

Molecular Phylogeny of Long-Tailed Giant Rats (Muridae: Genus *Leopoldamys*) Based on Mitochondrial Cytochrome *B* Sequences

(Filogeni Molekul Tikus Gergasi Berekor Panjang (Muridae: Genus *Leopoldamys*) Berdasarkan Jujukan Sitokrom *B* Mitokondria)

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ABSTRACT

Two species of *Leopoldamys* long-tailed giant rats are found in Peninsular Malaysia. They are currently referred to as *Leopoldamys ciliatus* which inhabits montane habitat, and *Leopoldamys vociferans* which usually inhabits the lowland forest. To date, there is no report on the phylogenetic relationship of *L. ciliatus* with the other *Leopoldamys* taxa. The present study was carried out to determine its relationship, based on the mitochondrial cytochrome *b* (cyt *b*) gene sequence, with *L. vociferans* of Peninsular Malaysia and other congeners. Phylogenetic analysis shows that *L. ciliatus* is a sister-species to the lineage L1 of *L. herberti* and *L. revertens*, and is distantly related to *L. edwardsi*. *L. vociferans*, and *L. sabanus* form a distinct clade (lineage L5) from the other *Leopoldamys* taxa from Indochina. The Sumatra taxon currently known as *L. sabanus* is genetically distinct to *L. vociferans* with K2P distances between 0.065 and 0.069. Contrary to previous opinions, *L. herberti*, *L. revertens*, and *L. neilli* of Indochina are valid species based on more than 2.5% threshold genetic distance. Both the *L. edwardsi* and *L. neilli* species complexes are represented by several sibling species. A more extensive taxon sampling from various regions (particularly Sumatra and other regions of Indonesia) as well as the use of morphological and molecular (mitogenomes or multiple genes) data sets are needed to provide a robust phylogeny and systematics.

Keywords: *Leopoldamys ciliatus*; Malaysia; molecular phylogeny; Murinae; polyphyletic; Sundaland

ABSTRAK

Dua spesies tikus gergasi berekor panjang (genus *Leopoldamys*) boleh dijumpai di Semenanjung Malaysia. Ia kini dirujuk sebagai *Leopoldamys ciliatus* yang mendiami habitat pergunungan dan *Leopoldamys vociferans* yang biasanya mendiami hutan dataran rendah. Sehingga kini, tiada laporan mengenai hubungan filogenetik *L. ciliatus* bersama takson *Leopoldamys* yang lain. Kajian ini dijalankan untuk menentukan hubungan genetik tersebut berdasarkan jujukan gen mitokondria sitokrom *b* (cyt *b*), bersama *L. vociferans* dari Semenanjung Malaysia dan kongener lain. Analisis filogenetik mendedahkan bahawa *L. ciliatus* ialah spesies rapat kepada cabang keturunan L1, *L. herberti* dan *L. revertens* dan hubungan jauh dengan *L. edwardsi*. *L. vociferans* dan *L. sabanus* membentuk klad yang berbeza (keturunan L5) daripada takson *Leopoldamys* lain dari Indochina. Takson Sumatera yang kini dikenali sebagai *L. sabanus* secara genetik berbeza dengan *L. vociferans* bersama jarak K2P antara 0.065 dan 0.069. Bertentangan dengan pendapat sebelumnya, *L. herberti*, *L. revertens* dan *L. neilli* dari Indochina adalah spesies yang sah berdasarkan jarak genetik lebih daripada 2.5%. Kedua-dua kompleks spesies *L. edwardsi* dan *L. neilli* diwakili oleh beberapa spesies adik-beradik. Pensampelan takson yang lebih meluas dari pelbagai kawasan (terutamanya Sumatera dan kawasan lain di Indonesia) serta penggunaan set data morfologi dan molekul (mitogenom atau gen pelbagai) diperlukan untuk membentuk filogeni dan sistematik yang teguh.

Kata kunci: Filogeni molekul; *Leopoldamys ciliatus*; Malaysia; Murinae; polifiletik; Sundaland

INTRODUCTION

Nine species are currently recognized in the genus *Leopoldamys* worldwide: *L. ciliatus*, *L. diwangkarai*, *L. edwardsi*, *L. herberti*, *L. milleti*, *L. neilli*, *L. sabanus*, *L. siporanus*, and *L. vociferans* (Balakirev et al. 2013; Latinne et al. 2013b; Yong et al. 2013). A recent study, based on two mitochondrial (cyt *b*, COI) and three nuclear (GHR, IRBP and RAG1) genes, indicates that *L. edwardsi* is a species complex with at least three distinct species in China - *L. hainanensis* (previously *L. e. hainanensis*) endemic to Hainan Island, a cryptic species in southern China, and the nominotypical species *L. edwardsi* (Li et al. 2019). Most of this diversity is in Indochina, but three species are distributed south of the Isthmus of Kra in Sundaland.

