THE SARAWAK MUSEUM JOURNAL

Vol. LXXIV No. 95 (Supplement 1) (New Series) Since 1911 ISSN. 0375-3050 June 2015

TIKUS PURBAKALA
A Guide for Zooarchaeologists on the Identifications of Rats from Borneo Caves Excavations by Dental Characters

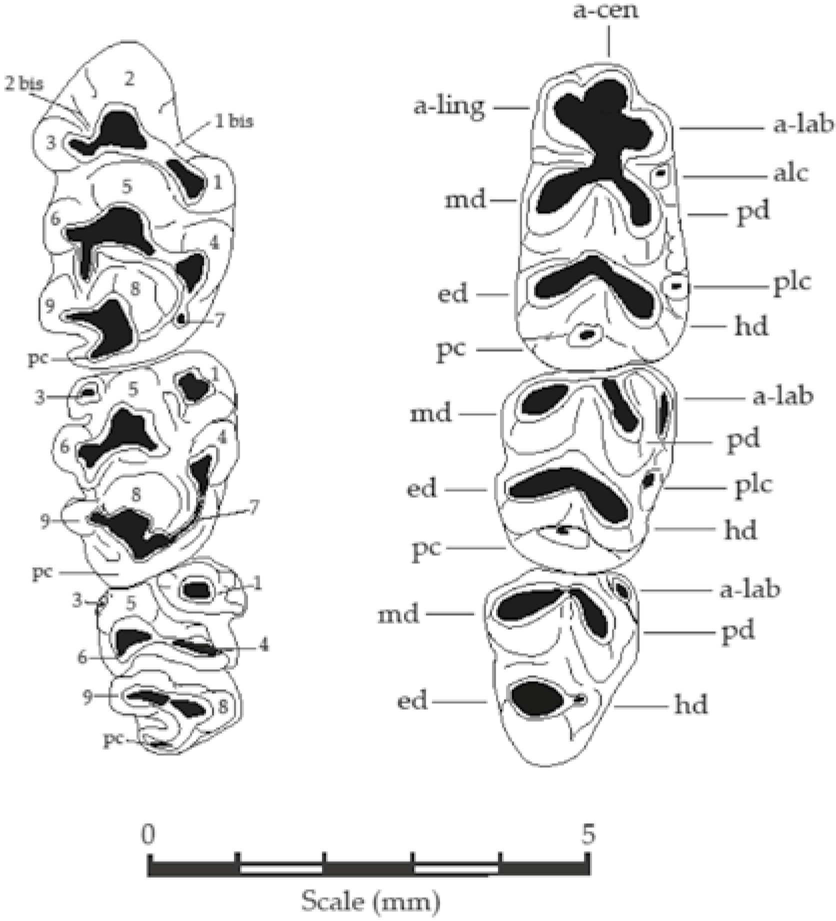
by

Earl of Cranbrook and Philip J. Piper

SARAWAK MUSEUM DEPARTMENT

HONORARY CURATORS, 2015

Archaeology	Stephen Chia Ming Soon, *Ph.D.*
Art Materials	Sylvester Wielding ak. Jussem, *M.A.*
Beads	Heidi Munan, *B.A.,* P.B.S., P.B.D.
Birds	Slim Sreedharan
Botany	Paul Chai, *Ph.D.*
Ceramics	Datuk Lucas Chin, P.G.B.K., P.B.S., A.M.N., P.P.B.
History	Datu Haji Sanib bin Haji Said, *M.A., Ph.D., D.I.M. (Arch.),* D.J.B.S.
Mammals	Dato Sri Earl of Cranbrook, *M.A., Ph.D., D.Sc. (Hon.),* J.B.S. (K), P.N.B.S. (K)
Reptiles and Amphibians	Dato Robert F. Inger, *Ph.D.*
Social Anthropology	Peter M. Kedit, *Ph.D.*



Occlusal aspect of left upper molar row and right lower molar row of Grey tree rat *Lenothrix canus*, prepared by PJP to illustrate the terminology of G. G. Musser (1981) (see Figure 2 for detail).

THE SARAWAK MUSEUM JOURNAL

Vol. LXXIV No. 95 (Supplement 1) (New Series) Since 1911 ISSN. 0375-3050 June 2015

SARAWAK MUSEUM DEPARTMENT

EDITORIAL BOARD

Policy

The Sarawak Museum Journal is devoted to the advancement of knowledge in the natural and human sciences. It publishes articles pertaining to the Asian region in general, but particularly to Borneo and Sarawak. Generally, it will accept manuscripts from international scientists, but specifically it serves the need of local scientists especially those working with, and through the Sarawak Museum; to publish their research findings and to provide a forum for their scholastic discourse. As the Sarawak Museum Department is a Government Department in the State of Sarawak, it should be clearly understood that responsibility for facts and opinion rests exclusively with authors of signed articles, and their writings do not necessarily reflect the views or policy of the Sarawak Museum Department, or that of the State Government of Sarawak.

Guidelines for Contributors

All manuscripts submitted for publication should be addressed to The Chief Editor, *The Sarawak Museum Journal,* Sarawak Museum Department, Jalan Barrack, 93200 Kuching, Sarawak, Malaysia. They should be typed with double-line spacing throughout with liberal margins. Footnotes should be assembled at the end of the text. References should be given with the authors' names and dates of publication in the text and works listed at the end of the paper in alphabetical order of authors' names. Contributors should ensure that any drawings submitted are bold enough to remain legible after the reduction which is nearly always necessary; this applies particularly to lettering on illustrations. Prints of photographs should have a glossy finish and should not normally be less than 16.5 x 12 cm.

To expedite publication all contributors are strongly urged to submit their articles in both hard copy and diskette using IBM Microsoft programmes.

Submitted article is considered a final and finished work of a contributor and therefore proofs will not be referred to him/her.

Contributors are provided with 20 offprints of articles free of charge; further offprints are supplied at cost.

Subscription

The subscription price for Peninsular Malaysia is RM15.00 per issue (inclusive of RM5.00 postage), and for Sarawak and Sabah is RM13.50 (inclusive of RM3.50 postage). For ASEAN and foreign countries, it is USD5.00 per issue (excluding postage). Please contact us at the following address, for postage rates and any other information: The Director, Sarawak Museum Department, Jalan Barrack, 93200 Kuching, Sarawak, Malaysia. Email: webmaster@museum.sarawak.gov.my.

The Sarawak Museum Journal is also obtainable in exchange for journal of related fields written in English. *The Sarawak Museum Journal* is published annually by the Sarawak Museum Department.

CONTENTS

FOREWORD

The many years of active archaeological research and cave excavations, undertaken by the Sarawak Museum since the 1950s, have confirmed the place of archaeozoology as a significant contributor to the understanding of the prehistory and palaeo-ecology of Borneo. Among the animal remains recovered in cave deposits, the past presence of some large mammals now extinct in the island has been demonstrated: a giant pangolin (globally extinct), the tiger, Malayan tapir and Javan rhinoceros. Analysis of mammalian teeth and bones has identified the main quarry species of ancient peoples of Borneo, and has shed light on their remarkable hunting skills. Moreover, because mammals provided the raw material, it has also been shown how bones and teeth were worked to create artefacts for special purposes, including presumed projectile tips and other functional and decorative items.

Not all the mammal remains owe their presence in these archaeological sites to the activities of people. In some cases more numerous than the products of human activity, are the skeletal remains of natural casualties of small mammals, such as bats, that roost within the cave and emerge daily to feed, and others that live mainly outside but enter caves to take advantage of the resources provided, including food and shelter. Important among the latter group, known as ‘troglophiles’, are the rats (Murinae). The rats of Borneo are numerous, and diverse in their habits and favoured habitats, from old forest to scrub, cultivation or other vegetation altered by human presence and activity. The remains of rats in dated archaeological contexts can therefore provide valuable information on the prevailing environment surrounding a cave. Hitherto, a major impediment to interpretation of the evidence offered by rats in archaeological sites has been the difficulty in identifying the remains to genus and species.

