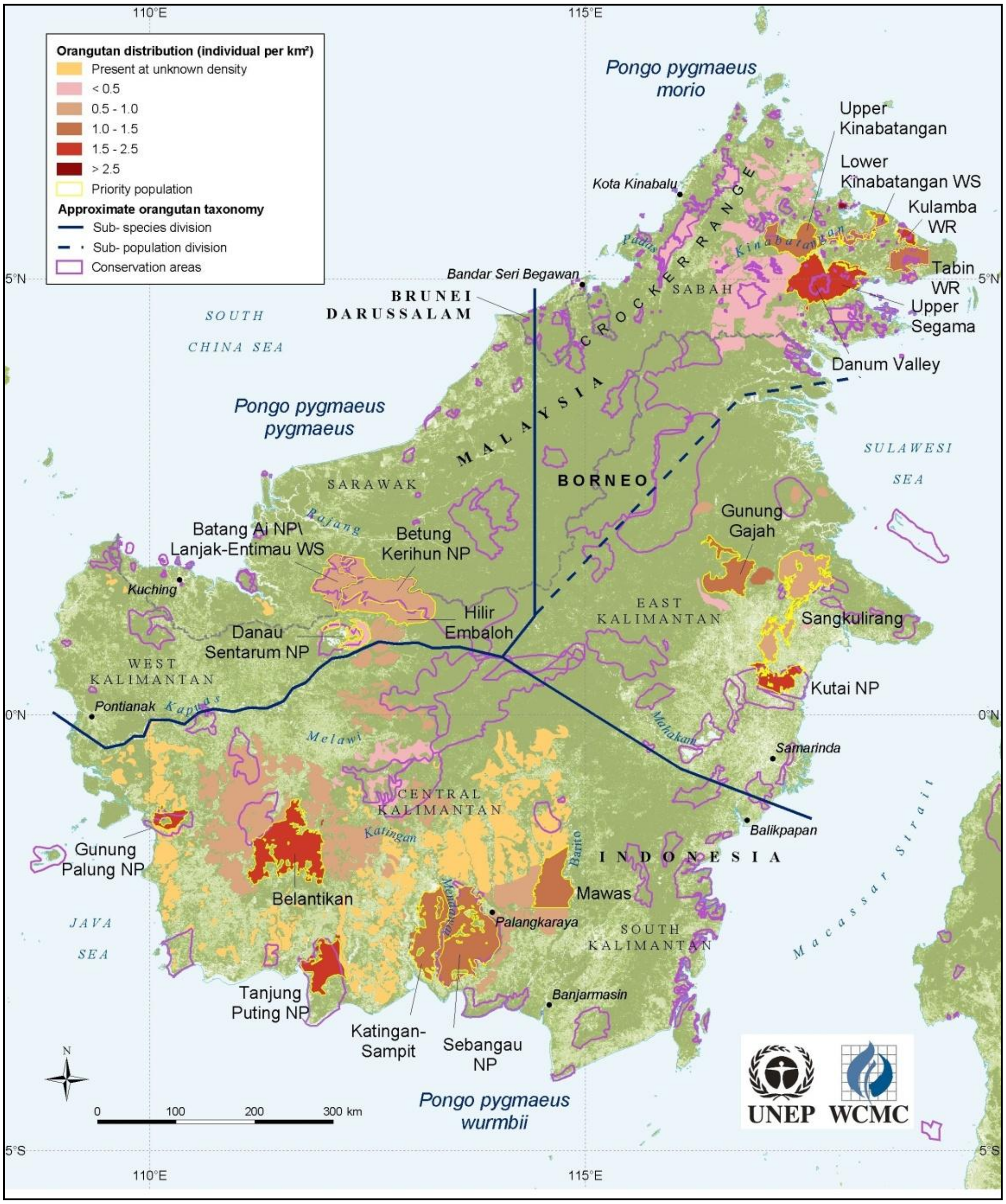


Figure 3.4 Bornean Orangutan distribution map, source: Caldecott, J., Miles, L., eds (2005) World Atlas of Great Apes and their Conservation. Prepared at the UNEP World Conservation Monitoring Center. University of California Press, Berkeley, USA. Remodified By Rona Dennis, Erik Meijard & Lee Shan Khee for GRASP, September 2005.

The *Pongo* fossil record was formerly widespread in Quaternary Southeast Asia. Dental remains (molars) of Pleistocene age discovered at Trinil, Java, by Dubois (1891) were assigned to *Pongo* by Von Koenigswald (1940) and Hooijer (1948). These molars have since been re-identified as *Homo erectus* (Smith *et al*., 2009). Groesbeek, (1996) concluded that it was impossible to determine the serial positions of the Trinil molars.

