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First Systematic Study of Late Pleistocene Rat Fossils from Batu Caves: New Record of Extinct Species and Biogeography Implications

(Kajian Sistematik Pertama Fosil Tikus Akhir Pleistosen dari Batu Caves: Rekod Baharu Spesies yang Telah Pupus dan Implikasi Biogeografi)

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ABSTRACT

This paper presents the first systematic study of rat (Murinae) isolated dental fossils collected from Late Pleistocene (66000 years ago) cave breccia deposits in Cistern Cave, Batu Caves, Selangor. The cave is partly deposited with fine, coarse and pebbly breccia mixed with abundant mammal fossil cemented to the wall and ceiling of the cave. A total of 39 specimens of teeth and jaw fragments of Murinae were recovered among other large and small mammal remains. Dental morphology and size comparisons suggest that the fossils belong to extinct and extant species which occurred in Peninsular Malaysia and adjacent regions. The species identified are Chiropodomys gliroides, Leopoldamys sabanus, Leopoldamys minutus, Maxomys whiteheadi, Maxomys rajah *and* Rattus rattus. *Almost all species identified from the fossils are known as markers for lowland forested environments.*

Keywords: Caves fossils; Murinae; Peninsular Malaysia; quaternary

ABSTRAK

Kertas ini membentangkan kajian sistematik pertama fosil gigi tikus (Murinae) yang ditemui di dalam endapan breksia gua yang berusia Akhir Pleistosen (66000 tahun dahulu) di Gua Cistern, Batu Caves, Selangor. Sebahagian daripada gua ini dilitupi endapan breksia berbutir halus, kasar dan berpebel, bercampur aduk dengan fosil mamalia yang melekat pada dinding dan siling gua. Sejumlah 39 spesimen gigi dan serpihan rahang Murinae telah ditemui bersama pelbagai fosil mamalia besar dan kecil yang lain. Kajian terhadap perbandingan morfologi dan saiz menunjukkan bahawa fosil gigi ini terdiri daripada spesies yang telah pupus dan yang masih hidup di Semenanjung Malaysia serta negara yang berdekatan. Spesies yang telah dikenal pasti adalah Chiropodomys gliroides, Leopoldamys sabanus, Leopoldamys minutus, Maxomys whiteheadi, Maxomys rajah *dan* Rattus rattus. *Hampir semua spesies fosil yang telah dikenal pasti merupakan fauna yang hidup di sekitaran hutan tanah rendah.*

Kata kunci: Fosil gua; kuaterner; Murinae; Semenanjung Malaysia

INTRODUCTION

The work presented here is based on fossil materials gathered between 2015-2017 from Cistern Cave, part of the cave system located at Batu Caves, a 329 m isolated tower karst surrounded by housing and urban developments in the Gombak district of Selangor (Figure 1). The tower karst is part of Ordovician-Silurian Kuala Lumpur Limestone, which had been altered or metamorphosed to marble during the Triassic orogeny and underlies the flat plain of Kuala Lumpur where some of it had been eroded and covered by Quaternary alluvium (Stauffer & Morgan 1971). Plenty of caves were formed at various levels on the hillside and one of the caves is known as Cistern Cave.

Cistern Cave located about 30 m east of the famous Batu Caves Temple steps and generally formed in an east-west direction with shorter connecting passages oriented north-south. The main entrance of Cistern Cave is accessible at about 3 m above ground level. Cistern cave is divided based on the elevation into three main chambers: lower, middle and upper chambers.

Lim (2006) first reported an *in situ* fossil mammalian fauna in this cave, and later systematic study on large mammal fossils was done by Yasamin et al. (2013) where the team dated the fossil-bearing breccia to the Late Pleistocene period, 66000 years ago (ka) by U/Th and luminescene dating methods. There is few research on micromammal fossils in Peninsular Malaysia compared to the neighbouring countries. Some archaeological studies in Peninsular Malaysia have reported micromammal remains associated with past human activities in caves (Adi Taha 2007; Velat Bujeng 2009), however, they have not been the subject of detailed palaeontological investigation. Therefore, the aims of this study were to conduct a first systematic study on micromammal fossils, specifically on rat (Murinae) dental remains, to highlight new fossil records in Sundaic subregion and their implications for understanding the paleobiogeography and palaeoenvironment of Peninsular Malaysia during Pleistocene times.

Materials and Methods

All fossil samples examined here were collected from breccia that embedded to the ceiling and walls throughout most areas of the chambers. These breccia are poorly sorted with the clast ranging from fine sand to cobble, partially cemented by calcite, while some are unconsolidated. The finer grain breccia shows discerning layers of various thickness especially on the wall sections. Fossil localities were assigned as CC1 to CC9 (Figure 1). Only samples collected from middle chambers (CC3, CC4, CC5 and CC7) contained Murinae dental fossils.