I therefore applaud the work done by Dato Sri Gathorne, Earl of Cranbrook and Dr Philip J. Piper in providing this manual to guide present and future zooarchaeologists towards the identification of the dental remains of rat genera and species. Throughout the six decades of archaeological investigation by the Sarawak Museum, and others, the *Sarawak Museum Journal* has served as a key outlet for progress reports and final publication of zooarchaeological discoveries. I am therefore very pleased to be able to offer a supplement in the

SMJ series as an illustrated guide to the identification of rat remains in Borneo archaeological contexts, by reference to dental anatomy.

Earl of Cranbrook began working as a technical assistant in the Sarawak Museum in 1954. His work on animal remains from the excavation of Niah Caves under Tom Harrisson was outstanding. There were abundant zooarchaeological materials available when Philip Piper arrived to do his postgraduate research on the subject in the early 2007. Together, they have published many new findings on the ancient fauna of Niah caves.

I congratulate the authors on their achievement, and I recommend this *Guide* as a model of clear exposition of a difficult subject that I am sure will be of use to all mammalogists, and notably to present and future zooarchaeologists working with the rich resources of Borneo caves. I hope it will be the first of a series of guides to support future zooarchaeologists working in Borneo.

Ipoi Datan, *M.A.*
Director, Sarawak Museum Department

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF PLATES

Glossary of terms

Anterior : towards the front (of the toothrow)

Posterior : towards the rear (of the toothrow)

Labial : towards the outer or cheek-side of the tooth

Lingual : towards the inner or tongue-side of the tooth.

Distal : away from the midline (therefore, in the toothrow carrying the same meaning as ‘posterior’)

Mesial : towards the midline (therefore, in the rat toothrow, carrying the same meaning as ‘anterior’)

INTRODUCTION

The existing mammal fauna of Borneo includes 26 named species of the rodent family Muridae, subfamily Murinae (Emmons 1993; Payne & Francis, 2005; Maryanto & Sinaga, 2008; Achmadi *et al.*, 2012). Of these, 19 middle-sized to large species belong to genera formerly grouped within the single genus *Rattus* by regional systematists including Chasen (1940), and Ellerman & Morrison-Scott (1951). Now divided among six genera, *Lenothrix, Leopoldamys, Sundamys, Maxomys, Rattus* and *Niviventer* (Wilson & Reeder, 2005), these species (Table 1) are collectively regarded as 'rats' for present purposes: *tikus* in Bahasa Malaysia.

Huge numbers of whole and fragmentary animal bones and teeth have been recovered in archaeological investigations of Borneo caves by the Sarawak Museum, notably the famous excavations at Niah (Harrisson, 1958, 1959; Barker *et al.*, 2007; Piper & Rabbet, 2013). These assemblages of animal remains are mainly the result of two non-exclusive processes of accumulation: (1) the natural deposition of carcases of bats, rats, swiftlets and other cave-roosting species that emerge to find resources to support their existence (termed 'trogloxenes'), or the remains of visiting individuals of species that inhabit the surroundings but also enter caves to exploit the resources of this environment ('troglophiles'); and (2) human activity, depositing in the cave mouth whole or parts of animal remains originally brought there as food, for tool manufacture and use, or other purposes. The second process produces material of prime interest to anthropologists and prehistorians but, for the biologist and palaeo-ecologist, the occurrence of troglophiles among animal remains provides valuable information on the contemporary environment outside the cave.

The present work has been developed in preparation for the authors' study of the rat remains from excavations by the Sarawak Museum at the Niah caves, which have yielded over 40 jaws with teeth. At other sites investigated by the Sarawak Museum, such as Sireh cave, the presence of broken incisors in the excavated area provided confirmation of the occurrence of rats throughout the archaeological deposit, although no identifiable items were found (Cranbrook, 2012). Among the animal remains from caves at Jambusan, Sarawak, excavated by A.H. Everett in 1878-79, Cranbrook (2013) found teeth of rats, so far unidentified. Re-excavating Gua Tupak, one of the caves investigated by Everett, Gani *et al.* (2013) noted rats among mammalian remains that were not identified. The frequent occurrence of rat remains has therefore confirmed that these rodents are among habitual troglophiles, to be expected in archaeological deposits in cave sites in Borneo.

These rats comprise an ecologically diverse group of small mammals, shown by their present ecology to be sensitive to environmental factors such the nature and extent of forest cover, and to other ambient features reflecting altitude. If confidently identified, the species of rats in archaeological contexts therefore become potentially valuable members of the troglophile community to provide palaeo-ecological information. The identification of post-cranial bones of Bornean rats in archaeology is challenging and at present has not been attempted. However, as shown below, dental remains can provide undisputed confirmation of identity at genus level and, in some cases, strong evidence at species level.

Although molecular phylogenetics have become a tool in the systematics of regional Murinae (Md Tamrin & Abdullah, 2011), traditional taxonomists have defined the genera of Borneo rats mainly on morphological characteristics such as body size, pelage and integument coloration and, especially, on anatomical features of the skull with the teeth of the upper molar row borne on the maxillary bone. Unfortunately, whole skulls of rats are rarely recovered undamaged in archaeological contexts. At the best, partial skull fragments of the maxillary region have been found, some bearing teeth of the upper molar row. More frequent are detached lower jaws (mandibles), often fragmentary but retaining some or all teeth in place. For practical purposes, therefore, while dependable features for identification of archaeological specimens can be found in diagnostic characters of the molars of the upper (maxillary) toothrow, it is the less-studied lower (mandibular) molar rows that must often be relied upon by the zooarchaeologist.

It is therefore the aim of this *Guide* to provide the means to identify the remains of rats from archaeological excavations in Borneo by the molar teeth only, with special emphasis on those of the lower jaw. In addition to the instances cited above, it can be predicted that there will be further discoveries of the remains of rats from Borneo archaeological cave sites. As modern procedures for excavation and recovery are applied, there will be opportunities for extended work on identification, and new interpretations to be made.

ACKNOWLEDGMENTS

The Natural History Museum, London, (BMNH) provided comparative material used in this study from recent populations of rats inhabiting Borneo. We gratefully thank all staff of the Mammal Section for access to the collections in their charge. BMNH retains copyright of all photographs of specimens in the collections. Many thanks also to Dr. Larry Heaney of the Field Museum of Natural History, Chicago for providing modern comparative measurements of rat taxa from Borneo. Research by P.J.P. was funded by ARC Discovery grant DP14103650. All figures were prepared by P.J.P. from original scale photographic images of identified rat maxillary or mandibular dentition using Adobe Illustrator CS5. The tooth outline was first traced and then the pattern of the occlusal surfaces of each molar was illustrated. Where the enamel surface of the specimen had worn through, the exposed dentine was shaded black. Thus the stage of tooth wear in the figure corresponds to the wear observed in the original specimen (Figure 1).

Figure 1. Photograph of the occlusal aspect of an archaeological specimen, identified as a worn lower molar row of Müller's rat *Sundamys muelleri*, with the corresponding scale figure prepared by P.J. Piper. Areas of exposed dentine are coloured black and enamel is white.

Table 1. Named species of Borneo 'rats', as defined in the text: Head and body lengths (H&B), weights, length of upper molar row, and distribution within Borneo and Habits/ Habitats from Payne *et al*. (2005), or alternative sources as noted.

Genus	***Species***	***H&B length*** (*mm*)	***Weight*** (*g*)	***Upper molar row*** (*mm*)
Lenothrix	*canus*	165-220	80-220	8.2-8.6
Leopoldamys	*sabanus*	215-273	250-532	9.1-10.0
	diwankarai	197-255	189-190	8.5-9.3
Maxomys	*alticola*	139-176	n/a	5.4-6.1
	baeodon	126-140	n/a	4.1-5.0
	ochraceiventer	140-171	n/a	5.4-6.0
	rajah	139-218	95-218	6.9-8.1
	surifer	160-202	n/a	5.8-6.8
	whiteheadi	91-111	30-83	5.1-6.2
	tajuddinii	95-122	50-70	5.2-6.4
Niviventer	*cremoriventer*	106-160	53-100	5.6-6.6
	rapit	122-163	n/a	5.8-6.1
Rattus	*argentiventer*	140-210	85-180	6.8-7.5
	baluensis	150-188	80-135	6.5-7.0
	exulans	101-138	45-65	4.7-5.6
	norvegicus	163-265	50-400	7.0-7.4
	tanezumi	122-219	100-200	6.2-7.0
	tiomanicus	140-188	78-125	6.0-6.8
Sundamys	*infraluteus*	226-295	237-600	10.6-11.6
	muelleri	179-244	160-305	8.2-10.0

Notes

1. Measurements of all species from Payne *et al*. (2005) or other sources, as indicated.
2. Distribution and habitats from Wilson and Reeder (2005).
3. Measurements of *Leopoldamys diwangkarai* from Maryanto & Sinaga (2008). The species was described from three specimens, two from Borneo: the type from Pemantang Murawai, Central Kalimantan, and a paratype from Bukit Baka, West Kalimantan.