Two species of long-tailed giant rats are found in Peninsular Malaysia, one inhabiting montane habitat and the other lowland forest (Musser & Carleton 2005). In earlier taxonomic treatment, the montane species was referred to as *Rattus edwardsi* (Thomas 1882) and the lowland species as *Rattus sabanus* (Thomas 1882; Harrison 1966; Medway 1969; Yong 1968, 1970). They were accorded subspecies rank (*R. e. ciliatus*, *R. s. vociferans* for the mainland taxon, *R. s. lancavensis* for the Langkawi taxon, *R. s. dictatorius* for the Penang taxon, and *R. s. stridens* for the Tioman taxon) to distinguish them from morphologically very similar taxa named as the same species in other geographical regions (Medway 1969; Yong 1968). These species were grouped/classified as members of the subgenus *Leopoldamys* (Ellerman 1947, 1949; Yong 1968, 1969). With the elevation of the subgenus to generic status (Musser 1981), they are now members of the genus *Leopoldamys* (Yong et al. 2013).

The montane long-tailed giant rat of Peninsular Malaysia is now regarded as a distinct species, *L. ciliatus* (Musser 1981; Musser & Carleton 2005; Yong et al. 2013) – referred to as *Rattus ciliatus* in passing by Medway and Yong (1976). The taxon was first described by Bonhote (1900) from Mount Inas, Perak, Malaysia but it was also reported to be distributed in the highlands of Sumatra (Aplin 2016). The lowland counterpart is now named *L. vociferans* (Miller 1900) (Balakirev, Abramov & Rozhnov 2013). It was first described from Trong Province, Thailand at a low elevation (300 m) and shares close similarities in terms of sizes, coloration and cranial shape with the Bornean *L. sabanus*.

The phylogenetic relationship between several *Leopoldamys* species is still unresolved. Whilst most of the species have been included in molecular

phylogenies, some more narrowly distributed taxa are not included, so there is no comprehensive phylogeny. For example, neither *L. ciliatus* from Peninsular Malaysia, nor *L. diwangkarai* and *L. siporanus* from Indonesia have been sequenced (Balakirev, Abramov & Rozhnov 2013; Latinne et al. 2013a).

In view of the lack of study on the molecular phylogeny of *L. ciliatus* and other *Leopoldamys* taxa, the present study was carried out to determine its relationship, based on mitochondrial cyt *b* sequences, with *L. vociferans* of Peninsular Malaysia and other *Leopoldamys* taxa.

MATERIALS AND METHODS

SAMPLE COLLECTIONS

This study was ethically approved (S24012019/26112018-02/R) by the Institutional Animal Care and Use Committee, Universiti Malaya (UMIACUC). Field work was conducted under a permit (#100-24/1.24 Jld 9(8)) from the Department of Wildlife and National Parks of Peninsular Malaysia using mesh wire box live traps (28 cm × 15 cm × 12 cm) baited with banana, palm kernel or salted fish.

The two Peninsular Malaysia species of *Leopoldamys* long-tailed giant rats collected in the present study were *L. ciliatus* (n = 5) from Genting Highlands, Pahang (elevations 1554 – 1727 m, GPS 3.439878, 101.783444); *L. vociferans* from Fraser's Hill, Pahang (n = 3; elevation 1045 m, GPS 3.726419, 101.717111), Lubuk Yu, Pahang (n = 1, elevation 210 m, GPS 3.753211, 102.651122), and Tioman Island, Pahang (n = 6, elevations 200 – 250 m, GPS 2.821131, 104.169686) (Figure 1). Thirty traps were set up for five nights in Genting Highlands for a total of 150 trap nights, while 40 to 50 traps (five nights) in Fraser's Hill, Lubuk Yu and Tioman Island for a total of 200, 210 and 250 trap nights, respectively. Captured rats were identified, based on morphology and ecology (Table 1, Figure 2), with reference to published literature (Medway 1983; Pimsai et al. 2014; Yong 1970). *L. ciliatus* had been previously collected from Gunung Ulu Kali (Genting Highlands) and *L. vociferans* from Fraser's Hill (Chan, Dhaliwal & Yong 1979; Yong 1970).