Figure 3.3 Bornean Orangutan *Pongo pygmaeus* with infant, source: www.arkive.org

In the Sangiran area, Grine and Franzen (1994) subsequently commented on the difficulty in distinguishing between the molars of hominids (human) and *Pongo* from the classic Sangiran sites based on the isolated and undated surface finds reported by Aziz and Saefudin (1996) and Kaifu *et al*. (2001) which were of uncertain provenance and identity (cf. Grine and Franzen, 1994). None the less, in an extensive review, Smith *et al*. (2011) have left open the likelihood that some specimens remain attributable to *Pongo* among the classic Sangiran sites, i.e., Middle Pleistocene.

A collection of *Pongo* teeth from caves in the Padang Highland of Sumatra itemized by Hooijer (1948) has an estimated relative age range of 80 - 60 ka (de Vos, 1983; Drawhorn, 1995 a, b).

Excavations at Niah Cave, Sarawak, have yielded abundant remains of *Pongo* continuously through the terminal Pleistocene and Holocene (Hooijer, 1960; Barker *et al*., 2007). Remains of *Pongo* had also been recovered from Holocene archeological sites in the Madai Caves of Sabah (Cranbrook, 1988a; Harrison, 1998).

Middle and Late Pleistocene fossils had been found in Thailand (Tougard, 1998; Tougard and Ducrocq, 1999), Laos (Kahlke, 1972; Arambourg & Fromaget, 1938; Fromaget, 1940; Lê, 1998 in Tougard & Ducrocq, 1999; Louys *et al*., 2007; Bacon *et al*., 2008a, 2011), Vietnam (Schwartz *et al*., 1994, 1995; Long *et al*., 1996; Bacon & Long, 2001; Bacon *et al*., 2008b; Zeitoun *et al*., 2005, 2010) and Cambodia (Beden & Guérin, 1973). Dates for *Pongo* remains from Vietnamese caves vary from 475 ±125 ka for Tham Khuyen Cave (Ciochon *et al*., 1996) to 23 ka for Nguom rock shelter in northern Vietnam (Cuong, 1992 reported in Bacon & Long, 2001). In China, abundant Early, Middle and Late Pleistocene dental specimens of *Pongo* have been reported, concentrated in the southern provinces (Pei, 1935; Hooijer, 1948; Kahlke, 1972; Gu *et al*., 1987; Ho *et al*., 1995; Wang *et al.*, 2009; Zhao *et al*., 2009).

Ten isolated fossil *Pongo* teeth from two cave sites were found in the current study representing a new discovery in Peninsular Malaysia. Casts of seven teeth were given to both the National Museum of Natural History (Leiden) housed with the Dubois collection of casts, and the Natural History Museum (London). Measurements of these teeth and casts registration numbers are given in (Table 3.3).

Table 3.3 Dimensions of the upper and lower teeth with computed dental crown area attributed to *Pongo* recovered in this study.

Tooth Type	No.	L	W	Crown Area $(mm)^2$	Casts registration No. in NHM
P^4 (dex.)	CC 3-6	11.6	16.3	189.1	M83837
P^4 (dex.)	SC 6-2	8.9	13.0	115.7	M83839
P^4 (dex.)	BDC 1-28U	9.2	13.0	119.6	M83835
M^3 (dex.)	CC 6-3	12.7	15.6	198.1	
I_2 (dex.)	SC 3-4	10.0	11.3	113.0	
P_3 (dex.)	BDC 1-10L	15.0	10.6	159.0	M83833
P_4 (dex.)	SC 3-3	11.3	12.5	141.3	M83838
P_4 (sin.)	BDC 1-19U	9.7	11.5	111.6	M83834
M_1/M_2 (sin.)	VC 4-4	17.6	14.8	260.5	
M_1/M_2 (dex.)	BDC 5-3	15.3	13.4	205.0	M83836

No. = field number of specimen; L= mesio-distal length; W= bucco-lingual width; NHM=Natural History Museum (London). All measurements are in mm.

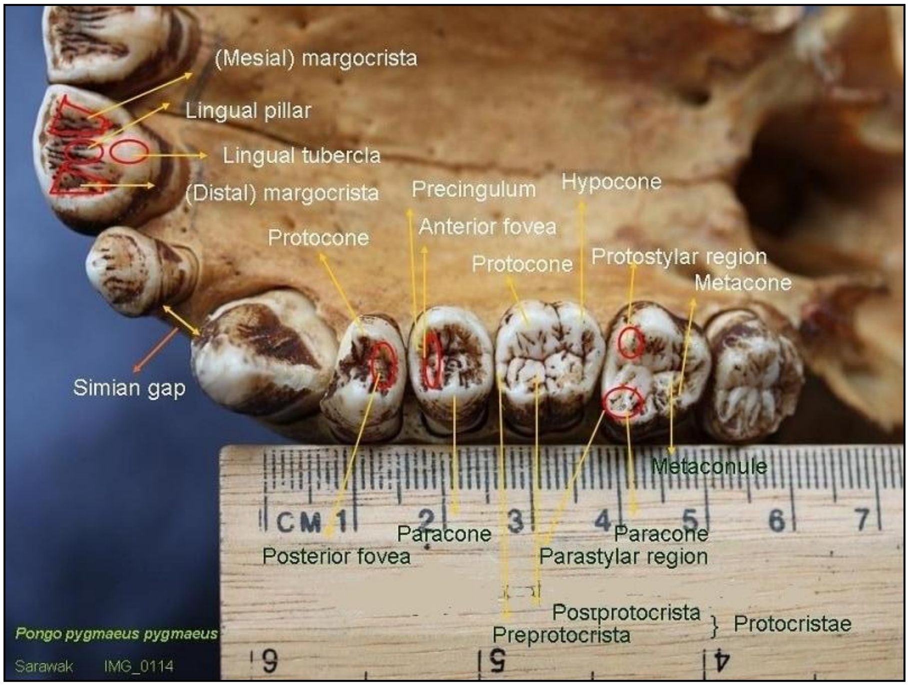
3.2.2.1.1 Teeth description (Figure 3.5)

