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)

ISHLAHUDDIN HANI SAHAK, LIM TZE TSHEN, ROS FATIHAH MUHAMMAD*, NUR SYIMAH IZZAH ABDULLAH THAN & MOHAMMAD AMIN ABD AZIZ

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

INTRODUCTION
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

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 luminescence 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 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, showed 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 sorted residues were observed under a microscope (AmScope SM2T2) 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 (M¹–M³) and left lower (M₁–M₃) 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 M¹ (CC5-i18: Figure 3(A)); three left lower M₁ (CC3-i80: Figure 3(B), CC3-i84 and CC4-i1).

Description - The outline of M¹ crown is oval and has three rows of cusps with three roots. The central cusps are larger than the lingual and labial cusps. The central 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 M₁ crown is roughly rectangular in shape and all specimens have two roots, one located at anterior and the other one at posterior. The M₁ has a round anterocentral cusp located in the middle front of the two
| Species       | Materials | M¹                  | M²                  | M³                  | M¹                  | M²                  | M³                  |
|--------------|-----------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| Modern       |           |                     |                     |                     |                     |                     |                     |
|              |           | L: 1.56-2.00 (44)   | W: 1.00-1.28 (44)   | L: 1.65-1.84 (6)    | W: 1.10-1.17 (6)    | L: 1.57-1.90 (44)   | W: 0.87-1.20 (44)   |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
| Modern       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           | L: 1.50-1.80 (6)    | W: 0.99-1.11 (6)    | L: 1.20-1.32 (6)    | W: 0.99-1.14 (6)    | L: 1.57-1.90 (44)   | W: 0.87-1.20 (44)   |
| Fossil       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
| Modern       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           | L: 1.50-1.80 (6)    | W: 0.99-1.11 (6)    | L: 1.20-1.32 (6)    | W: 0.99-1.14 (6)    | L: 1.57-1.90 (44)   | W: 0.87-1.20 (44)   |
| Fossil       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
| Modern       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           | L: 1.14-1.55 (44)   | W: 0.95-1.17 (44)   | L: 1.20-1.32 (6)    | W: 0.99-1.14 (6)    | L: 1.57-1.90 (44)   | W: 0.87-1.20 (44)   |
| Fossil       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
| 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       |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
|              |           |                     |                     |                     |                     |                     |                     |
| 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)         |
(Continued) TABLE 1.