In CC3, approximately 1.7 m thick of cave breccia was attached to the cave wall, covering the upper part of the wall and the floor. Here, samples were taken from breccia at 1.5 m from cave floor where white patches of small mammal bones can be observed *in situ*. In CC4, samples were taken from remnant breccia that strongly cemented to the ceiling located next to stalagmite and rim stone pool. CC5 is a breccia layer that had been dated by Yasamin et al. (2013), 0.5 m below a mushroom-shaped flowstone. CC7 located west of CC5, shown observable laminated sediments deposited in between flowstone.

The fossil-bearing cave breccia was extracted using hammer and chisel. The breccia samples were dissolved in 7:3 ratio of 70% diluted formic acid and buffer solution (made by reacting samples with acid) and left overnight or until no reaction observed to the samples. The residues left from dissolution were washed under running water, and then put in the oven to dry. Then, the dried residues were screened by sieve of 4 mm to 500 µm meshes. Finally, the sorted residues were observed under a microscope (AmScope SZMT2) to search for small mammal fossils.

Measuring methods and terminology for Murinae teeth (Figure 2) follow Musser (1981). The Murinae teeth were measured to 0.01 mm using an ocular eyepiece measurement lens attached to Amscope SZMT2, Leica M125C, Leica S6D and Wild M5A stereoscopic microscopes. Tooth crown measurements taken include length (L, the maximal length of molar crown in the anterior-posterior axis) and width (W, the maximal width of molar crown in the labial-lingual dimension) (Figure 2).

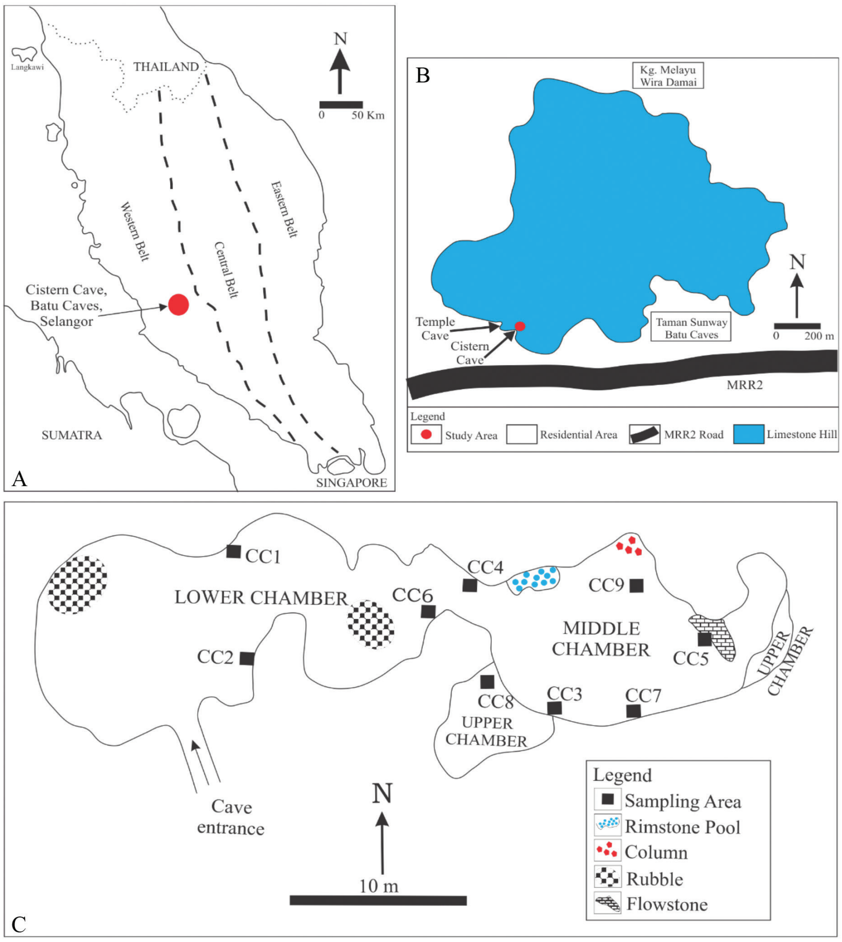

FIGURE 1. A) Batu Caves location in Peninsular Malaysia, B) Cistern Cave location in Batu Caves limestone hill complex, C) Plan view of Cistern Cave (modified from Yasamin 2013) indicating three main chambers of the cave and the location of the sampling areas. Fossils distributed throughout most of the breccia deposits that attached to the wall and ceiling of the cave