The rats were euthanized with an overdose of Zoletil® 50 (>50 mg/kg of body weight). Small pieces of their liver (over 10 mm in size) were preserved in 90% ethanol in 1.5 mL tube and kept in a -20 °C freezer for molecular work.

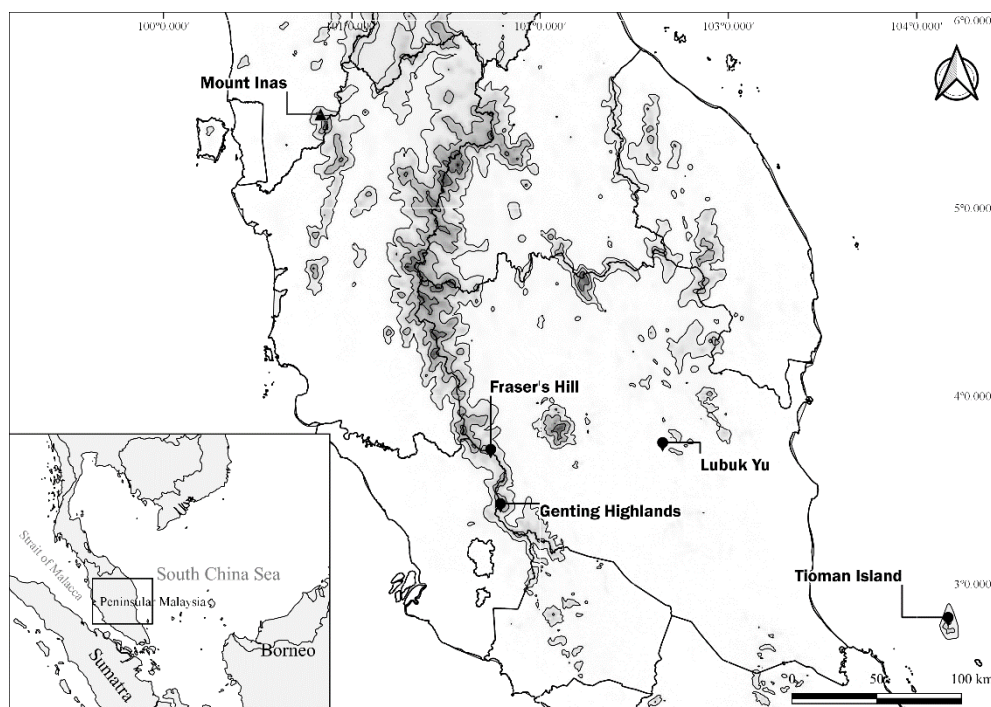


FIGURE 1. Study sites of Peninsular Malaysia *Leopoldamys* long-tailed giant rats. Darker shades represent elevation of 500 m onwards. *Leopoldamys ciliatus* was first described from Mount Inas, Perak, Malaysia by Bonhote (1900) (black triangle)

TABLE 1. Descriptive statistics of external measurements (mm) on *Leopoldamys* species collected in Peninsular Malaysia, Pimsai et al. (2014) and Yong (1970). Mean \pm standard deviation (SD), range (in parentheses) and sample size (n) are stated. Sexes are combined and samples range from sub-adult to adult

Character	Measurement			
	<i>L. vociferans</i>	<i>L. ciliatus</i>	<i>L. sabanus</i>	<i>L. ciliatus</i>
	Current study (n = 10)	Current study, Genting Highlands (n = 5)	Pimsai et al. (2012) (n = 14)	Yong (1970) (n = 22)
Head-body length (Hb)	207.6 \pm 15.6 (185-229)	253 \pm 30.0 (205- 278)	224.6 \pm 16.1 (190-252)	251.2 \pm 2.8 (220-275)
Tail (T)	298.7 \pm 53.3 (167- 361)	322 \pm 32.6 (272- 355)	328.5 \pm 19.5 (295-362)	334.6 \pm 4.5 (310-355)
Ear (E)	25.4 \pm 2.5 (22-30)	27.7 \pm 1.7 (26-31)	-	28.5 \pm 0.15 (27-29)
Hindfoot (Hf)	43.6 \pm 3.3 (36-48)	51.2 \pm 3.6 (45-54)	44.2 \pm 3.8 (37-51)	53.2 \pm 0.4 (51-56)
Forefoot (Ff)	21.3 \pm 3.1 (15-26)	22.8 \pm 2.2 (21-26)	-	-
Weight (g)	241.5 \pm 72.8 (114- 388)	389 \pm 120.0 (251-534)	-	-