| Species                  | Materials       | M¹   | M²   | M³   | M¹   | M²   | M³   |
|--------------------------|-----------------|------|------|------|------|------|------|
| **Fossil**               |                 |      |      |      |      |      |      |
| *M. pliosurifer*         | Myanmar         | L: 3.17-3.24 (2) | L: 2.18-2.50 (3) | L: 1.83 (1) | L: 2.67-2.78 (3) | L: 2.25 (1) | L: 1.79 (1) |
|                          |                 | W: 2.11-2.14 (2) | W: 2.13-2.33 (3) | W: 1.67 (1) | W: 1.62-1.83 (3) | W: 2.06 (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        | L: 2.83-3.61 (19) | L: 2.10-2.28 (5) | L: 2.61-3.01 (19) | L: 1.89-2.32 (10) | L: 1.40 (1) | L: 1.13 (1) |
|                          |                 | W: 1.75-2.21 (19) | W: 1.86-1.99 (5) | W: 1.62-1.95 (19) | W: 1.69-1.89 (10) |       |       |
| *M. whiteheadi*         | Cistern Cave    | L: 2.39 (1) | W: 1.49 (1) | L: 2.39 (1) | W: 1.49 (1) | L: 2.39 (1) | W: 1.49 (1) |
| **Modern**              |                 |      |      |      |      |      |      |
| *R. argetiventer*       | Peninsular Malaysia | L: 2.75-3.57 (32) | L: 2.03-2.43 (32) | L: 2.86-2.98 (32) | L: 1.90-2.35 (32) | L: 1.28-2.10 (32) | L: 1.10-1.79 (32) |
|                         |                 | W: 2.09-2.36 (32) | W: 1.50-2.25 (32) | W: 1.50-2.10 (32) | W: 1.55-2.19 (32) | W: 0.95-1.10 (22) |       |
| *R. exulans*            | Peninsular Malaysia | L: 2.40-2.80 (22) | L: 1.50-1.80 (22) | L: 2.00-2.30 (22) | L: 1.35-1.68 (22) | L: 0.85-1.20 (22) | L: 1.56-2.22 (14) |
|                         |                 | W: 1.36-1.65 (22) | W: 1.28-1.50 (22) | W: 1.20-1.38 (22) | W: 1.20-1.50 (22) | W: 0.95-1.10 (22) |       |
| *R. norvegicus*         | Peninsular Malaysia | L: 3.03-3.90 (16) | L: 2.30-2.68 (16) | L: 2.73-3.35 (16) | L: 2.00-2.37 (16) | L: 1.56-2.22 (14) | L: 1.59-1.88 (14) |
|                         |                 | W: 2.06-2.40 (16) | W: 1.91-2.31 (16) | W: 1.57-2.20 (16) | W: 1.67-2.28 (16) | W: 1.59-1.88 (14) |       |
| *R. rattus*             | Peninsular Malaysia | L: 2.94-3.46 (20) | L: 1.80-2.32 (20) | L: 2.37-3.03 (20) | L: 1.82-2.26 (20) | L: 1.52-2.08 (20) | L: 1.38-1.71 (20) |
|                         |                 | W: 1.74-2.21 (20) | W: 1.74-2.04 (20) | W: 1.43-1.82 (20) | W: 1.59-2.05 (20) | W: 1.38-1.71 (20) |       |
| **Fossil**              |                 |      |      |      |      |      |      |
| *R. jaegari*            | Thailand        | L: 3.13-3.59 (45) | L: 2.14-2.53 (56) | L: 2.66-3.03 (23) | L: 1.97-2.35 (45) | L: 1.66-2.16 (20) | L: 1.53-1.93 (20) |
|                         |                 | W: 1.81-2.10 (45) | W: 1.77-2.24 (56) | W: 1.51-1.88 (23) | W: 1.70-2.07 (45) | W: 1.66-2.16 (20) |       |
|                         | Myanmar         | L: 2.86-3.17 (3) | L: 2.12 (1) | L: 2.85 (1) | L: 2.13 (1) | L: 2.00 (1) | L: 1.83 (1) |
|                         |                 | W: 1.79-1.93 (3) | W: 1.94 (1) | W: 1.96 (1) | W: 2.11 (1) |       |       |
| *R. rattus*             | China           | L: 2.50-3.40 (17) | L: 1.70-2.50 (19) | L: 1.70-2.50 (17) | L: 1.50-2.30 (19) | L: 1.50-2.00 (8) | L: 1.10-1.80 (8) |
|                         |                 | W: 1.45-2.00 (17) | W: 1.50-2.30 (19) | W: 1.50-2.30 (17) | W: 1.50-2.30 (19) | W: 1.10-1.80 (8) |       |
|                         | Thailand        | L: 3.16-3.63 (10) | L: 2.61-3.09 (31) | L: 2.06-2.41 (25) | W: 1.46-1.89 (31) | W: 1.71-1.99 (25) |       |
|                         |                 | W: 1.84-2.00 (10) | W: 1.46-1.89 (31) | 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: ¹IMR, ²LKCNHM, ³ZMUM, ⁴NHMP, ⁵KIZ, ⁶IVPP, ⁷Chaimanee (1998), ⁸Bacon et al. (2006), ⁹Nishioka 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\textsubscript{1} specimens.

**GENUS LEOPOLDAMYS ELLERMAN 1947**

*Leopoldamys minutus* (Chaimanee 1998)

*Fossil* - a right upper M\textsubscript{1,2} (CC3-i68: Figure 3(C)).

**Description** - The outline of M\textsubscript{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 slightly anteriorly and cusp t2 and t3 fused horizontally. Cusp t4, t5 and t6 are rounded, separated from each other. The whole crown of M\textsubscript{1} is without t7, with large cusp t8 and very small cusp t9. No posterior cingulum in M\textsubscript{1}. It has four roots. The outline of M\textsubscript{1} is long and slender with rounded cusps t1 and t4. Cusp t5 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 centrically, 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)

*Fossils* - a right upper M\textsuperscript{1} (CC3-i123); a left upper M\textsuperscript{1} (CC7-i1: Figure 3(D)).

**Description** - The outline of M\textsuperscript{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\textsuperscript{1} is without t7, with linguually bulging of t1 and t4. It is a simple crown with large cusp t8 and very small cusp t9. No posterior cingulum in M\textsuperscript{1}.

**GENUS MAXOMYS SODY, 1936**

*Maxomys rajah* (Thomas 1894)

*Rajah Sundaic Maxomys*

*Fossil* - right M\textsubscript{1,3} (CC5-i19: Figure 3(E)).

**Description** - The outline of M\textsubscript{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.

*Maxomys whiteheadi* (Thomas 1894)

*Whitehead’s Sundaic Maxomys*

*Fossil* - a left M\textsubscript{1} (CC3-i77: Figure 3(F)).