Distribution	***Habits/Habitat***	***Notes***
Sarawak, Sabah, Kalbar	Arboreal. Lowland forests, to 550 m on Kinabalu	*1,2*
Throughout	Scansorial. Lowland and montane forest, up to 3100 m on Kinabalu.	
Two specimens, West & Central Kalimantan	Lowland forest	3
Kinabalu and Trus Madi, Sabah	Montane forest; 1070 - 3360 m on Kinabalu	4
Rare; in Sarawak and Sabah	Lowland forests; to 1400 m on Kinabalu	4
Sabah	Lowland & submontane forests, to 1700 m on Kinabalu	4
Throughout	Strictly terrestrial Lowland forests, including second growth.	4
Throughout, including many islands	Terrestrial. Lowland and submontane forests, to 1680 m on Kinabalu	4
Throughout, including larger islands	Terrestrial. Lowland forest, to 2100 m on Kinabalu	5
Uncertain	Peatswamp forest	5
Throughout, and north Borneo islands	Scansorial. Lowland and submontane forest, up to 1530 m on Kinabalu	
Uplands of Borneo	Montane forests, Taken at 940 – 3360 m on Kinabalu	
Scattered localities, perhaps under-collected	Ricefields, grassland and and plantations; lowlands, to 1646 m on Kinabalu	6
Kinabalu only	Kinabalu only, above 1524 m to summit	
Throughout	Semi-commensal, entering rural houses, and in ricefileds, plantations and secondary forest, up to 1650 m on Kinablau.	
Some Borneo ports and adjoining land	Towns, plus records from ricefields in western Sabah	
Poorly recorded, but probably throughout	Commensal with people. Houses, gardens, crops and rice-field to the edge of secondary forests.	7
Throughout	Secondary forests and disturbed habitats	
Uplands of northwest Borneo	Disturbed and primary forests, uplands from 700 m, to 2930 m on Kinabalu	8
Throughout	Lowland forests, up to 1650 m on Kinabalu	

4. Distribution from Achmadi (2010).
5. Measurements from Achmadi *et al.* (2012).
6. Upper molar measurements from Maryanto (2003), n = 17 specimens from Kalimantan.
7. n = 42 Synonym of *Rattus rattus diardii* in Payne *et al.* (1885). Habitat from Pagès *et al.* (2010).
8. For new distribution records, extending the range reported by Payne *et al*. (1985), see Cranbrook *et al*. (2014).

RECOGNITION OF RATS OF BORNEO BY DENTAL CHARACTERS

There have been few zooarchaeological studies of rats of the South-east Asian region. The most comprehensive is that of Chaimanee (1998), covering cave sites of Plio-Pleistocene age in Thailand. From Java, Indonesia, Musser (1982) described an extinct species *Rattus trinilensis* from the Trinil Middle Pleistocene deposits. Later Java cave sites have yielded examples of *Rattus exulans* at Sampung cave, *Rattus tiomanicus* at Wajak, and *Leopoldamys sabanus* at Gua Jimbe (Chaimanee, 1998).

In the process, an agreed terminology of the dental anatomy of rat molars has been slow to develop. Chaimanee (1998:16) utilised a system modified from Misonne (1969). Although the differences are slight, in the following pages the terminology for dental structures is based on the work of G.G. Musser, an exceptional specialist who combined the numbering system of Miller (1912) for the upper molars with his own anatomical correlates for those of the lower jaw, as reproduced in Figure 2 (see Musser 1981: Fig. 1). Expanding on Musser's work, descriptions of the principal features of the dental anatomy of the lower (mandibular) molar row of the genera of rats of Borneo are amplified below in greater detail. On the basis of these features of dental anatomy, it has proved possible to determine generic identity independently of metric characters. Further identification to species is more conjectural, largely dependent on comparative measurements.

Because lower jaws are more frequent in archaeological contexts, and because the dimensions of the lower molar row are not normally published in systematic or descriptive literature, this *Guide* places particular emphasis on these teeth. The authors' measurements given in the tables below were taken to 0.01 mm with electronic vernier callipers, but have been reduced to the nearest 0.1 mm (0.05 being rounded up). Tooth crown measurements were taken as the greatest length (L) in the anterio-posterior (= mesio-distal) axis of the jaw, and greatest breadth (B) in the labio-lingual dimension. Because of its tapered profile, we found difficulty in obtaining consistent repeatability in the measurements of 3rd molars, which are therefore omitted from several tables.

In these pages, English names for the species of Borneo rats follow Payne & Francis (2005).

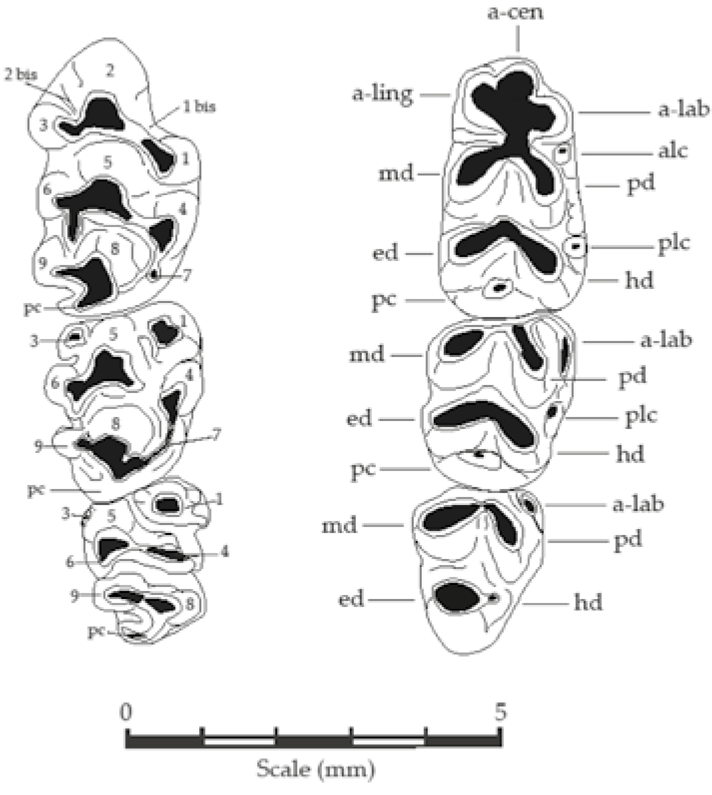


Figure 2. Left upper (maxillary) and right lower (mandibular) molar rows of *Lenothrix canus*, showing nomenclature of dental structures following Musser (1981). In the upper molars, cusps of the three lophs of each tooth are numbered t1 to t9; pc = posterior cingulum. On the lower molars, a-cen = antero-central cusp of the first loph; a-lab = anterolabial cusp; a-ling = anterolingual cusp; pd = protoconid, hd = hypoconid; md = metaconid; ed = entoconid; pc = posterior cingulum; alc = anterolabial cusplet; plc = posteror labial cusplet.

1. Large Rats

Lenothrix

Among larger rats, i.e., with upper and lower molar rows both exceeding 8 mm, the Grey tree rat *Lenothrix canus*, sole representative of its genus in Borneo, shows the most complete dental anatomy (Figure 2). This rat was accordingly selected by Musser (1981) and Musser & Newcomb 1983: 542, & fig. 95) to typify the generalised (primitive) form. It is a scansorial species, rare in present environments, with published records only in Sarawak from the neighbourhood of Kuching (Medway, 1977), and in Sabah at Sepilok and at Poring, at 1800 ft (~550 m) (Payne & Francis, 2005). There have so far been no identifications from archaeological sites.