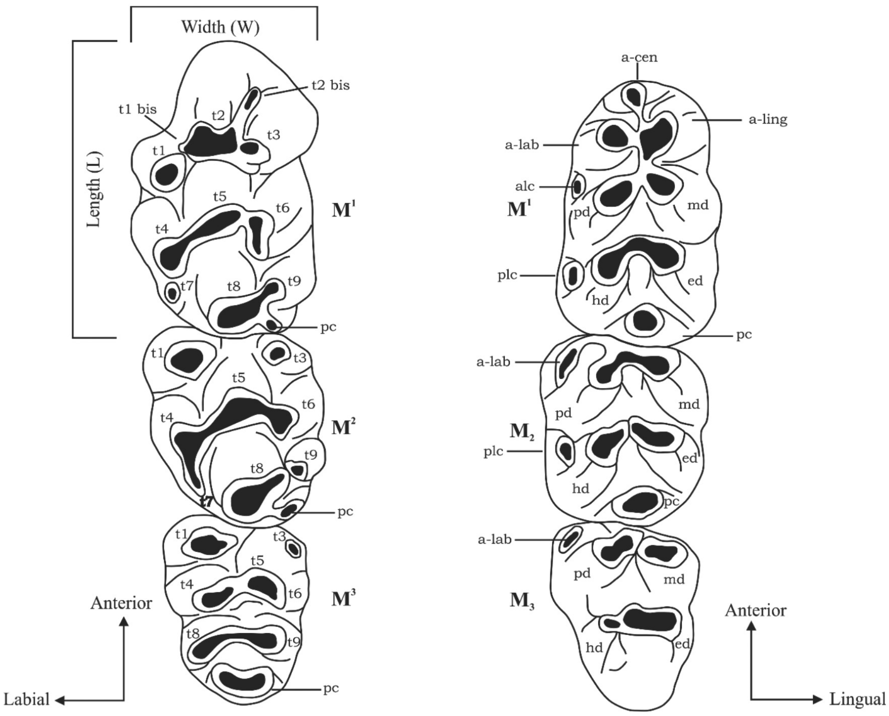

FIGURE 2. Nomenclature of dental structures using left upper (M^1–M^3) and left lower (M_1–M_3) molars of Lenothrix canus (modified from Musser 1981). M1 (first upper molar), M2 (second upper molar), M3 (third upper molar), M1 (first lower molar), M2 (second lower molar) and M3 (third lower molar). Upper molars cusps (t) are numbered sequentially from labial to lingual, cusp t1 to cusp t9; t1 bis is a small cusp between cusp t1 and t2; t2 bis is a small cusp between cusp t2 and t3. Lower molars cusps denoted as, a-lab: anterolabial cusp; a-ling: anterolingual cusp; a-cen: anterocentral cusp; pd: protoconid; hd: hypoconid; md: metaconid; ed: entoconid; pc: posterior cingulum; alc: anterior labial cusplet; plc: posterior labial cusplet

For species identification, the external morphology of fossils was compared with extant Indochinese and Sundaic species. These comparative studies and measurements were carried out on the modern specimens of Murinae stored in the Lee Kong Chian Natural History Museum of the National University of Singapore (LKCNHM), Kunming Institute of Zoology in Yunnan (KIZ), Institute for Medical Research Kuala Lumpur (IMR), Natural History Museum of Putrajaya (NHMP) and Zoological Museum of University Malaya (ZMUM). Fossil specimens of Murinae from Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing were also measured and compared with the fossils found in Cistern Cave. References from various article reporting Murinae fossil in both subregions were used as a secondary data for comparative study.

Results

A total of 39 fossil specimens consist of teeth and jaw fragments, have been identified as Murinae amongst 190 small mammal fossils recovered. Broadly speaking, the genera of fossils can be differentiated based on their size and roots numbers but detailed occlusal morphology is needed for the identification to species level. Most of the fossils show several stages of worn condition but the outline still gives a reliable feature for identification purposes except for some specimens with incomplete crown and/or without roots preserved. All identified species are presented here and the comparative teeth measurements are shown in Table 1.

Genus *Chiropodomys* Peters 1869

Chiropodomys gliroides (Blyth 1856)
Pencil-tailed tree mouse

Fossils - a left upper M^1 (CC5-i18: Figure 3(A)); three left lower M_1 (CC3-i80: Figure 3(B), CC3-i84 and CC4-i1).

Description - The outline of M^1 crown is oval and has three rows of cusps with three roots. The central cusps are larger than the lingual and labial cusps. The lingual cusps are in turn smaller than the labial cusps. There is no t1 bis and t2 bis. Cusp t1 located more posteriorly than cusps t2 and t3 within the same row. On the second row, cusps t4, t5 and t6 are separated with each other, and all cusps located at the same level. The cusp t7 in the third row is isolated and elongated in shape. Cusp t8 is large. Cusp t9 is nearly the same size as cusp t6, connected to cusp t8 by a long crest and it is situated anteriorly just behind the cusp t6. The posterior cingulum is well developed.