**Description** - The outline of M\textsubscript{1} crown is rectangular in shape. The posterior part is wider than the anterior. From occlusal view, M\textsubscript{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\textsuperscript{1} (CC3-i73: Figure 3(G)) and a left M\textsubscript{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 M₁ 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 M₁ 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. M₁ 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 M₁), from Thailand and Myanmar Late Pliocene localities, respectively.
Fossil evidence of these species therefore supports the early presence or origin of *Chiropteryx, 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. moii*) 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. ochraceiventervent*, *M. pagensis*, *M. panglina*, *M. tajuddinii*) since at least Late Pleistocene times.

While the extinct *L. minutus* from Late Pleistocene Cistern Cave did not chronos stratigraphically correlated with the Plio-Pleistocene *L. minutus* found in central Thailand, it shares the following occlusal morphology with the Thailand specimens: long and slender M1 and M2; M1 without cusp t7; cusp t9 on M1 is discrete and merged with the large cusp t8; no posterior cingulum on M1; cusps t1 and t4 on M1 and M2 are rounded; and the second cusp rows on M1 and M2 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

---

**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)

| Species        | Age       | C. glimoides | L. subanuax | L. minutus | M. whiteheadi | M. rajah | R. rattus |
|----------------|-----------|--------------|-------------|------------|---------------|----------|----------|
| Modern         | Θ         | Θ            | X           | O          | O             | Θ        |          |
| Holocene       | T         | T, B,        | -           | -          | -             | J        |          |
| L. Pleistocene | C, T      | C, T, 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 - Dummerman (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).
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: Chirodopodamy gliroides, Leopoldamys sabanus, Leopoldamys minitus, 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.

ACKNOWLEDGEMENTS

The research is supported by funds from University of Malaya under Postgraduate Research Grant (PPP)-PG064-2015A, MyBrain Malaysia and partly supported by RU Grant-Faculty Program GPR21B-2018. Our heartfelt gratitude for the help and support of staff members from Lee Kong Chian Natural History Museum of National University of Singapore, Kunming Institute of Zoology, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, Institute for Medical Research, Kuala Lumpur, Zoological Museum of University of Malaya and Natural History Museum of Putrajaya. We are very grateful to Yaowalak Chaimanee, Guy Musser, Earl of Cranbrook and Wang Yuan for thoughtful advice, providing references and initial discussions throughout the study.

REFERENCES

Adi Taha. 2007. Archaeology of Ulu Kelantan. Kuala Lumpur: Departments of Museum Malaysia.

Andrews, P. 1990. Owls, Caves and Fossils: Predation, Preservation, and Accumulation of Small Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip, Somerset. London: The University of Chicago Press.

Aplin, K.P., Suzuki, H., Chinen, A.A., Chesser, R.T., Have, J.T., Donnellan, S.C., Austin, J., Frost, A., Gonzalez, J.P., Herbreteau, V., Catzeff, F., Soubrier, J., Fang, Y.P., Robins, J., Matissoo-Smith, E., Bastos, A.D.S., Ibmu, M., Sinaga, M.H., Denys, C., van den Bussche, R.A., Conroy, C., Rowe, K. & Cooper, A. 2011. Multiple geographic origins of commensalism and complex dispersal history of black rats. PLoS ONE 6(1): 1-20.

Bacon, A.M., Demeter, F., Duringer, P., Rousse, S., Dodo, Y., Matsumura, H., Long, V.T., Thuy, N.K., Huang, N.T.M. & Anezaki, T. 2006. Records of murine rodents (Mamalia, Rodentia) in the Pleistocene localities of Tan Vinh and Ma U’Oi (Northern Vietnam) and their implications to past distribution. Annales de Paléontologie 92: 367-383.

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

Cranbrook, Earl of & Piper, P.J. 2015. Tikus Purbakala. A guide for Zooarchaeologists on the identifications of rats from Borneo caves excavations by dental characters. The Sarawak Museum Journal LXXIV: 1-38.

Dammernan, K.W. 1932. On prehistoric mammals from the Sampoeng Cave, Central Java. Tresvilia XIV: 477-487.

Demeter, F., Shackelford, L., Westaway, K., Barnes, L., Düringer, P., Ponche, J.L., Dumoncel, J., Sénégas, F., Sayavongkhamdy, T., Zhao, J.X., Sichanthongpit, P., Elise, P.E., Dunn, T., Zacwieja, A., Coppen, Y., Willerslev, E. & Bacon, A.M. 2017. Early modern humans from Tam Pà Lìng, Laos: Fossil review and perspectives. Current Anthropology 58: S527-S538.