Upper molar row: As among other genera of rats, in *Lenothrix* in the upper (maxillary) toothrow the 1st molar is composed of three lophs (or laminae). On the first (anterior) loph, t2 forms a large central lobe, and t1bis and t2bis are present; on the second loph t4 and t6 extend from the central t5 posteriorad for about an equal distance, t7 and t9 are distinct, and there is again a small pc; on the third loph, t1 is prominent and there may be a small t3, with wear, t4, t5 and t6 conjoin to form a median loph, t8 and t9 form a narrow horizontal loph, behind which there is a distinct pc (Figure 2).

Lower molar row: In the lower (mandibular) toothrow the anterior (mesial) loph of the 1st molar has an anterocentral cusp, forming a trefoil-shaped lobe with roughly equal-sized antero-labial and antero-lingual cusps. Both 1st and 2nd molars have anterolabial and posterolabial cusplets. The 3rd molar has a distinct anterolabial cusplet and a posterior loph clearly divided into hypoconid and entoconid (Plate 1).

Figure 3. Left upper molar row and right lower molar row of Long-tailed giant rat *Leopoldamys sabanus*: See text for description.

Leopoldamys

The dental characters of *Leopoldamys* were described by Musser (1981: 261-263). Within the range of the genus, at least eight species of *Leopoldamys* have been recognised from morphological and molecular evidence (Balakirev *et al.*, 2013). In Peninsular Malaysia the *sabanus*-lineage is represented by *L. vociferans*, frequenting forest habitat up to around 750 m elevation, occasionally higher, where it is ecologically replaced in montane habitats by a larger species *L.* (*edwardsi*) *ciliatus* (Corbet & Hill, 1992). In Borneo, a second species *Leopoldamys diwangkarai* was described by Maryanto & Sinaga (2008) based on three rats of this genus trapped at lowland elevations in Borneo and Java: the type from Murung Raya, Central Kalimantan, and one paratype from Bukit Bata, West Kalimantan; the second paratype from Java.

In total samples from Kalimantan and Java there was overlap in crown length of the upper molar row (Maryanto & Sinaga, 2008), in *L. sabanus* 9.07-10.51 mm (n = 48), and *L. diwankarai* 8.54-9.28 mm (n = 3), so that in mid-range this measurement would not separate archaeological specimens. The three specimens of *L. diwankarai* were found in the same localities as 'typical' *L. sabanus*. The dorso-ventrally bicoloured tail of *L. diwankarai* resembles the coloration of juvenile Bornean *L. sabanus*, as seen among a small sample in BMNH, and the form and measurements of the skull also indicate that the three specimens were subadult. Further experience is needed to verify the existence in Borneo of two species of *Leopoldamys* with overlapping distribution and similar ecology.

Upper molar row: On the upper 1st molar of *Leopoldamys*, the labial cusp t3 is generally lacking but, if present, is small and partially merged with t2, so that the anterior loph appears to be formed of only a small lingual and wide central cusp; t7 is lacking, t8 & t9 are merged to form a wedge-shaped loph. This molar has four roots: anterior, posterior and lingual roots are large; the lingual root is small (Chaimanee, 1998). The upper 2nd molar usually lacks t3, and always lacks t7; cusp t9 is small, and incorporated into the adjacent and larger cusp t8 to the extent that its outline is nearly lost. The 3rd molar lacks t3; t4 and 5 are merged, as are t8 and t9; there is no pc.

Lower molar row: the 1st molar lacks an anterocentral cusp and the anterolabial and anterolingual cusps are compressed together; only a posterior labial cusplet is present. This molar has four roots, large anterior and posterior, small labial and lingual. On the 2nd molar, only a posterior labial cusplet may be present; no labial cusplets are present on the 3rd molar, which is proportionally small in comparison with the first molar (Table 1; Figure 3, Plate 2).

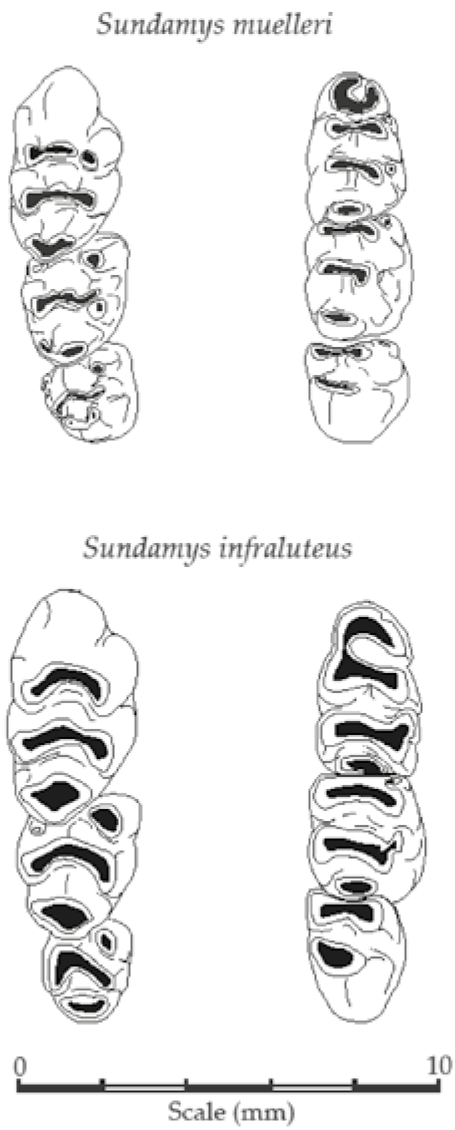


Figure 4. Left upper and right lower molar rows of the two species of *Sundamys* of Borneo, Müller's rat *S. muelleri* and Mountain giant rat *S. infraluteus*.

Sundamys

The dentition of *Sundamys,* simpler than that of *Lenothrix,* was described in further detail by Musser & Newcomb (1983: 420-423). Two species of this genus occur in Borneo. Widespread is Müller's rat *Sundamys muelleri* frequenting forest habitats from the lowlands, including residual plots of *kerangas* heath forest in Brunei Darussalam (Charles & Ang, 2010), to Lower Montane forest up to 5400 feet (~1650 m) on Gunung Kinabalu (Medway, 1977). In forest and in rural areas Mueller's rat enters occupied human habitation and camp sites, as noted at the Kinabalu Base Camp in 1964 (Cranbrook, 2005: 120). At higher elevations, above ~1000 m in the north and north-western uplands of Borneo, the Mountain giant rat *Sundamys infraluteus* occurs in forest of all sorts, including logged forests (Cranbrook *et al.,* 2014). It is equally 'tame' in behaviour, and will come into informal shelters and camp sites. The dental anatomy is similar in the two Borneo species, but measurements of molar rows and individual teeth distinguish the larger *S. infraluteus* from *S. muelleri* (Table 2).

Upper molar row: The 1st molar consists of three broad, arcuate lophs in which the central cusps t2, t5 & t8 are prominent; in each loph there are smaller labial cusps t3, t6 & t9, and lingual cusps t1 & t4 in the anterior and mesial lophs; t1bis, t2bis and t7 are lacking. There was a wedge-shaped posterior cingulum (pc) in 50% of the sample of *Sundamys muelleri* of Musser & Newcomb (1983: 421). The 1st molar has five roots, anterior, posterior, labial and two lingual. In the upper 2nd molar t1 and t3 are large, and t7 and pc are absent. In the upper third molar t1 is large, t3 present, t4, t5 & t6, and t8 & t9 are coalesced to form two arcuate laminae; pc is absent.

Lower molar row: The 1st molar lacks an anterocentral cusp and the anterolabial and anterolingual cusps are merged to form a broad, curved lamina; there was a small anterior labial cusplet in half the sample studied by Musser & Newcomb (1983) and "in almost every specimen" a large and conspicuous posterior labial cusplet. On the 2nd molar, there is invariably a large anterolabial cusplet (the presence of which is diagnostic in comparison with *Leopoldamys*) and a large posterior labial cusplet; similarly, the 3rd molar is also distinguished by an anterolabial cusp in 68% of specimens examined, again a feature absent in *Leopoldamys*. In proportion to the first molar, the third is comparatively robust (Figure 4, Plates 3 & 4).