The outline of M_1 crown is roughly rectangular in shape and all specimens have two roots, one located at anterior and the other one at posterior. The M_1 has a round anterocentral cusp located in the middle front of the two

TABLE 1. Measurements of Murinae fossil teeth from Cistern Cave and comparative materials. L: range of length, W: range of width, sample size within brackets. All measurements in millimetres. See Materials and Methods for abbreviations of institutions

Species	Materials	M^1	M^2	M^3	M^1	M^2	M^3
Modern							
C. gliroides	Peninsular Malaysia[1,2]	L: 1.56-2.00 (44) W: 1.00-1.28 (44)			L: 1.57-1.90 (44) W: 0.87-1.20 (44)	L: 1.14-1.55 (44) W: 0.95-1.17 (44)	
	Yunnan, China[5]	L: 1.65-1.84 (6) W: 1.10-1.17 (6)			L: 1.50-1.80 (6) W: 0.99-1.11 (6)	L: 1.20-1.32 (6) W: 0.99-1.14 (6)	
Fossil							
C. gliroides	Thailand[7]	L: 1.52-1.97 (64) W: 0.95-1.21 (64)			L: 1.45-1.88 (46) W: 0.88-1.16 (46)	L: 1.12-1.39 (32) W: 0.95-1.18 (32)	
	Cistern Cave	L: 1.63 (1) W: 1.04 (1)			L: 1.70-1.81 (3) W: 1.01-1.13 (3)	L: 1.25 (1) W: 1.02 (1)	
Modern							
L. neili	Thailand[7]	L: 3.98-4.38 (3) W: 2.48-2.62 (3)					
L. sabanus	Peninsular Malaysia[1,2,3]	L: 4.35-5.44 (65) W: 2.61-3.10 (65)	L: 2.80-3.60 (65) W: 2.60-3.00 (65)			L: 2.79-3.36 (65) W: 2.20-2.94 (65)	L: 2.06-3.00 (65) W: 1.92-2.69 (65)
Fossil							
L. minutus	Thailand[1]	L: 3.16-3.73 (62) W: 1.92-2.19 (62)	L: 2.22-2.81 (66) W: 1.75-2.17 (66)				
	Cistern Cave	L: 3.80 (1) W: 2.22 (1)	L: 2.59 (1) W: 2.13 (1)				
L. sabanus	Thailand[7]	L: 4.12-5.18 (49) W: 2.49-3.00 (49)				L: 2.61-2.95 (38) W: 2.39-2.87 (38)	
	Vietnam[8]	L: 4.21-5.36 (20) W: 2.85-3.62 (20)				L: 3.08-3.93 (34) W: 2.49-3.41 (34)	L: 2.43-3.04 (7) W: 2.26-2.75 (7)
	Cistern Cave	L: 4.82-4.96 (2) W: 2.49-2.53 (2)				L: 3.10 (1) W: 2.92 (1)	L: 2.53 (1) W: 2.40 (1)
Modern							
M. rajah	Peninsular Malaysia[1,2,3]	L: 3.04-3.40 (35) W: 1.84-2.40 (35)	L: 2.00-2.50 (34) W: 1.56-2.28 (34)	L: 1.57-1.85 (34) W: 1.16-1.78 (34)	L: 2.65-3.16 (36) W: 1.64-1.96 (36)	L: 2.00-2.37 (36) W: 1.62-2.00 (36)	L: 1.55-2.07 (35) W: 1.35-1.74 (35)
M. surifer	Peninsular Malaysia[1,2,3]	L: 2.73-3.54 (40) W: 1.87-2.64 (40)	L: 1.92-2.48 (40) W: 1.65-2.20 (40)	L: 1.44-2.15 (40) W: 1.10-1.85 (40)	L: 2.42-3.00 (40) W: 1.57-2.03 (40)	L: 1.80-2.23 (40) W: 1.60-2.00 (40)	L: 1.50-1.99 (40) W: 1.38-1.88 (40)
M. whiteheadi	Peninsular Malaysia[1,2]	L: 2.40-2.88 (30) W: 1.36-1.65 (30)	L: 1.62-1.90 (30) W: 1.20-1.60 (30)	L: 1.00-1.27 (30) W: 0.85-1.28 (30)	L: 2.13-2.42 (30) W: 1.24-1.42 (30)	L: 1.58-1.81 (30) W: 1.23-1.50 (30)	L: 1.14-1.46 (30) W: 0.95-1.24 (30)

continue

(Continued) TABLE 1.