A. *Pongo* in Batu Caves

Upper premolars

P^4: CC 3-6 (dex.), Plate 1 (C1)

The slightly worn crown of this tooth is bicuspid and oval in shape. Both mesial and distal surfaces are flat though the former is somewhat convex vertically and transversely. Interproximal contact facets are visible on both surfaces. The lingual and buccal surfaces are gently curved. Contact angles between the marginal and mesial and distal ridges are all rounded with no clear prominence of the mesio-external angle. The paracone (buccal cusp) is shaper and higher in profile than the protocone (lingual cusp) but both are sub-equal in size and aligned on the same coronal plane. Both are situated closer to the posterior marginal ridge which accounted for the longer anterior marginal ridge. The latter is also set lower in profile than the posterior marginal ridge. The two cusps are separated by a shallow but clear mesio-distal developmental groove which does not cut through the marginal ridges. The course of this major groove tends to follow the longitudinal axis of the tooth except for its posterior section which bends lingually towards the distal part of the protocone. The posterior transverse ridge runs distally from the paracone and reaches the tip of the protocone. Another transverse ridge connecting the anterior parts of the two cusps runs almost parallel to its posterior counterpart. The anterior transverse ridge is clearly bisected by the major developmental groove, whereas owing to the lingual bending of the back half of this groove, the posterior transverse ridge does not seem to be so affected. The anterior fovea is larger in extension than the posterior but the central fovea occupies most of the surface area. Shallow furrows and the coarse enamel wrinkles which they define radiate from the center of these depressions towards their margins. No traces of the cingulum are visible on both lingual and buccal surfaces. The marginal ridges appear smooth and no accessory cusps or tubercles are detected. The upper and middle parts of the roots are preserved with three roots observable: one lingually and two buccally. The former is the most robust while the antero-external is the smallest. The antero-external root has a longitudinal depression along its anterior surface and is elongated in cross section whereas the lingual root is more rounded. All three are fuse together on the upper part where the fused section on the posterior surface exhibits a shallow depression.



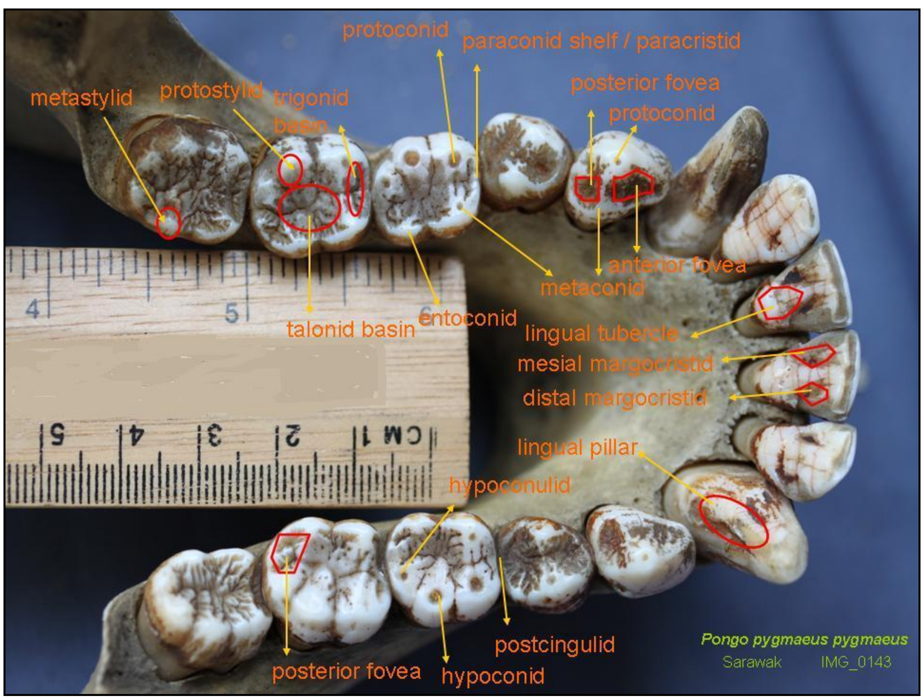


Figure 3.5 Nomenclature to describe the upper cheek teeth (top) and lower cheek teeth (bottom) structures of *Pongo*.