Table 2: Comparative measurements of the molar rows of Borneo examples of Müller's rat *Sundamys muelleri borneanus* and Mountain giant rat *Sundamys i. infraluteus*, to nst 0.1 mm. Upper (Max) molar row from Payne & Francis (2005). Other measurements from specimens in the Natural History Museum, London. Molar row (M1-M3), mesiodistal length of 1st molar (M1L), labiolingual breadth of 1st molar (M1B), length of 2nd molar (M2L), breadth of 2nd molar (M2B); n = number in sample.

Species		n	M1 - M3	M1L	M1B	M2L	M2B
Sundamys muelleri borneanus	Max molar row	63	8.2-10.0				
	Mnd molar row	8	8.4-9.0	3.3-3.7	2.1-2.5	2.3-2.7	2.3-2.5
Sundamys i. infraluteus	Max molar row	13	10.6-11.6				
	Mnd molar row	12	10.2-11.4	4.0-4.5	2.7-3.0	2.9-3.4	2.8-3.2

2. Moderate-sized Rats

The remaining genera, *Maxomys, Rattus* and *Niviventer*, are middle-sized rats with the length of the molar rows overlapping in the range >5 - < 8.1 mm. Separation of the genera therefore again relies on differences in dental anatomy.

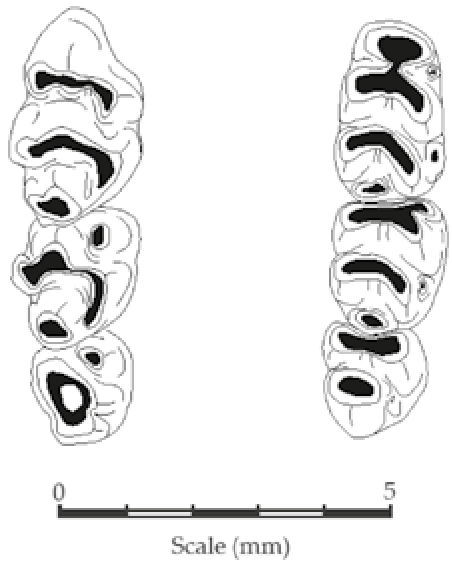


Figure 5. Left upper and right lower molar row of Brown spiny rat *Maxomys rajah,* wear moderate to heavy.

Maxomys

From morphological studies, Musser *et al.* (1979) recognised 16 species of the South-east Asian genus *Maxomys* of which seven occurred in Borneo: Brown spiny rat *Maxomys rajah*, Red spiny rat *M. surifer,* Mountain spiny rat *M. alticola,* Chestnut-bellied rat *M. ochraceiventer,* Small spiny rat *M. baeodon* and Whitehead's rat *M. whiteheadi.* The last was divided by Achmadi (2010) into two taxa of species rank, differing in average size. The larger form, also characterised by colour of the pelage, was subsequently named *Maxomys tajuddinii* by Achmadi *et al.* (2013), who distinguished the species by statistical treatment from *M. ochraceiventer* and *M. baeodon.*

There is considerable overlap in dental dimensions among *Maxomys* rats of Borneo, but all share a relatively simplified dental anatomy (Musser, 1981; and Figure 5). In dental dimensions, *Maxomys rajah* appears to be the largest member of the genus in Borneo, though our small sample size shows overlap with *M. surifer* (Table 3). Both these species are larger than *M. alticola, M. ochraceiventer* and *M. whiteheadi* (with *M. tajuddinii*), all of which all have overlapping dental dimensions. *M. baeodon* is smaller (Table 3). All *Maxomys* species are rats of forest habitat; *M. tajuddinii* frequents lowland swamp forest (Achmadi *et al*., 2013).

Upper molar row: In the 1st molar cusps t1 and t2 are conjoined and, with wear, merge with t3; cusps t1bis, t2bis and t7 are lacking. On both 1st and 2nd molars showing moderate wear, cusps t4, t5 and t6 merge to form a rounded rectangular lobe in which t4 extends distad so that the rear margin of t4 is notably posterior to the rear margin of t6; cusps t8 and t9 are merged, but t9 forms a distinct forward (mesial)-projecting lobe. Cusp t3 is present on the 2nd molar; pc is present on first and second molars, occasionally on the third. The upper 1st molar has three or four roots (Chaimanee, 1998).

Lower molar row: In *Maxomys surifer* and *M. rajah* the lower first molar sometimes possesses a small anterocentral cusp, a feature that is diagnostic, if present (Plate 5 a). This cusp is lacking in specimens of other Bornean species of *Maxomys* examined in the present study. In the lower 1st molar of all *Maxomys* species, the anterolingual and anterolabial cusps are subequal in size, although the anterolabial cusp is invariably slightly larger. Both cusps are more or less level in *M. rajah* (Plate 6) and *M. ochraceiventer* while in *M. surifer*, *M. alticola* and *M. baeodon* the larger anterolingual cusp protrudes further anteriorly than the anterolabial, yet not so markedly as in *Rattus* species (Figure 6). An anterolabial cusplet is absent in most specimens, but a posterolabial cusplet is present in all but three species (Musser *et al.*, 1979). This molar has two roots. On the lower 2nd molar small anterolabial and posterolabial cusplets are present in most specimens. All *Maxomys* specimens studied lacked an anterolabial cusp on the lower 3rd molar, illustrated by *M. whiteheadi* (Place 5 b).

Table 3. Comparative dental measurements of Borneo examples of *Maxomys* species, to nst 0.1 mm. Maxillary molar row measurements marked * from Payne & Francis (2005), " from Achmadi *et al.* (2012). Other measurements from specimens in the Natural History Museum, London.

Species		**n**	**M1 - M3**	**n**	**M1L**	**M1B**	**M2L**	**M2B**	**M3L**	**M3B**
Maxomys surifer	Max. molar row Mnd molar row	5 4	5.4-5.9 5.5-6.3	5 4	2.9-3.5 2.9-3.2	2.0-2.3 1.4-1.8	1.8-2.2 1.9-2.1	1.6-2.1 1.5-1.6	1.4-1.7 1.4-1.7	1.6-1.7 1.0-1.0
Maxomys rajah	Max. molar row Mnd molar row	5 2	5.9-7.1 5.4-7.0	5 7	3.0-3.8 2.7-3.5	2.2-2.4 1.5-2.0	1.5-2.4 1.9-2.0	1.9-2.1 1.5-2.0	1.1-1.4 1.4-1.8	1.4-1.9 1.4-1.9
Maxomys alticola	Max. molar row Mnd molar row	23* 1	5.4-6.1* 5.4	1	2.4	1.3	1.8	1.4		
Maxomys ochraceiventer	Max. molar row Mnd molar row	13* 3	5.4-6.0* 5.1-5.3	3	2.4	1.3-1.5	1.6-1.8	1.4-1.5		
Maxomys baeodon	Max. molar row Mnd molar row	5* 1	4.1-5.0* 4.2	1	1.9	1.1	1.4	1.2		
Maxomys whiteheadi	Max. molar row Mnd molar row	21* 2	5.1-6.2* 5.2-5.4	2	2.3, 2.4	1.2, 1.5	1.7, 1.7	1.2, 1.3		
Maxomys tajuddinii	Max. molar row Mnd molar row		5.2-6.4" n/a							

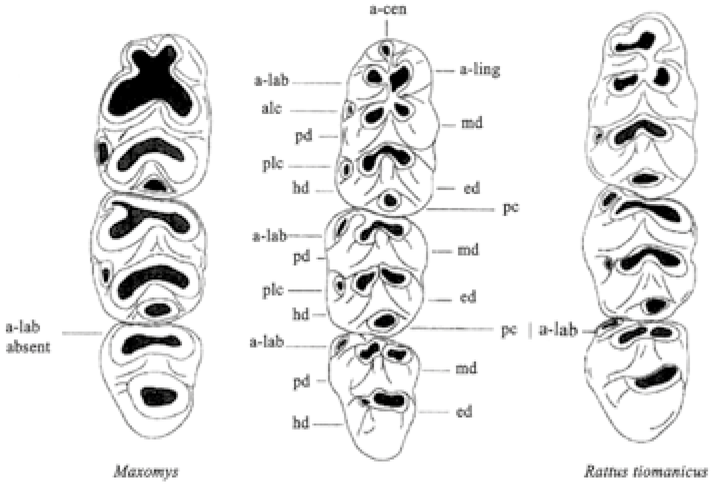


Figure 6. Left lower molar row of *Maxomys* and *Rattus* compared with (centre) *Lenothrix.* The tooth of *Maxomys* shows greatest wear, and that of *Lenothrix* the least. Not to scale.