FIGURE 2. Representative specimens of *Leopoldamys ciliatus* from Genting Highlands (GH7) and *Leopoldamys vociferans* from Lubuk Yu (LY2) from three different angles (dorsal, ventral and lateral)

DNA EXTRACTION AND AMPLIFICATION

Total genomic DNA was extracted from the liver using Vivantis GF-1 Tissue DNA extraction Kit, according to the manufacturer's protocols. Mitochondrial *cyt b* was amplified by polymerase chain reaction (PCR) and sequenced using the universal primers from Irwin, Kocher and Wilson (1991): L14723 (5'-ACCAATGACATGAAAAATCATCGTT-3') and H15915 (5'-TCTCCATTTCTGGTTTACAAGAC-3'). The 25 μ L PCR reaction and the protocol to amplify the *cyt b* region were performed following Saarani et al. (2021) in a Mastercycler® (Eppendorf) machine. The products were then checked by electrophoresis using 1% agarose gel in a 1 \times TAE buffer and stained with SYBR® Safe DNA Gel Stain. Electrophoresis was run at 80 V, 180 mA in 1 \times TAE running buffer for 45 min and checked under ultraviolet light (Alpha Imager Gel Documentation System, Siber Hegner, Germany). Lastly, purification and Sanger sequencing of the PCR products were performed by First Base Co. (Selangor, Malaysia). Representative *cyt b* sequences of *Leopoldamys* taxa (total of 79 sequences) from the Genbank were used for phylogenetic comparison, with *Sundamys muelleri*, *Maxomys surifer*, and *M. ochraceiventer* as outgroup taxa (Table 2). The taxonomic names of the sequences in the GenBank were emended where relevant according to published literature (Balakirev, Abramov & Rozhnov 2013; Latinne et al. 2013a; Li et al. 2019).

MOLECULAR ANALYSES

All sequences were edited using BioEdit Sequence Alignment Editor (version 7.2.6.1) software (Hall 1999) and aligned using Clustal W multiple alignment algorithms in MEGA X (version 10.2.5) (Kumar et al. 2018). The basic sequence parameter calculations such as variable sites and parsimony informative sites were also performed using MEGA X. Phylogenetic analysis was carried out using maximum-likelihood (ML) and Bayesian inference (BI). The ML phylogenetic tree was constructed using the Tamura Nei model with 1000 bootstrap replications. Net genetic distances between localities and *Leopoldamys* species were also calculated in MEGA X using the Kimura-2-parameter (Table 2).

The best-fit model of DNA evolution was determined in jModel test (version 0.1.1) using the Akaike Information Criterion (AIC). The best evolutionary model for the data set was the TPM2uf+I+G, however, because this model is not implemented in MrBayes software, we used the GTR+I+G substitution model. BI was investigated using MrBayes software (version 3.1.2) (Huelsenbeck & Ronquist 2001). Markov chain Monte Carlo (MCMC) sampling was performed for 1730000 generations. Treeview software (version 1.6.6) was used to view the BI tree (Page 1996).

The minimum spanning network of the haplotypes for the *L. sabanus/L. vociferans* complex was constructed using NETWORK (version 10.2.0.0) (Brandelt, Forster &

Röhl 1999) to visualize their evolutionary relationships. A median-joining algorithm was used to construct the minimum-spanning network (MNS).

RESULTS

PHYLOGENETIC ANALYSES

A total of 15 *cyt b* sequences of Peninsular Malaysia *Leopoldamys* with various lengths ranging from 862 to 1142 base pairs (bp) were sequenced and deposited into the Genbank database. (Accession number: MZ221531–MZ221545) (Supplementary data). We compared 94 individuals of *Leopoldamys* species, of which 720 sites were conserved, 420 sites were variable of which 365 sites were parsimony informative. Both ML and BI trees had identical topology (Figure 3) with *L. milleti* as basal to lineage L1. All phylogenetic trees were consistent with Balakirev, Abramov and Rozhnov (2013).