P^4: SC 6-2 (dex.), Plate 1 (C2)

The crown is well-preserved, slightly worn, but with only a minor portion of root remnants still attached mesio-lingually. Oval in outline shape with somewhat flattened mesial and distal surfaces. Interproximal contact facets are discernible on both surfaces. The wider buccal surface, however, is higher and less convex than the lingual surface. This is a typical bicuspid tooth with the protocone (lingual cusp) shorter and blunter than the prominent paracone (buccal cusp). Both are situated at the edge of the crown and the paracone appears slightly larger than the protocone. The lingual crown surface of the protocone is flaring. Even though only slightly worn with clear fine enamel wrinkles on the occlusal surface observable, there are still a number of occlusal attrition facets seen on some of the ridges. Parts of enamel on the posterior surface of the paracone and most on the protocone have broken off during extraction. A shallow but distinct mesio-distal developmental groove separates the two cusps but without cutting through the mesial and distal marginal ridges. An anterior transverse ridge passes down from the tip of the paracone and runs inwards and forwards across the occlusal surface and ultimately joins one of the few minor ridges in front of protocone. An almost parallel posterior ridge connects the protocone to the distal aspect of the paracone. Both ridges, however, are bisected by the mesio-distal developmental groove at the bottom of the central depression. These ridges, together with the marginal ridges, divide the occlusal surface into three parts. The central fovea is the largest where a few shallow grooves can be seen to radiate from the center and touch the anterior and posterior ridges of the fovea at right angles. The posterior fovea seems to be shallower and smaller in size than the anterior fovea owing to a more advance stage of attrition in the distal part of the occulsal surface. No traces of a cinglum are seen on either side of the tooth.

Upper molar

M^3: CC 6-3 (dex.), Plate 1 (C3)

Four major cusps with moderately degree of wear are observable on this tooth. The subtriangular outline of the crown is caused by the distinct regression in the postero-buccal border, owing to the more inward position of the metacone relative to the paracone. The crown is generally well-preserved but worn, especially on the buccal side around the paracone and metacone. There is a small occlusal attrition facet posterior to the paracone and close to the buccal margin. Lingual cusps appear to be more emerged than those on the buccal side. The sulcus obliquus is well-marked on the crown surface separating the hypocone from the other cusps but not extending down towards the lingual surface between protocone and hypocone. The obliquely oriented postprotocrista (crista oblique) is visible on the posterior slope of the protocone. Its presumed extension towards metacone, however, is obliterated by the advanced stage of wear. The presence of an anterior fovea is determinable since this part of the tooth has been corroded by dental pathology. The central basin occupies the largest surface area. The posterior fovea, located disto-lingually, is clear but small and bounded mesially by a ridge running down from the posterior surface of the hypocone and posteriorly by the distal marginal ridge. Coarse wrinkles are concentrated around the depression created by the sulcus obliquus and at the base of the posterior fovea running at right angles towards the margins of these basins. A number of minor furrows are still observable on the smoothly worn occlusal surface at the buccal cusps area. A big and deep carious cavity had developed on the anterior side of the occlusal surface extending from the anterior interproximal surface to the front part of the central basin almost obscuring the protocone and only leaving the lingual edge of the cusp visible. Both the lingual and buccal surfaces are smooth and no traces of cingulum are observable. The buccal surface is more distended horizontally at the paracone area than the relatively flat lingual surface. No posterior contact facet is detected on the rather smoothly curved posterior surface. Only a small section of the root is preserved.

<u>Lower incisor</u>

I_2: SC 3-4 (dex.), Plate 1 (C4)

The lower part of the lateral (distal) surface is slightly worn and its associated root was broken during extraction. A portion of the root attached to the mesial (median) surface is preserved. The mesial surface of the crown is higher and more vertical than the lateral surface and is somewhat convex labio-lingually towards the gingival border. Even though much of the mesial surface and the adjoining incisal (cutting/occlusal) border are still lightly covered with matrix, it is clear that it rises and forms an almost acute angle with the incisal edge whereas the latero-incisal angle is blunted, which accounted for the asymmetrical shape of the otherwise typical shovel outline for the tooth. The incisal edge shows only slight wear but no traces of the middle tubercle such as are observable in unworn teeth are discernible. The labial surface is flat but shows a small degree of convexity vertically and transversely at the section of the crown where the mesio-lateral diameter is largest. The labio-mesial margin is constricted sharply from then on towards the central part of the crown at the base in contrast to the gentler curve of the labio-lateral margin. There is also a series of thin and finely separated horizontal lines across much of the surface In addition to a number of small shallow vertical grooves in the middle section of the labial surface., A moderately developed cingulid rises from the relatively well-marked central tubercle on the lingual side which tapers towards the incisal margin but not touching the edge. The tuberculum dentale is clear on the lingual surface with some minor vertical ridges and grooves on both the shallow lateral and mesial margocristae, defined by the central tubercle and the lateral and mesial ridges, respectively.