Rattus

This genus is distinguished by a set of dental characters considered by Musser & Newcomb (1983, Table 38) to be a mix of primitive and derived within Murinae. The *Rattus* rats are notable for species that are commensal with humans and/or dependent on human activity for the creation and maintenance of habitat favourable for their existence. Extreme examples of reliance on urban habitats are the cosmopolitan Norway rat *Rattus norvegicus* and Asian house rat *Rattus tanezumi* (as *Rattus rattus diardii* in Payne & Francis, 2005; but see Pagès *et al.,* 2010). Probably more ancient, the Ricefield rat *R. argentiventer* may have been a grassland specialist before it became a widespread regional pest of paddy fields. In an analysis of morphological variation of the species across mainland and island South-east Asia, Maryanto (2003) concluded that the species has diverged into four groups sufficiently distinct to be recognised as subspecies, including the form widespread in Borneo which he described as a new subspecies *R. argentiventer kalimantanensis*. The Polynesian rat *Rattus exulans*, despite its vernacular name, is widespread in continental and island South-east Asia. In Borneo, this little rat frequents a variety of habitats associated with people, notably rural houses, gardens, cultivations and disturbed or secondary forest. Resulting from this close association, *Rattus exulans* has accompanied humans in their historic expansion through the Pacific islands in past centuries (Wilmshurst *et al.,* 2008). The Malaysian field rat *R. tiomanicus* is less closely commensal with humans. This rat does not normally occur in houses, but does frequent man-made habitats, such as disturbed and secondary forests, plantations, gardens, scrub and grassland; rarely occurring in tall dipterocarp forests (Payne & Francis, 2005). Last of the group in Borneo, Summit rat *R. baluensis* has no ecological contact with other members of the genus, being confined to the upper slopes of Kinabalu above 2100 m. Of these five *Rattus* species, in our small samples of Borneo specimens (Table 4) there is general similarity in measurement of upper molar row between *Rattus argentiventer*, *R. tiomanicus* and *R. baluensis,* but greater separation in length of the lower toothrow, with marginal overlap between the three species.

Upper molar row: On the upper 1st molar cusp t1 is joined to t2 and a prominent t3 is distinct and t4 is separate or weakly joined to t5; on both 1st and 2nd molars, t1bis and t2bis are absent, and t8 is larger than t9 which, although more or less conjoined, retains its identity except in heavily worn specimens; pc is present at the rear of the 1st molar, sometimes the 2nd and occasionally the 3rd. On the 3rd molar, t3 may be present or lacking. The upper 1st molar has five roots (Chaimanee, 1998).

Lower molar row: The lower 1st molar invariably lacks an anterocentral cusp; the anterolingual cusp is distinctly larger than the anterolabial and, in occlusal aspect, is expanded anteriorly, extending almost parallel to the long axis of the tooth, while the anterolabial cusp is offset, with its anterior margin notably posterior to the anterior margin of the anterolabial cusp. Consequently, the shape of the anteroloph of the 1st molar distinguishes members of the genus *Rattus* from *Maxomys.* A small anterolabial cusplet is always present; pc is relatively large. The 1st molar has four roots. The lower 2nd molar of *Rattus* has both anterolabial and posterolabial cusplets; pc is present. The 3rd molar has two lophs only, and an anterolabial cusp, the presence of which provides a second character to distinguish the genus from *Maxomys*; there is no pc. Unlike *Maxomys* and *Niviventer* (below), the lower 3rd molar is relatively large in comparison with 1st and 2nd molars (Plate 7).

Table 4. Comparative dental measurements of Borneo examples of *Niviventer* and *Rattus* species, to nst 0.1 mm. Maxillary molar row measurements marked * from Payne & Francis (2005). Other measurements from Borneo specimens in the Natural History Museum, London.

Species		n	M1 - M3	n	M1L	M1B	M2L	M2B
Niviventer cremoriventer	Max. molar row	17*	5.6-6.6*					
	Mnd molar row	2	5.4, 5.6	2	2.4, 2.4	1.1, 1.2	1.7, 1.9	1.2, 1.4
Niviventer rapit	Max. molar row	5*	5.8-6.1*					
	Mnd molar row	1	5.7	1	2.7	1.4	1.9	1.4
Rattus tiomanicus	Max. molar row	8	6.0-6.8					
	Mnd molar row	9	5.7-6.2	8	2.5-2.7	1.4-1.6	1.8-1.9	1.5-1.8
Rattus argentiventer	Max. molar row	3	6.6-7.0	3	3.1-3.3	2.0-2.1	2.2-2.2	1.7-1.9
	Mnd molar row	3	6.2-6.4	3	2.7-3.2	1.5-1.8	1.5-2.0	1.7-1.8
Rattus baluensis	Max. molar row	5*	6.5-7.0*					
	Mnd molar row	15	6.4-6.8	3	2.4-2.4	1.3-1.5	1.6-1.8	1.4-1.5
Rattus exulans	Max. molar row	5*	4.1-5.0*					
	Mnd molar row	1	4.2	1	1.9	1.1	1.4	1.2

Niviventer

In *Niviventer*, the occlusal pattern of the molars is the least complex among Borneo rats (Plate 8). The genus is mainly continental in distribution, but two species occur in Borneo, both believed to be scansorial in habit: Dark-tailed tree rat *N. cremoriventer* is widespread but nowhere common in forest and woodland habitats, and the (mis-named) Long-tailed mountain rat *N. rapit* has been recorded only in the northern third of Borneo, in forest habitats from the lowlands (including Niah, Sarawak) and uplands to 3360 m on Kinabalu (Payne & Francis, 2005).

Upper molar row: The upper 1st and 2nd molars are long and slender, while the 3rd molar is round or oblong and relatively very small. Except for cusps t1 on the 2nd and 3rd molars, other cusps (even in unworn teeth) are merged to form chevron-shaped lophs. The 1st molar consists of two such lophs, and a large posterior cusp representing merged t8 and t9. All upper molars lack t1bis, t2bis, t7 and pc; cusp t3 is usually absent from the 2nd and 3rd molars (Musser 1981: 240-241). In most species, the upper 1st molar has five roots.

Lower molar row. The lower molars repeat this simplified occlusal pattern. In the lower 1st molar there is no anterocentral cusp; the anterolingual and anterolabial cusps are relatively small, usually joined into an oblong or triangular lamina, with the anterolingual cusp protruding to a moderate degree beyond the anterolabial cusp (Musser 1981: 244), but not in the exaggerated manner of *Rattus*; a posterolabial cusplet is present in most individuals of most species. On the lower 2nd molar, there is no anterolabial cusplet; a posterolabial cusplet is present in some species, but generally absent in *Niviventer cremoriventer* (96% of 157 individuals examined) and Bornean examples of *Niviventer r. rapit* (83% of 6 individuals) (Musser 1981, Table 2). The lower 3rd molar is small in relation to the 1st and 2nd molars and lacks labial cusplets, thus distinguishing the genus from *Rattus* (Plate 8).

CONCLUSION

This *Guide* describes the dental anatomy of six murine genera occurring in Borneo in the present era: *Lenothrix, Leopoldamys, Sundamys, Maxomys, Rattus* and *Niviventer*. These were formerly considered to be members of a single genus *Rattus* and therefore, for present purposes, are grouped under the English vernacular name ‘rats’. For the zooarchaeologist, dental anatomy of the molars is shown to provide confident identification of genus, sometimes even in difficult cases when only a partial toothrow is present in the specimen.