Species	Materials	M^1	M^2	M^3	M^1	M^2	M^3
Fossil							
M. pliosurifer	Myanmar[9]	L: 3.17-3.24 (2) W: 2.11-2.14 (2)	L: 2.18-2.50 (3) W: 2.13-2.33 (3)	L: 1.83 (1) W: 1.67 (1)	L: 2.67-2.78 (3) W: 1.62-1.83 (3)	L: 2.25 (1) W: 2.06 (1)	L: 1.79 (1) W: 1.68 (1)
M. rajah	**Cistern Cave**				L: 2.92 (1) W: 1.64 (1)	L: 2.26 (1) W: 1.76 (1)	L: 1.87 (1) W: 1.66 (1)
M. surifer	Thailand[7]	L: 2.83-3.61 (19) W: 1.75-2.21 (19)	L: 2.10-2.28 (5) W: 1.86-1.99 (5)		L: 2.61-3.01 (19) W: 1.62-1.95 (19)	L: 1.89-2.32 (10) W: 1.69-1.89 (10)	
M. whiteheadi	**Cistern Cave**				L: 2.39 (1) W: 1.49 (1)		L: 1.40 (1) W: 1.13 (1)
Modern							
R. argetiventer	Peninsular Malaysia[1,2,3]	L: 2.75-3.57 (32) W: 2.09-2.36 (32)	L: 2.03-2.43 (32) W: 1.50-2.25 (32)		L: 2.86-2.98 (32) W: 1.50-1.60 (32)	L: 1.90-2.35 (32) W: 1.55-2.19 (32)	L: 1.28-2.10 (32) W: 1.10-1.79 (32)
R. exulans	Peninsular Malaysia[1,2,3]	L: 2.40-2.80 (22) W: 1.36-1.65 (22)	L: 1.50-1.80 (22) W: 1.28-1.50 (22)		L: 2.00-2.30 (22) W: 1.20-1.38 (22)	L: 1.35-1.68 (22) W: 1.20-1.50 (22)	L: 0.85-1.20 (22) W: 0.95-1.10 (22)
R. norvegicus	Peninsular Malaysia[1,2,3]	L: 3.03-3.90 (16) W: 2.06-2.40 (16)	L: 2.30-2.68 (16) W: 1.91-2.31 (16)		L: 2.73-3.35 (16) W: 1.57-2.20 (16)	L: 2.00-2.37 (16) W: 1.67-2.28 (16)	L: 1.56-2.22 (14) W: 1.59-1.88 (14)
R. rattus	Peninsular Malaysia[1,2,3,4]	L: 2.94-3.46 (20) W: 1.74-2.21 (20)	L: 1.80-2.32 (20) W: 1.74-2.04(20)		L: 2.37-3.03 (20) W: 1.43-1.82 (20)	L: 1.82-2.26 (20) W: 1.59-2.05 (20)	L: 1.52-2.08 (20) W: 1.38-1.71 (20)
Fossil							
R. jaegari	Thailand[7]	L: 3.13-3.59 (45) W: 1.81-2.10 (45)	L: 2.14-2.53 (56) W: 1.77-2.24 (56)		L: 2.66-3.03 (23) W: 1.51-1.88 (23)	L: 1.97-2.35 (45) W: 1.70-2.07 (45)	L: 1.66-2.16 (20) W: 1.53-1.93 (20)
	Myanmar[9]	L: 2.86-3.17 (3) W: 1.79-1.93 (3)	L: 2.12 (1) W: 1.94 (1)		L: 2.85 (1) W: 1.96 (1)	L: 2.13 (1) W: 2.11 (1)	L: 2.00 (1) W: 1.83 (1)
R. rattus	China[6]				L: 2.50-3.40 (17) W: 1.45-2.00 (17)	L: 1.70-2.50 (19) W: 1.50-2.30 (19)	L: 1.50-2.00 (8) W: 1.10-1.80 (8)
	Thailand[1]	L: 3.16-3.63 (10) W: 1.84-2.00 (10)			L: 2.61-3.09 (31) W: 1.46-1.89 (31)	L: 2.06-2.41 (25) W: 1.71-1.99 (25)	
	Cistern Cave	L: 3.36 (1) W: 2.24 (1)			L: 3.09 (1) W: 1.84 (1)		

Sources: [1]IMR, [2]LKCNHM, [3]ZMUM, [4]NHMP, [5]KIZ, [6]IVPP, [7]Chaimanee (1998), [8]Bacon et al. (2006), [9]Nishioka et al. (2015)

anterior cusps. The anterolabial cusp is separate from the anterolingual cusp. In second row, the protoconid is separate from metaconid. In third row, the hypoconid is also separate from entoconid. Four labial cusplets are developed from the anterolabial cusp to the posterior end. Labial cusplets usually join together to form a ridge, only posterior labial cusplet is isolated and well-marked. Posterior cingulum is present at the edge of all M_1 specimens.

GENUS *LEOPOLDAMYS* ELLERMAN 1947

Leopoldamys minutus (Chaimanee 1998)

Fossil - a right upper M^{1-2} (CC3-i68: Figure 3(C)).

Description - The outline of M^1 crown is oval, long and slender with a simple cusps pattern. It has two gentle chevron-shaped laminae and a posterior lamina. The first row consists of isolated and rounded cusp t1 which located slight anteriorly and cusp t2 and t3 fused horizontally. Cusp t4, t5 and t6 are rounded, separated from each other. The whole crown of M^1 is without t7, with large cusp t8 and very small cusp t9. No posterior cingulum in M^1. It has four roots. The outline of M^2 is long and slender with rounded cups t1 and t4. Cusp t3 is absent. Cusp t4 is also rounded, located at the same level with cusp t6 and it is separated from cusp t5.

Cusp t5 is larger and located centrally, more anteriorly and fused with cusp t6. The second horizontal ridge is much narrower than the first ridge, with large cusp t8 and small t9, without cusp t7.

Leopoldamys sabanus (Thomas 1887)
Long-tailed giant rat

Fossils - a right upper M^1 (CC3-i123); a left upper M^1 (CC7-i1: Figure 3(D)).