Lower premolar

P_4: SC 3-3 (dex.), Plate 1 (C5)

The crown of this slightly worn multicuspid tooth is roughly trapezoid in shape, narrower at the anterior and broadens towards the posterior end. All angles are rounded with a flaring antero-buccal surface with gingival line located lower towards the roots than the lingual side of the crown. Parts of the crown are still lightly covered with matrix and the enamel layer was detached from the antero-lingual surface, thereby exposing the underlying white dentine. This seems to be a damage caused during extraction or preparation in the laboratory as the rather clean breakage surface indicates. Two major cusps of sub-equal size and height are observable on the rim of the occlusal surface: the buccal protoconid and lingual metaconid. The former is higher than the latter as measured from the cervico-enamel junction owing to the bulging buccal surface. A transverse ridge (protocristid) connects the tips of both cusps. This is bisected by a mesio-distal developmental groove (antero-posterior sulcus) and is placed nearer to the anterior marginal ridge and not in the middle of the crown surface. A medium sized shallow depression (trigonid) is thus formed in the anterior part of the crown surrounded by the anterior marginal ridge and the protocristid. Posterior to the tips of these cusps run two longer parallel vertical ridges merging ultimately in the posterior marginal ridge. These, together with the protocristid as the anterior border enclose a larger and deeper depression (talonid), occupies more than two-thirds of the crown area. Coarse enamel wrinkles are seen in both trigonid and talonid basins but with different radiating patterns. Wrinkles run from a central bucco-lingual groove in the trigonid basin vertically towards the anterior marginal ridge and the protocristid.

There are two centers of radiation for such wrinkles in the talonid basin, one from the posterior half of the mesio-distal developmental groove and the other on the central lingual section of the basin. One minor cusp (hypoconid) is discernible on the disto-buccal side of the crown and is separated from the posterior ridge of the protoconid by a small notch. Posterior to the notch and directly from the distal surface of the hypoconid runs a short shallow oblique ledge spreading across the disto-buccal surface and merging ultimately into the flaring buccal surface. The entoconid is present on the disto-lingual side in the form of a weak bump on the crown border. An interproximal contact facet is present only on the distal surface and an occlusal attrition facet has caused the posterior ridge of the protoconid to be less sharp than the ridge posterior to the metaconid. Only part of the confluent posterior roots is preserved and this shows a posterior vertical groove between the buccal and lingual components. Both are mesio-distally compressed and elongate in cross section. The pulp chamber is exposed underneath the anterior half of the tooth crown.

Lower molar

M_1/M_2 : VC 4-4 (sin.), Plate 1 (C6)

This is a heavily worn low-cusped tooth with only remnants of roots preserved. Its crown is roughly rectangular in outline with five primary cusps located at the edge of the occlusal surface. The mesial surface, with a clear interproximal contact facet at the upper middle section, is smooth and flat and turns into the lingual and buccal surfaces at almost right angles. The distal surface, however, is convex vertically and forms an obtuse angle with both the lingual and buccal surfaces. It too contains an interproximal contact facet but smaller and located closer to the buccal side than the case for the mesial surface. The bilobate lingual surface is smooth and only moderately convex vertically especially towards the cervico-enamel junction. The comparatively low-crowned buccal surface is distinctly trilobed in outline with a more convex curvature from the occlusal to cervico-enamel junction.

No traces of cingulid are observable on both the lingual and buccal surfaces. The two lingual cusps, metaconid and entoconid are higher and sharper than the three cusps on the buccal side (protoconid, hypoconid and hypoconulid) with the metaconid highest among the five cusps. The protoconid and metaconid are aligned in a position roughly oppose to one another whereas the hypoconid is located in opposition to a minor cusp in between metaconid and entoconid. The smallest cusp, the hypoconulid, is positioned buccally closer to the hypoconid and slightly distal to the entoconid. Occlusal attrition facets are seen on the tops of the three blunted buccal cusps but only the protoconid shows signs of advanced wear with the dentine disk exposed. All three, together with parts of the posterior and anterior marginal ridges adjoining the hypoconulid and protoconid, respectively were smoothened by attrition. The protoconid and metaconid are linked by a single transverse ridge (protocristid), which together with the anterior marginal ridge, delineates a narrow and shallow trigonid basin. The majority of the crown surface is occupied by the deep talonid basin which is bounded by the protocristid anteriorly and distally by another transverse ridge (post-protocristid) between the entoconid and hypoconulid. This latter ridge, however, is not as well-marked and distinct as the protocristid. A third depression, a vestigial posterior fovea (post-talonid basin) bounded by the post-protocristid and posterior marginal ridge, was discernible behind the spacious talonid basin. This small depression is located centrally at the distal end of the longitudinal axis. All three depressions and the protocristid and post-protocristid are bisected by a shallow mesio-distal developmental groove. The major 5 cusps and grooves are only loosely arranged in the '*Dryopithecus* (Y-5) type' (Schwartz, 1988), with the dividing grooves not very clearly marked but metaconid and hypoconid in contact at the base of the talonid basin. Remnants of enamel crenulations are seen in both the trigonid and talonid basins. In both cases these seem to fall from the defining ridges or from the tops of the cusp towards their respective centers.