Genomic studies indicate that these genera of rats (as defined) are probably of Late Pliocene or Early Pleistocene origin. Available palaeontological and archaeological evidence supports this conclusion. Thus, *Rattus trinilensis* of early Middle Pleistocene age from Trinil, Java (consisting of a partial lower jaw with 1st and 2nd molars in place), although matching no living species, displayed in the 1st molar the fully developed cusp pattern characteristic of the genus *Rattus* (Musser, 1982). In Thailand, the main layer of Snake Cave, with a minimum age of 169,000±15,000 years, i.e., late Middle Pleistocene, yielded specimens identified as *Leopoldamys sabanus, Maxomys surifer,* two species of *Rattus* and *Niviventer fulvescens* (Chaimanee, 1998).

Troglophile habits of rats of these genera are confirmed by the recovery of these specimens from cave deposits of varying age in Thailand (Chaimanee, 1998). From other cave excavations there are additional records of *Sundamys muelleri* and *Leopoldamys sabanus* from terminal Pleistocene levels at Niah cave, Sarawak (Medway, 1964) and *Rattus tiomanicus* from early Holocene Wajak cave, Java (Brink, 1982). Remains of *Lenothrix* have yet to be found in an archaeological context, but evidently member species of the other five genera of rats can be expected to occur in any Borneo cave that provides the right conditions of preservation.

The living rats of Borneo vary in body size and correspondingly in dental dimensions (Table 1). Consequently, tooth size may serve to differentiate between some related species of the same genus (see Tables 3 and 4). For archaeological specimens, however, caution is advisable in relying on tooth measurements for species identification. Biometric studies have shown that past populations of mammal species of differing size and habits (including two rats) appear to have diminished in tooth or body dimensions during the Late Quaternary. Included in this trend are Long-tailed macaque *Macaca fascicularis* (Harrison, 1996), Sumatran rhinoceros *Dicerorhinus sumatrensis* (Cranbrook, 1986), Bornean shrew *Crocidura foetida* (Cranbrook & Piper, 2008a) and the rats *Leopoldamys sabanus* and *Sundamys muelleri* (Medway, 1964). Past vagaries in climate and consequent modifications of vegetation (see chapters 4, 5 and 6, in Barker, 2013) are among ecological factors that may exert selective pressure, potentially affecting mammals of all kinds, with consequences including adaptive modifications in body size towards diminution (Cranbrook, 2010; Cranbrook & Piper, 2008b). It is therefore important to emphasise that the anatomical characters of rat molars, described herein, are dependable indicators of generic identity, regardless of size, but do not necessarily provide positive identification of different species within genera.

In their present ecological requirements, all species of the genera *Lenothrix, Leopoldamys, Maxomys* and *Niviventer* are characteristically confined to natural forest habitats, notably closed Mixed Dipterocarp Forest and lowland swamp forests The presence of any members of these genera in an archaeological context would therefore indicate the local persistence of forest habitat of some form. Both *Sundamys* species, however, are evidently tolerant of disturbed or altered habitat, including (in the case of *S. muelleri*) the depauperate *kerangas* environment. Both, moreover, opportunistically associate with humans in rural locations and might, therefore, be expected to enter cave sites occupied by people.

Rats of the genus *Rattus* are more variable in their ecology and in the extent to which they are commensal with people. Both *Rattus norvegicus* and *R. tanezumi* are presumed to be introductions within historic times. These species were therefore not expected in archaeological contexts by Musser (1982), although either may perhaps be found in the future in new cave deposits near urban settlements. The recognition of a distinct, endemic Borneo subspecies of *R. argentiventer* implies a period of isolation sufficient to evolve this level of differentiation. Although now a pest of paddy fields, the species may have been present, occupying grassy habitat, before the introduction of rice cultivation to northwest Borneo some 4500 years ago (Bellwood, 1997). The presence of *R. argentiventer* in a cave deposit would therefore be a sure sign of a local deforested environment, but might not be an unchallenged indicator of the local cultivation of rice. The discovery of remains of *Rattus exulans* in an archaeological context would, however, be a strong signal of human alteration of the local environment and the neighbourhood of a permanent or regularly inhabited settlement of rural character. The nature of the habitat indicated by the presence of *R. tiomanicus* is more conjectural. The identification of *R. tiomanicus* in an early Holocene context at Wajak cave (Brink, 1982) testifies to the antiquity of the species in the region. Today this rat is associated mainly with wooded vegetation affected by human activity, including plantation and disturbed or secondary forest. Its original habitat is likely to have been natural vegetation with similar characteristics, perhaps maintained by the activity of large herbivorous mammals rather than humans. Its larger, upland congener, *R. baluensis* frequents naturally stunted, open montane forest. The altitude zone in which this rat occurs on Kinabalu experiences average ambient temperatures at least 7°C lower than at sea level, more extreme than the ~5°C drop postulated at the Last Glacial Maximum. Prima facie, this species is likely to be found in an archaeological context only at high altitude, where its presence would be an indicator of both local vegetation and ambient temperature.

Further conjecture on the palaeo-ecological inferences to be drawn from the presence of genera or species of rats in archaeological contexts now depends on the discovery and examination of more specimens. We hope that the publication of this *Guide* to the recognition of rat genera (and, sometimes, species) will provide the means for further identifications by zooarchaeologists and others drawn into the search for and study of mammal remains from Borneo archaeological sites.

REFERENCES

Achmadi, A.S. (2010). Taxonomic status of spiny rats (*Maxomys* Jentink, Rodentia) from Indonesia and Malaysia based on morphological study. *Treubia* 37: 49-82.

Achmadi, A.S., I. Maryanto & Maharadatunkamsi (2012). Systematic and description of new species of *Maxomys* (Muridae). *Treubia* 39: 1-26.

Balakirev, A.E., A.V. Abramov & V.V. Rozhnov (2013). Revision of the genus *Leopoldamys* (Rodentia, Muridae) as inferred from morphological and molecular data, with special emphasis on the species composition in continental Indochina. *Zootaxa* 3640 (4): 521-549.

Barker, G. (Ed.) 2013. *Rainforest foraging and farming in Island Southeast Asia. The archaeology of Niah Caves, Sarawak.* Vol. 1, pp. i-xx, 1-410.

Barker G., H. Barton, M. Bird, & 22 others (2007). New investigations in Niah Great Cave (Sarawak, Borneo) verify the antiquity of the anatomically-modern 'Deep Skull' and reveal foraging strategies *c*.45bp indicative of behavioural modernity. *Journal of Human Evolution* 52: 243-261.

Bellwood, P. (1997). *Prehistory of the Indo-Malaysian Archipelago.* Revised edn. Honolulu, University of Hawai'i Press.

Brink, L.M. van den (1982). On the mammal fauna of the Wajak cave, Java (Indonesia). *Modern Quaternary Research in Southeast Asia* 7: 177-193.

Chaimanee, Y. (1998). Plio-Pleistocene rodents of Thailand. *Thai Studies in Biodiversity* 3: 1-303.

Charles, J.K. & B.B. Ang (2010). Non-volant small mammal community response to fragmentation of kerangas forests in Brunei Darussalam. *Biodiversity Conservation* 19: 543-561.

Chasen, F.N. (1940). A handlist of Malaysian mammals. *Bulletin of the Raffles Museum, Singapore* 15: i-xx, 1-209.

Corbet, G.B., & J.E. Hill (1992). *The mammals of the Indomalayan Region.* Oxford & London, Natural History Museum Publications.

Cranbrook, Earl of (1986). A review of fossil and prehistoric remains of rhinoceroses of Borneo. *Sabah Museum and Archives Journal* 1(1): 50-110.

Cranbrook, Earl of (2005). Kinabalu, Class of '64: personal recollections. *In* Mandalam, K. R., G.W.H . Davison & P. Regis (Eds). *East Kinabalu.Royal Society Expeditions 40th Anniversary Monograph.*pp. 115-132. Sabah Society, Kota Kinabalu.

Cranbrook, Earl of (2010). Late Quaternary turnover of mammals in Borneo: the zooarchaeological record. *Biodiversity Conservation* 19: 373-391.