Phylogenetic analyses showed two very distinct lineages of *Leopoldamys* in Peninsular Malaysia. These two lineages were not sister taxa. The higher elevation *L. ciliatus* was sister to lineage L1 containing *L. revertens* and *L. herberti* (Figure 3), with K2P distance values of 0.062 with L1a (*L. revertens* from Vietnam) and 0.057 with L1b (*L. herberti*) (Table 2).

Leopoldamys vociferans from Peninsular Malaysia and southern Thailand (Surat Thani) was part of the Sundaland *L. sabanus* complex and formed a monophyletic group (Figure 3), with K2P distance of 0.008. The mainland and island (Tioman Island) taxa of *L. vociferans* from Peninsular Malaysia had a K2P distance of 0.003. *Leopoldamys sabanus* s.s. (from Sabah, Sarawak and Kalimantan) formed a distinct lineage. The genetic affinity of these taxa was also reflected in the minimum spanning network of *cyt b* haplotypes (Figure 4). No haplotypes were shared between the three landmasses (Malay Peninsula, Sumatra and Borneo). Although the Sumatra taxon formed a sister lineage with *L. vociferans* s.s., with K2P distance of 0.065, it was supported with low bootstrap values (BS = 62) and posterior probabilities (PP = 0.68).

Lineage L3 consisted of *L. edwardsi* s.s. (from the type locality Fujian, China) and related taxa (*L. hainanensis* and other taxa of the *edwardsi* complex), while lineage L2 consisted of *L. neilli* and related taxa. A specimen from Tuyen Quang (L3b) was closer to specimens from northern lineage from China, and lineage L3 showed closer affinity to lineage L1 than to lineage L2. These lineages formed a group distinct from lineage L5 which contained taxa of the *L. sabanus/vociferans* complex.

DISCUSSION

In their revision of the genus *Leopoldamys* (Rodentia, Muridae) from Indochina, Balakirev, Abramov and Rozhnov (2013) divided the congeners into three sections based on five main genetic lineages: (1) the *edwardsi* section comprising *L. revertens* (lineage L1), *L. herberti* (lineage L2) and *L. edwardsi* (lineage L3); (2) the *milleti* section comprising *L. milleti* (lineage L4); and (3) the *sabanus* section comprising *L. sabanus*, *L. vociferans* and the unverified Sumatra taxa (lineage L5). *L. neilli* (lineage L2) was considered as a junior synonym of *L. herberti*. The taxonomic position of *L. ciliatus* was stated to be uncertain and might well be more closely related to *L. milleti* from the highlands of southern Vietnam (Balakirev, Abramov & Rozhnov 2013); however, *L. ciliatus* was not included in this study. Latinne et al. (2013a) subsequently revised the nomenclature by Balakirev, Abramov and Rozhnov (2013) as follows: lineage L1 = *L. herberti* (instead of *L. revertens*), L2 = *L. neilli* (instead of *L. herberti*), L3 = *L. edwardsi*, L4 = *L. milleti*, and L5 = *L. sabanus*; and *L. neilli* (lineage L2) should not be considered as a junior synonym of *L. herberti*.

Our present study based on *cyt b* sequences, shows that *L. ciliatus* from Peninsular Malaysia is closely related to the *L. revertens/L. herberti* lineage, and is distantly related to *L. edwardsi* s.s. and related taxa (Figure 3). It is also related closer to *L. milleti* than to *L. edwardsi* and *L. neilli* complexes (Figure 3). Study is needed to confirm whether the Sumatra taxon *setiger* is conspecific to *L. ciliatus*.

Assuming correct identification of the taxa and based on the threshold K2P distance of >2.5% (Tobe, Kitchener & Linacre 2010) as well as without overlapping of the haplotypes, the present study indicates that *L. revertens*, *L. herberti*, and *L. neilli* are valid species (Figure 3). A previous study based on *cyt b*, GHR and IRPB genes indicates that *L. herberti* is sister to *L. neilli* in the lineage also containing *L. revertens* (Fabre et al. 2013). The K2P distance of 0.024 between *L. herberti* and *L. revertens* in the present study is low for sister taxa. However, a low *cyt b* genetic distance has been reported for other rodents, e.g., *Cavia* (3.1%), *Cynomys* (1.3%, range 1.2-1.3%) and *Oxymycterus* (3.6%, range 1.9-6.8%) (Baker & Bradley 2006).