No deflecting wrinkle is detected due to occlusal wear. Two weakly developed accessory cusps around the entoconid are observable, one between it and the hypoconulid which may represent the tuberculum sextum (C6), and the other between the metaconid and entoconid which may indicate the occurrence of the tuberculum intermedium (C7). The accessory cusp posterior to the entoconid is separated from it by a shallow groove visible on the lingual surface. On the same surface a small depression can be seen between the entoconid and the anterior accessory cusp. Immediately under the tooth crown are remains of the confluent anterior and posterior roots which show signs of gnaw marks by rodents.

B. *Pongo* in Lenggong Valley

<u>Upper premolar</u>

P^4: BDC 1-28U (dex.), Plate 1 (C7)

The heavily worn crown is oval in outline with two major cusps preserved. Root remnants are attached to the mesio-buccal surface. All angles between the marginal ridges and mesial and distal borders are rounded. The paracone (buccal cusp) is higher than the protocone (lingual cusp) in profile, though both are blunt and worn down, exposing the underlying dentine. The area around the latter is in a more advance stage of wear so that the exposed dentine disk is considerably larger. Enamel crenulations and most of the ordinary major ridges are weakly discernible due to the worn down condition of the tooth. The small anterior fovea and its defining margins are almost obliterated, and the equally small posterior fovea can, however, still be located at the distal end of the tooth closer to the paracone. Interproximal contact facets are clear on both mesial and distal surfaces.

Lower premolars

P_3: BDC 1-10L (dex.), Plate 1 (C8)

This is a slightly worn unicuspid tooth with a sectorial crown surface outline. The mesio-distally extended protoconid is prominent and pointed, with a convex buccal surface. The flaring of this surface brings the antero-buccal part of the gingival line further down towards the roots as compared to the condition in the distal half of the tooth. The lingual surface is generally flat and slightly concave in the middle. The ridge (paracristid) passes mesially down from the protoconid is straight and runs smoothly along the anterior margin of the tooth before merging with the front part of a rather weakly developed but clearly defined lingual cingulid. A transverse ridge (protocristid/ metaconid ridge) runs down internally and distally from the protoconid tip terminating in a minor cusp (metaconid) before converging with a thickened section of the distal marginal ridge. The metaconid is distinctly smaller and less well-marked than the protoconid. Another relatively short and smooth ridge (posterior ridge) passes distally from the protoconid to meet with a minor tubercle (? hypoconid) at the disto-buccal corner of the tooth that ultimately connects with the distal marginal ridge. These ridges and lingual cingulid make up the defining borders of the two major occlusal depressions: a trigonid fossa in the anterior and a talonid fossa in the posterior. The former is equilateral triangle in shape and larger. It occupies about two thirds of the total crown area or as much as the talonid fossa. There is one vertical groove running from its shallow basin at the center across the surface towards the lingual side and passes down onto the lingual surface of the crown. This groove divides the trigonid fossa into two parts with the front part concave and the distal part convex especially on its lingual section. The talonid fossa is deeper and circular in outline. Enamel crenulations are weak and only occur in both basins. Posterior to the distal marginal ridge and close to the minor tubercle (? hypoconid) at the base of the posterior ridge from the protoconid are two very small basins with closely packed crenulations radiating from their centers. Interproximal contact facets are seen on both mesial and distal surfaces, the former being larger than the latter. Only parts of the anterior and posterior roots are preserved.

P_4: BDC 1-19U (sin.), Plate 1 (C9)