Cranbrook, Earl of (2012). Sireh cave bone in retrospect. Bone, teeth and other animal remains from Sarawak Museum excavations of 1954 and 1959. *The Sarawak Museum Journal* 70 (91 ns): 55-87.

Cranbrook, Earl of (2013). The 'Everett collection from Borneo caves' in the Natural History Museum, London: its origin, composition and potential for research. *Journal of the Malaysian Branch Royal Asiatic Society* 86 (1): 79-112.

Cranbrook, Earl of, A. H. Ahmad & I. Maryanto (2014). The mountain giant rat of Borneo *Sundamys infraluteus* and its relations. *Journal of Tropical Biology and Conservation* 11: 49-62.

Cranbrook, Earl of, & P.J. Piper (2008a). Post-Pleistocene evolution of Bornean shrews *Crocidura foetida* (Mammalia, Soricidae). *Biological Journal of the Linnean Society* 94: 413-419.

Cranbrook, Earl of, & P.J. Piper (2008b). Sarawak through the ice ages to present time: Environmental change and human impacts on the past and present distribution of mammals. *In* Robert B. Stuebing, Joanes Unggang, Jodi Ferner, John Ferner, Belden Giman & Kee Kum Ping (eds.) *Proceedings of the Regional Conference: Biodiversity Conservation in Tropical Planted Forests in South East Asia*. Kota Kinabalu, Natural History Publications (Borneo) pp. 81-104.

Ellerman, J.R., & T. C. S. Morrison-Scott (1951). *Checklist of Palaearctic and Indian mammals 1758 to 1946.* London, British Museum (Natural History).

Emmons, L.H. (1993). A new genus and species of rat from Borneo (Rodentia: Muridae). *Proceedings of the Biological Society of Washington* 106: 752-761.

Gani, N., S. Chia & V. Bujeng (2013). Faunal remains from Gua Tupak, Bau, Sarawak. *The Sarawak Museum Journal* 71 (92 ns): 123-168.

Harrison, T. (1996). The palaeoecological context at Niah Cave, Sarawak: Evidence from the primate fauna. *Indo-Pacific Prehistory Association Bulletin* 14 (Chang Mai Papers Vol. 1): 90-100.

Harrisson, T. (1958). The caves of Niah: a history of prehistory. *The Sarawak Museum Journal* 8 (12 ns): 549-595.

Harrisson, T. (1959). New archaeological and ethnological results from Niah Caves. *Man* 59: 1-8.

Maryanto, I. (2003). Taxonomic status of the ricefield rat *Rattus argentiventer* (Robinson and Kloss, 1916) (Rodentia) from Thailand, Malaysia and Indonesia based on morphological variation. *Records of the Western Australian Museum* 22: 46-65.

Maryanto, I. & M.H. Sinaga (2008). New species of *Leopoldamys* (Mammals, Rodentia, Muridae) from Kalimantan and Java. *Treubia* 36: 23-36.

Md Tamrin, N.A. & M.T. Abdullah (2011). Molecular phylogenetics and systematic of Malaysian murine rodents (*Maxomys, Sundamys, Leopoldamys, Niviventer* and *Rattus*) inferred from partial mitochondrial cytochrome *c* oxidase subunit I (COI) gene. *Journal of Science and Technology in the Tropics* 7: 75-86.

Medway, Lord (1964). Niah cave bone – VII: Size change in the teeth of two rats, *Rattus sabanus* Thomas and *R. muelleri* Jentink. *The Sarawak Museum Journal* 11 (23-24 ns): 616-623, plates XVI-XIX.

Medway, Lord (1977). *Mammals of Borneo.* Monographs of the Malaysian Branch of the Royal Asiatic Society 7: i-xii, 1-172.

Miller, G. S., Jr (1912). *Catalogue of mammals of Western Europe in the collection of the British Museum, London.* London, British Museum (Natural History).

Misonne, X. (1969). African and Indo-Australian Muridae: evolutionary trends. *Annales Museum Royal Afrique Central* Sërie IN-8. Sciences Zoologiques 172: 1-219.

Musser, G. G., J. T. Marshall, Jr. & Boeadi (1979). Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). *Journal of Mammalogy* 60: 594-606.

Musser, G. G. (1981). Results of the Archbold Expeditions. No. 105. Notes on the systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bulletin of the American Museum of Natural History* 168: 225-334, figures 1-51, tables 1-12.

Musser, G. G. (1982). The Trinil rats. *Modern Quaternary Research in SE Asia* 7: 65-85.

Musser, G. G. & C. Newcomb, 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* 174: 329-598.

Pagès, M., Y. V. Chaval, S. Herbreteau, J-F. Waengsothorn, J-P. Cosson, S. Hugot, J. Morand & J. Michaux (2010). Revisiting the taxonomy of the Rattini tribe: a phylogeny-based delimitation of species boundaries. *BMC Evolutionary Biology* 10: 184-211.

Payne, J. & C.M. Francis (2005). *A field guide to the mammals of Borneo.* 4th reprint. Kota Kinabalu, Sabah Society.

Piper, P.J. & R.J. Rabbet (2013). Vertebrate fauna. *In* G. Barker (Ed.), *Rainforest foraging and farming in Island Southeast Asia. The Archaeology of the Niah Caves, Sarawak.* 1: 198-208. University of Cambridge, McDonald Institute Monographs.

Wilmshurst, J. M., A. A. Anderson, T.F.G. Higham & T.H. Worthy (2008). Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences* 105 (22): 7676-7680.

Wilson, D. E., & D. M. Reeder (2005). *Mammal species of the world: a taxonomic and geographic reference.* 3rd edn., Vol. 2. Baltimore, Johns Hopkins University Press.

(a)


(b)


Plate 1. (a) Right upper molar row and (b) right lower molar row of *Lenothrix canus* (BMNH 49.6725, from Kepong, Selangor, Peninsular Malaysia). Scale in mm. See text for distinguishing features.

(a)

(b)

Plate 2. (a) Right upper molar row and (b) right lower molar row of female *Leopoldamys sabanus* (BMNH 71.2977). Scale mm. See text for distinguishing features.

(a)

(b)

Plate 3. (a) Right upper molar row and (b) right lower molar row of juvenile male *Sundamys muelleri* (BMNH 99.12.9.74) from Mt Dulit, Sarawak. Scale mm. See text for description of diagnostic characters of the genus.

(a)

(b)

Plate 4. (a) Right upper molar row and (b) right lower molar row of *Sundamys infraluteus* (BMNH 71.2844), from Bundu Tuhan, Mt Kinabalu, Sabah.

(a)

(b)

Plate 5. (a) Right lower molar row of *Maxomys surifer* (BMNH 71.3004*),* showing a small anterocentral cusp on the anteroloph of the 1st molar, between anterolabial and anterolingual cusps of subequal size. Note also the posterolabial cusplet on M1 and on M2, only. Scale mm.

(b) Right lower molar row of *Maxomys whiteheadi* (BM 85.735). Note the lack of an anterocentral cusp on the first molar. Scale mm.

(a)

(b)

Plate 6. (a) Right upper molar row and (b) right lower molar row of female *Maxomys rajah* (BMNH 71.2938). Scale mm.

(a)

(b)

Plate 7. (a) Left upper molar row and (b) right lower molar row of *Rattus argentiventer* (BMNH 55.888), showing the characters of the genus *Rattus*. In the lower toothrow, on M1, note the lack of anterocentral cusp, the relatively large size and anterocentral position of the anterolingual cusp, and prominent posterolabial cusplet. On M2, note anterolabial and posterolabial cusplets, and on M3, the diagnostic anterolabial cusplet. Scale 0.5 mm.

(a)

(b)

Plate 8. (a) Right upper molar row and (b) right lower molar row of *Niviventer cremoriventer* (BMNH 71.2803). Scale in mm. See text for description of distinguishing features.

THE AUTHORS

Earl of Cranbrook *PhD*, JBS, PNBS
Hon. Curator of Mammals, Sarawak Museum Department
lordcranbrook@greatglemhamfarms.co.uk

Philip J. Piper *PhD*
School of Archaeology & Anthropology, Australian National University, Canberra ACT 0200, Australia
phil_piper2003@yahoo.ie