Gorog, A.J., Sinaga, M.H. & Engstrom, M.D. 2004. Vicariance or dispersal? Historical biogeography of three Sunda shelf murine rodents (Maxomys surifer, Leopoldamys sabanus and Maxomys whiteheadi). Biological Journal of the Linnean Society 81: 91-109.

Heslop, D., Dekkers, M.J. & Langereis, C.G. 2002. Timing and structure of the mid Pleistocene transition: Records from the loess deposits of northern China. Palaeogeography, Palaeoclimatology, Palaeoecology 185: 133-143.

IUCN. 2019. IUCN Red List of Threatened Species Version 2019.2. http://www.iucnredlist.org.

Lim, T.T. 2006. Fossil teeth from a limestone cave in Selangor. Pencinta Alam December: 2-3.

Medway, L. 1977. The Niah excavations and an assessment of the impact of early man on mammals in Borneo. Asian Perspectives XX(1): 51-69.

Musser, G.G. 1981. Results of the Archbold Expeditions No. 105. Notes on 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: 225-234.

Musser, G.G. & Carleton, M.D. 2005. Superfamily Muroidea. In Mammal Species of the World: A Geographic and Taxonomic Reference, edited by Wilson, D.E. & Reeder, D.A. Baltimore: The John Hopkins University Press. pp. 894-1531.

Nishioka, Y., Takai, M., Nishimura, T., Thaung-Thu, Zin-Maung-Maung-Then, Egi, N., Tsubamoto, T. & Maung-Maung-Maung-Maung. 2015. Late Pliocene rodents from the Irrawaddy sediments of central Myanmar and their palaeogeographical significance. Journal of Systematic Palaeontology 13(4): 287-314.

Ruedas, L.A. & Kirsh, J.A. 1997. Systematics of Maxomys Sody, 1936 (Rodentia): Studies of some Borneo-Javan species and allied Sundaic and Australo-Papuan genera. Biological Journal of the Linnean Society 61(3): 385-408.

Stauffer, P.H. & Morgan, R.P.C. 1971. Geology of Batu Caves. In The Malayan Nature Society and the Batu Caves Protection Association. pp. 5-11.

Storm, P. & de Vos, J. 2006. Rediscovery of the Late Pleistocene Punung hominin sites and the discovery of a new site Gunung Dawung in East Java. Senckenbergiana lethaea 86(2): 271-281.

Van der Meulen & Musser, G.G. 1999. New paleontological data from the continental Pleistocene of Java. In Elephants have a snorkel! Papers in Honour of Paul Y. Sondar, edited by Reumer, J.W. F. & De Vos, J. DEINSEA 7. pp. 361-368.
Velat Bujeng. 2009. Zooarchaeological evidence of the Late Pleistocene until Late Holocene at Lenggong Valley, Perak. Warisan Arkeologi Malaysia 2: 84-102.

Verneau, O., Catzeflis, F. & Furano, A.V. 1998. Determining and dating recent rodent speciation events by using L1 (LINE-1) retrotransposons. Proceedings of the National Academy of Sciences 95: 11284-11289.

Vu, T.L., de Vos, J. & Ciochon, R.S. 1996. The fossil mammal fauna of the Lang Trang Caves, Vietnam, compared with Southeast Asian fossil mammal faunas: The geographical implications. Bulletin of the Indo-Pacific Prehistory Association 14: 101-109.

Westaway, K.E., Morwood, M.J., Roberts, R.G., Rokus, A.D., Zhao, J.X., Storm, P., Aziz, F., van den Bergh, G., Hadi, P., Jatmiko & de Vos, J. 2007. Age and biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications for Pongo and Homo. Journal of Human Evolution 53: 709-717.

Yasamin Kh. Ibrahim, Lim, T.T., Westaway, K.E., Cranbrook, Earl of, Humphrey, L., Ros Fatihah, M., Zhao, J.X. & Lee, C.P. 2013. First discovery of Pleistocene orangutan (Pongo sp.) fossils in Peninsular Malaysia: Biogeographic and paleoenvironmental implications. Journal of Human Evolution 65: 770-797.

Zhang, Z., Liu, J., Zhang, H. & Yuan, C. 1997. A Pleistocene mammalian fauna from Panxian Dadong, Guizhou Province [in Chinese with English abstract]. Acta Anthropologica Sinica 16(3): 207-220.

Zou, S., Chen, X., Zhang, B., Zhao, K., Wen, J., Deng, L. & Tong, H. 2016. Preliminary report on the Late Pleistocene mammalian fauna from Shangli County, Pingxiang, Jiangxi Province [in Chinese with English abstract]. Acta Anthropologica Sinica 35(1): 109-120.