This is a relatively small and moderately worn tooth with only the crown preserved. The crown is roughly square in outline with a slightly wider posterior margin than anterior. The buccal surface is convex vertically and horizontally whereas the lingual surface is relatively flat. The antero-buccal crown bulge is not strongly developed so that the gingival line along this surface is only slightly lower than that in the antero-lingual side. The lingual cusp (metaconid) and the buccal cusp (protoconid) are arranged in a transverse line opposite each other with both located at the margine of the crown. The former is slightly larger than the latter but both are blunted by wear. Attrition has also worn down the enamel tip of the protoconid, thereby exposing a small circular dentine disk on the occlusal surface. Short ridges extend from the anterior part of both cusps curving smoothly into the anterior marginal ridge of the crown. A transverse ridge (protocristid) connecting the tips of the cusps are cut in the middle by the antero-posterior developmental groove (mesio-distal sulcus). Only traces of the anterior half of this groove are discernible as it has been obliterated by wear whereas the second half of it is less affected. From the posterior aspects of the protoconid and metaconid run two almost parallel vertical ridges which bend inwards and outwards, respectively, to converge with the posterior marginal ridge. All these ridges thus divide the occlusal surface into two basins: a small shallow anterior trigonid and a spacious and relatively deep concave posterior talonid that occupies about two-thirds of the total crown area. The trigonid is oval in shape and dips towards the mesial surface but the roughly circular talonid remains within the boundaries set by the surrounding ridges.

Most of the enamel wrinkles have been obliterated by wear and only remnants in the form of shallow tiny pits and shallow grooves are observable within the two fovea especially on the lingual side of the talonid. The clearly defined postero-buccal and postero-lingual corners and rims of the crown are rounded and worn, therefore no definite signs of the minor cusps (hypoconid and entoconid) are observable if present. A small concavity exists on the postero-buccal surface between the protoconid and the hypoconid. Interproximal contact facets are seen on both mesial and distal surfaces.

<u>Lower molar</u>

$M_1/M_{2:}$ BDC 5-3 (dex.), Plate 1 (C10)

This is a multicuspid bunodont tooth possibly in the early stage of advance wear. The crown is roughly squarish in outline containing five cusps located on the marginal edges. The lingual cusps (metaconid and entoconid) are sharper and higher in profile than the buccal cusps (protoconid, hypoconid and hypoconulid). The bluntness of these is mainly due to the more advanced degree of wear on the buccal cusps area. With the respective enamel caps eroded by attrition, dentine disks of varying sizes are observable on all three with the hypoconid having the largest and deepest, followed by those of the protoconid and hypoconulid. Even though it remains the highest cusp of all five, the metaconid still suffers a small degree of wear exposing the underlying dentine. It is, nevertheless, the least affected of all four worn down cusps with the size of the dentine disk being smallest. The entoconid, only slightly more emergent than the hypoconulid, remains perfect with enamel covering but with a clear occlusal attrition facet on its distal surface. The anterior cusps (protoconid and metaconid) are aligned along the same line but the hypoconid is placed in opposition to the interval between the two lingual cusps. The hypoconulid, smallest of all cusps, is positioned closer to the hypoconid rather than on the central axis.

The connecting transverse ridge between protoconid and metaconid (protocristid) is double with a weak shallow groove running from the side of the protoconid dentine disk to that on the metaconid. This ridge and the anterior marginal ridge form the borders of a small transverse slit (trigonid fossa) which has worn down almost to the base level of the fovea. Posterior to the vestigial trigonid fossa is the spacious talonid fossa which is deeper and occupies most area of the occlusal surface. Its posterior border, the transverse ridge connecting hypoconid and entoconid (postprotocristid), however, is not well-marked, being obliterated by wear along its course. A flattened remnant of it can still be seen on the crown area between hypoconulid and entoconid. This and the posterior marginal ridge make up the borders of a rather narrow and shallow postero-lingually positioned basin or vestigial post-talonid fossa. The major grooves and cusps are arranged in a typical "*Dryopithecus* (Y-5) pattern": the metaconid and hypoconid meet at the base of talonid fossa; only shallow traces of the separating groove between the lingual cusps are observable due to surface wear, but at the base of the talonid fossa it bifurcates into a mesial minor groove separating the protoconid and hypoconid while a posterior counterpart cuts between hypoconid and hypoconulid. The mesial minor groove continues onto the buccal surface as a vertical groove running down to about half of the crown height. A central mesio-distal developmental groove between the anterior cusps starts off from the anterior fovea, bisects the protocristid and runs through the anterior part of the talonid basin before joining up with the main 'Y' grooves at the base of the basin. Thereafter it leaves no clear traces of its course on the occlusal surface. Posterior to the contact surface between the metaconid and hyopoconid is another central groove passing between hypoconulid and entoconid, ultimately ending up in the post-talonid fossa. Most of the enamel wrinkles at the base of the basin are obscured by wear but remnants of which are readily observable around the dentine disks and on the two relatively unworn lingual cusps.

Both lingual and buccal surfaces are smooth and without any traces of a cingulid discernible. The mesial interproximal contact facet (located between protoconid and metaconid) is larger than the distal facet under the hypoconulid. Only remnants of the anterior and posterior roots, with gnaw marks by rodents, beneath the crown are preserved.