Description - The outline of M^1 crown is oval, long and slender with a simple cusps pattern. It has two chevron-shaped laminae and a posterior lamina. The first row consists of isolated cusps t1, located slightly posteriorly, and cusp t2 and t3, which fused horizontally. The cusp t3 is reduced in size. Cusp t4 is rounded and almost the same size with cusp t6, and cusp t6 is fused with cusp t5. The whole crown of M^1 is without t7, with lingually bulging of t1 and t4. It is a simple crown with large cusp t8 and very small cusp t9. No posterior cingulum in M^1.

GENUS *MAXOMYS* SODY, 1936

Maxomys rajah (Thomas 1894)
Rajah Sundaic Maxomys

Fossil - right M_{1-3} (CC5-i19: Figure 3(E)).

Description - The outline of M_1 crown is rectangular in the occlusal view. Roughly, the anterior part of the tooth is the same size with posterior. The first chevron is formed by anterolingual and anterolabial cusps. The anterolabial cusp is larger than anterolingual cusp and located more distally. Anterocentral cusp is absent. The second chevron composed of the nearly the same size as protoconid and metaconid. The metaconid in second row is connected to the anterolingual cusp in first row and forming a trefoil-shaped loph. The protoconid is isolated and located longer downwards to the edge. The third chevron is separated from the second chevron by a shallow valley. The third chevron is composed of hypoconid and entoconid, and both cusps are almost the same size. The elongated posterior labial cusplet is present and located beside the hypoconid. Anterior labial cusplet is absent, posterior cingulum is large and elongated labiolingually and it has two roots.

The outline of M_2 crown is square in shape. It composed of two chevrons and a posterior cingulum. The first chevron composed of nearly same size protoconid and metaconid. There is a small and well developed anterolabial cusp near the protoconid. The second chevron is composed of hypoconid and entoconid and does not connect with the first chevron. The posterior labial cusplet is present. The entoconid on the second chevron is slightly larger than the hypoconid. The posterior cingulum is separate from second chevron by a shallow valley. The outline of M_3 crown is roughly triangular in occlusal view. It is very simple and composed of two chevrons. There is no anterolabial cusp. The anterior part is slightly larger than the posterior. The protoconid on the labial side of the first row is larger than the metaconid on the lingual side. The second chevron is composed of hypoconid and entoconid. It has two roots.

Maxomys whiteheadi (Thomas 1894)
Whitehead's Sundaic Maxomys

Fossil - a left M_1 (CC3-i77: Figure 3(F)).

Description - The outline of M_1 crown is rectangular in shape. The posterior part is wider than the anterior. From occlusal view, M_1 tooth has a basic Murinae pattern with three simple chevrons and a posterior cingulum. The first chevron is formed by anterolingual and anterolabial cusps. The anterolabial cusp is larger than anterolingual cusp and located more distally. The second chevron composed of the protoconid and metaconid that are connected to the first chevron forming a quatrefoil-shaped loph or X- pattern form due to worn out. The protoconid and metaconid are of the same size, just that protoconid is longer downwards to the edge. The third chevron is separated from the second chevron by a shallow valley. The third chevron is composed of hypoconid and entoconid, and both cusps are almost the same size. The posterior labial cusplet is located just beside the hypoconid while anterior labial cusplet is absent. The posterior cingulum is large and elongated labiolingually. It has two roots.

GENUS *RATTUS* FISCHER, 1803

Rattus rattus (Linnaeus 1758)
House rat

Fossils - a right M^1 (CC3-i73: Figure 3(G)) and a left M_1 (CC3-i93: Figure 3(H)).

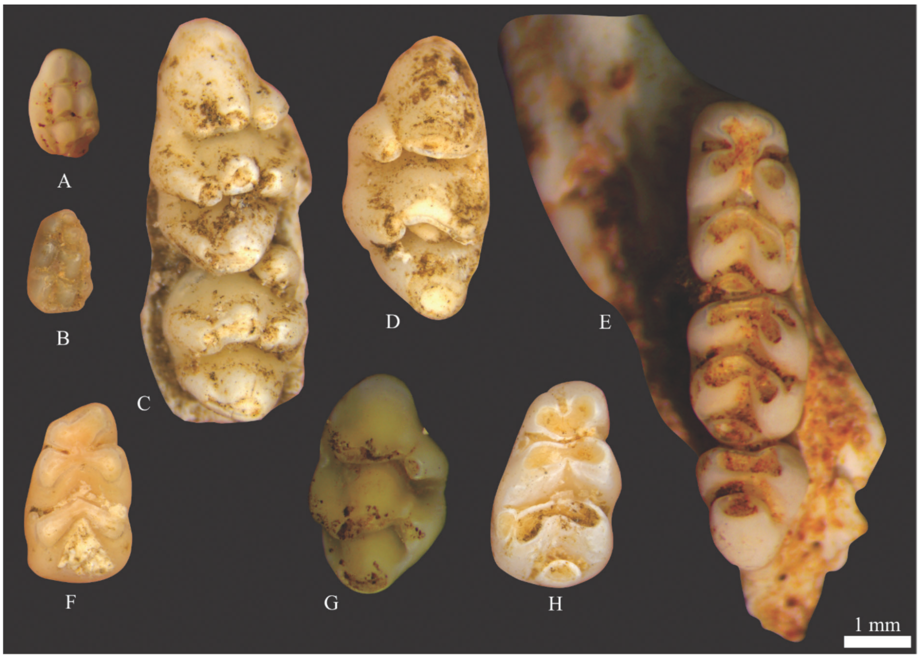

FIGURE 3. Isolated Murinae fossil teeth from Cistern Cave. *Chiropodomys gliroides*: A. CC5-i18 B. CC3-i80; *Leopoldamys minutus*: C. CC3-i68; *Leopoldamys sabanus*: D. CC7-i1; *Maxomys rajah*: E. CC5-i19; *Maxomys whiteheadi*: F. CC3-i77; *Rattus rattus*: G. CC3-i73 H. CC3-i93

Description - The crown outline of M^1 is roughly oval in shape from the occlusal view. In lateral view, all cusps are gently pointed. The first row consists of cusps t2 and t3, and they are located horizontally in the same row. Cusp t1 is isolated, located posteriorly and larger than cusps t2 and t3. In the second row, cusp t4 located separately and posteriorly while cusps t5 and t6 are at the same level. Cusp t5 is located a bit anteriorly and it is larger than cusps t4 and t6. From the occlusal view, it shows that the central cusps on first and second rows are larger than the lingual and labial cusps. Cusps t3 and t6 are smaller, but with clear delineation with neighbouring cusps t2 and t5. The cusps on the first and second row are unconnected to each other because there is a gap between the two rows and the horizontal dentine line. The third row is composed of cusps t8 and a small cusp t9, and they are connected to one another. Cusp t7 and posterior cingulum are absent.

The crown outline of M_1 is roughly trapezoidal in shape. The anterior part is narrower than posterior part. There are three simple chevrons and a posterior cingulum. There are anterolabial and anterolingual cusps. The first row is formed by anterolabial cusp and anterolingual cusp, and both cusps have nearly the same size. The second row composed of protoconid and metaconid, and it is separated from the first row. The protoconid is slightly larger than the metaconid. There is small anterolabial cusplet near to the protoconid. The third row composed of hypoconid and entoconid, and it is bended more downward compared to the cusps on second row. The third row is separated from second row by a valley. There is isolated posterior labial cusplet, oval in shape located near to the hypoconid cusp. The posterior cingulum has a rounded shape. M_1 has four roots.

Discussion

Murinae assemblage from Cistern Cave includes *Chiropodomys gliroides*, *Leopoldamys sabanus*, *Leopoldamys minutus*, *Maxomys whiteheadi*, *Maxomys rajah* and *Rattus rattus*. The current study shows that the Murinae fossils from Cistern Cave are of the same species with those found from cave sediments in South China, Vietnam, Laos, Thailand, Borneo and Java (Table 2). *Chiropodomys gliroides* is the only species in the genus which has a modern distribution range that includes both Indochinese and Sundaic subregions (Carleton & Musser 2005; IUCN 2019). Fossil records of the species (Table 2) show that such pattern of distribution has established itself at least from Early Pleistocene.

There are records of Murinae fossils of some of the genera dated back to Early Pliocene in the Indochinese subregion (Table 2). The fossil records are therefore in agreement with the rodent speciation study of Verneau et al. (1998) where it is estimated that fossil representatives of each of these Murinae lineages (*Maxomys*, *Rattus* sensu stricto and the *Niviventer*/*Leopoldamys*) should be present at post-Early Pliocene sites.

The earliest forms of *Leopoldamys* and *Chiropodomys* in Southeast Asia are an extinct species *L. minutus* and the extant *C. gliroides*, found in the cave deposits of Late Pliocene to Early Pleistocene age in Khao Samngam, central Thailand (Chaimanee 1998). Chaimanee (1998) and Nishioka et al. (2015) reported an early form of *Rattus*, *R. jaegari,* with a primitive dental character (posterior cingulum on M^1), from Thailand and Myanmar Late Pliocene localities, respectively.

TABLE 2. Temporal biogeographical distribution of fossil and extant Murinae from Indochinese and Sundaic subregions (**S** - South China; **V** - Vietnam; **L** - Laos; **T** - Thailand; **D** - Badak Cave C, Peninsular Malaysia; **C** - Cistern Cave, Peninsular Malaysia; **B** - Borneo; **J** - Java; Θ **-** Modern occurrence in both subregions; **O -** Modern occurrence in Sundaic subregion only; **X** - Extinct)

Age \ Species	*C. gliroides*	*L. sabanus*	*L. minutus*	*M. whiteheadi*	*M. rajah*	*R. rattus*
Modern	Θ	Θ	**X**	**O**	**O**	Θ
Holocene	T	**T, B,**	-	-	-	**J**
L. Pleistocene	C, T	T, C, B, J, V	C	C	C	S, T, C
M. Pleistocene	**T, D**	**V, L, T**	-	-	-	**S**
E. Pleistocene	**T, J**	-	**T**	-	-	**T**
L. Pliocene	**T**	-	**T**	-	-	-