3.2.2.1.2 Remarks

The *Pongo* teeth collection described above comprises one lower incisor, three upper premolars, three lower premolars, one upper molar and two lower molars extracted from Cistern, Swamp, and Villa Caves (Batu Caves sites) and from Badak Cave C (Lenggong Valley site). Most of the crowns of these ten isolated teeth are well preserved, with some parts of the roots showing clear signs of gnawing by rodents. Crown area measurements of the Orangutans are used here to provide a better reflection for size than just using the length and width measurements alone. Comparative crown area data for other modern and fossil *Pongo* teeth from different sites with mean and standard deviation are shown in (Table 3.4). Comparisons between equivalent tooth types show that specimens from the Late Pleistocene Batu Caves sites are larger than those from the Middle Pleistocene Lenggong Valley site. Collections from other South-east Asian sites have suggested a trend of diminution of tooth crown size among *Pongo* in the course of the Quaternary (Hooijer, 1948;, Koenigswald, 1982; Gu *et al*., 1987; Ho *et al*., 1995). The general tendency of dental size reduction of *Pongo* in the Quaternary might not be tied strictly to chronology (Cameron, 2001) and these new examples from Peninsular Malaysia, of widely different ages, show no consistent pattern. Compared with data presented by Harrison (2000), the Badak Cave teeth of Middle Pleistocene age fall within the range of modern *Pongo*, while two of the six Late Pleistocene teeth (Batu Caves sample) exceed the upper limits.

The upper P^4 specimen (SC 6-2) is smaller than its equivalent from Batu Caves (CC 3-6) and from Badak Cave C (BDC 1-28U) (Table 3.4). However, (SC 6-2) is the smallest upper P^4 among the collections and it should also be noted that (BDC 1-28U) has nearly similar dimensions in width to smaller teeth reported from other Mid-Pleistocene sites in Vietnam, Thailand and China. Its crown area however, is closer to the means of males of modern species, and also to fossils and sub-fossils from Late Pleistocene sites, including Punung (Java), Padang caves (Sumatra) and Niah Caves (Borneo) (Table 3.4). CC 3-6, moreover, is larger than the Vietnamese fossils and its dimensions are within the upper range of variation of teeth collected from caves in South China (Table 3.4).

The same is true for other comparable pairs of dentition (BDC 1-19U, SC 3-3 for lower P_4; BDC 5-3, VC 4-4 for lower M_1/M_2). In all three cases, the Badak Cave C teeth are consistently either smaller or with dimensions located in the lower ranges of teeth from chronologically comparable sites in continental Asia. Given the small sample size of materials from Badak Cave C (n=4), it is possible that only smaller sized female individuals are represented, thereby explaining the size difference between them and other Mid-Pleistocene forms. Alternatively, it may indicate that the Mid-Pleistocene *Pongo* population in Peninsular Malaysia represented a somewhat smaller form inhabiting a marginal distribution range compared to their larger counterparts further north.

The large lower P_3 (BDC 1-10L) is bigger than the average size of teeth from Punung and Niah and some of the Vietnamese materials- Morph 2b of *P. hooijeri* from Tham Khuyen (Schwartz *et al*., 1994 & 1995), a young individual from a cave in Hoa Binh Province (Bacon & Long, 2001), and specimens from Thailand (Tougard, 1998) but it is smaller than the presumed male form of *P. hooijeri* (Morph 2a of Schwartz *et al*., 1994), and has a crown area below the mean for the South China form, *P. pygmaeus weidenreichi* (Table 3.4).

Modern *Pongo* appears to have a shorter lower P_3 and P_4 than most fossil materials and it is interesting to note that while (BDC 1-10L) falls within the cluster for fossil *Pongo*, the other specimens (BDC 1-19U and SC 3-3) group with the modern materials. While the South China specimens are on average larger than those from Punung, the *Pongo* teeth from Badak Cave C are intermediate between the two forms and are not considerably larger than those of modern species.

The Batu Caves samples can be compared with contemporary Late Pleistocene, populations, i.e., those from the Padang caves, Sumatra, described as a large chrono-subspecies by Hooijer (1948), and those from Punung, Java. All teeth from the Batu Caves sites are larger than the mean size of equivalent tooth types from the Punung series (Table 3.4). The upper P^4 (CC 3-6), upper M^3 (CC 6-3) and the lower M_1/M_2 (VC 4-4) all have crown areas that exceed even the maximum values of equivalent teeth from Punung. Both (CC 3-6 and VC 4-4) have considerably larger crown areas than those from modern *P. abelii* and *P. pygmaeus*. (CC 6-3) and are relatively large compared to the crown areas of the Middle Pleistocene material from Trinil and the Late Pleistocene Mulanshan tooth but falls within the upper range of males of modern species. The lower I_2 (SC 3-4), again is larger than modern samples but smaller than a Niah specimen of *P. pygmaeus* and comparable with the Hoa Binh tooth from Vietnam.

The Punung Orangutan has been considered a smaller morph by Koenigswald (1940) as compared with remains from other parts of Java owing possibly to temporal or geographic isolation. The generally larger teeth from the Batu Caves sites might represent a larger continental form different from the insular Javan, Sumatran and Bornean population.