Sources: **S** - Zhang et al. (1997); Zou et al. (2016); **V** - Bacon et al. (2006); Vu et al. (1996); **L** - Demeter et al. (2017); **T** - Chaimanee (1998); **D** - Yasamin et al. (2013); **C** - This study; **B** - Medway (1977); Cranbrook & Piper (2015); **J** - Dammerman (1932); van der Muelen & Musser (1999); Storm & de Vos (2006); Westaway et al. (2007); Θ - Modern occurrence in both subregions (IUCN 2019); **O** - Modern occurrence in Sundaic subregion only (IUCN 2019); and **X** - Chaimanee (1998)

Fossil evidence of these species therefore supports the early presence or origin of *Chiropodomys*, *Maxomys*, *Leopoldamys* and *Rattus* genera in the Indochinese subregion before they disperse south to the Sundaic subregion. During Plio-Pleistocene times, a relatively stable humid climate had characterized the region for several million years and tropical rain forest was widespread, presumably on the Sundaic continental shelf as well as on the islands, peninsula and mainland (Gorog et al. 2004). Such climatic regime and the prevalent vegetation type may facilitate the dispersals of these genera into the Sundaic subregion.

This report recorded the first fossils of *M. rajah* and *M. whiteheadi* in Late Pleistocene Southeast Asia. It is important to note that both of these extant are endemic to the Sundaic subregion (absence only from the northern part of the Kra Isthmus and Java Island in the south, IUCN 2019). The genus *Maxomys* is said to begin to diverge 4.8 million years ago (Ruedas & Kirsch 1997) from the Indochinese subregion, and since then only two species (*M. surifer* and *M. moi*) still inhabit the subregion (IUCN 2019). Our findings of the fossils of *M. rajah* and *M. whiteheadi* suggested that the two species have split from their sister species (*M. inas*, *M. articola*, *M. baeodon*, *M. bartelsii*, *M. hylomyoides*, *M. inflatus*, *M. ochraceiventer*, *M. pagensis*, *M. panglima*, *M. tajuddinii*) since at least Late Pleistocene times.

While the extinct *L. minutus* from Late Pleistocene Cistern Cave did not chronostratigraphically correlated with the Plio-Pleistocene *L. minutus* found in central Thailand, it shares the following occlusal morphology with the Thailand specimens: long and slender M^1 and M^2; M^1 without cusp t7; cusp t9 on M^1 is discrete and merged with the large cusp t8; no posterior cingulum on M^1; cusps t1 and t4 on M^1 and M^2 are rounded; and the second cusp rows on M^1 and M^2 form gently arcuate laminae.

The Cistern Cave specimen shows smallest dimensions of measurement as compared to any other known living species of *Leopoldamys*, including the karst endemic *L. neili* (Chaimanee 1998). Measurements of the Cistern Cave specimen match those of the *L. minutus* from Thailand (Table 1). The Cistern Cave specimen may have come from a juvenile *Leopoldamys* as there is very little wear on the occlusal surfaces but this is unlikely, because it is known that once the molars erupt from the palate they do not change in size (per. comm. Musser 2017).

This is believed to be the first record of the extinct species outside of Thailand, and since the age difference between the central Thailand and Cistern Cave is large, hypothetically, *L. minutus* inhabited both Indochinese and Sundaic subregions prior to their extinction most probably by the end of Late Pleistocene. It could have migrated to Sundaic subregion during cooling period of Early Pleistocene (Heslop et al. 2002) and later extinct in Malay Peninsula.

Rattus rattus is a widely distributed species around the world (IUCN 2019) with dispersal usually facilitated by human activities. In modern days, it occurs in disturbed and human-modified landscapes throughout much of the world, typically occupying villages, field complexes and disturbed forests (Aplin et al. 2011). The presence of *R. rattus* fossils in Cistern Cave more likely represent remnants of prey items left behind by predator such as owls (Andrews 1990) as sign associated with human settlement is yet to be found in the Late Pleistocene deposits of Cistern Cave. Alternatively, the recovery of its remains may indicate the occurrence of a naturally disturbed habitat around the cave site during the Late Pleistocene times.

CONCLUSION

The following taxa were recorded from Cistern Cave Murinae fossils: *Chiropodamys gliroides, Leopoldamys sabanus, Leopoldamys minutus, Maxomys whiteheadi, Maxomys rajah* and *Rattus rattus*. The identified Murinae taxa are useful in reconstructing the palaeoenvironment conditions of the Cistern Cave area during the Late Pleistocene times. Generally, all species, except *Rattus rattus*, are known as markers for lowland forested environments. The discovery of Murinae fossils in Cistern Cave fulfilled a chronological and biogeographical gap in the Late Pleistocene fossil records of Sundaic subregion. Future systematic vertebrate palaeontological research would include additional localities in Peninsular Malaysia to increase our understanding of Malaysian Quaternary fauna and environments.

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