The *L. edwardsi* complex (lineage L3) is represented by taxa from China and Vietnam. As for the taxa from China (Li et al. 2019), the Vietnam counterparts consist of more than a single species (Figure 3). Likewise, as previously reported by Latinne et al. (2012), the *L. neilli* complex (lineage L2) shows distinct genetic differences for the Thailand and Vietnam taxa. Both the *L. edwardsi*

and *L. neilli* complexes need further study to resolve the taxonomic status of the component taxa.

The present findings on the *L. sabanus* complex concur with earlier reports that the taxa from Borneo (Sabah, Sarawak and Kalimantan), Peninsular Malaysia and Sumatra form distinct lineages (Figure 3) (Balakirev, Abramov & Rozhnov 2013; Gorog, Sinaga & Engstrom 2004). *Leopoldamys sabanus* from Borneo is basal to

the lineage containing *L. vociferans* from Peninsular Malaysia and the Sumatra taxon.

The Thailand taxon of *L. vociferans* is genetically distinct from the Peninsular Malaysia taxon, with K2P distance of 0.008 (Figure 3). The Tioman Island *L. vociferans* is closely related to the mainland Peninsular Malaysia taxon but genetically distinct, with K2P distance of 0.003 (Figures 3 & 4); the available subspecies name is *stridens* (Chasen 1940; Medway 1969; Yong 1968).

TABLE 2. Net average of Kimura-2-parameter distance values between *Leopoldamys* species of Peninsular Malaysia and its current lineages. The distances between groups are shown below diagonal, standard error estimates are shown above the diagonal and diagonals (in bold) represent the intra-taxon genetic diversity

Lineages	<i>L. ciliatus</i> (Genting Highlands)	L1a	L1b	L2a	L2d	L2e	L2f	L3a	L3b	Northern lineage	Southern lineage	Hainan lineage	L4	L5a	L5b	L5c
<i>*L. ciliatus</i> (Genting Highlands)	0.005	0.008	0.008	0.011	0.013	0.011	0.011	0.012	0.014	0.011	0.011	0.012	0.011	0.012	0.012	0.013
L1a	0.062	0.006	0.004	0.009	0.013	0.011	0.011	0.012	0.011	0.009	0.011	0.012	0.011	0.012	0.011	0.011
L1b	0.057	0.024	0.010	0.010	0.013	0.012	0.011	0.013	0.012	0.010	0.011	0.012	0.011	0.012	0.011	0.012
L2a	0.101	0.087	0.088	0.028	0.009	0.008	0.009	0.011	0.012	0.009	0.011	0.012	0.012	0.011	0.012	0.011
L2d	0.124	0.112	0.121	0.064	0.006	0.010	0.011	0.013	0.015	0.012	0.014	0.015	0.015	0.015	0.015	0.014
L2e	0.106	0.105	0.117	0.058	0.078	0.011	0.009	0.014	0.014	0.011	0.013	0.013	0.013	0.013	0.013	0.011
L2f	0.108	0.107	0.113	0.073	0.093	0.075	0.006	0.014	0.014	0.010	0.013	0.012	0.011	0.011	0.012	0.012
L3a	0.106	0.109	0.101	0.088	0.110	0.108	0.129	0.051	0.013	0.009	0.004	0.007	0.013	0.016	0.015	0.014
L3b	0.113	0.095	0.095	0.102	0.132	0.122	0.123	0.082	-	0.003	0.012	0.012	0.014	0.014	0.015	0.013
Northern lineage	0.105	0.091	0.089	0.084	0.111	0.101	0.104	0.061	0.010	0.022	0.008	0.009	0.011	0.012	0.012	0.011
Southern lineage	0.112	0.112	0.106	0.102	0.133	0.124	0.138	0.002	0.095	0.071	0.009	0.006	0.011	0.013	0.014	0.013
Hainan lineage	0.128	0.130	0.120	0.116	0.142	0.132	0.129	0.038	0.096	0.078	0.045	0.001	0.012	0.014	0.014	0.013
L4	0.118	0.108	0.106	0.115	0.138	0.123	0.115	0.116	0.129	0.119	0.119	0.132	0.001	0.013	0.012	0.013
L5a	0.120	0.115	0.109	0.106	0.143	0.122	0.112	0.129	0.127	0.112	0.137	0.143	0.133	0.006	0.010	0.010
**L5b	0.132	0.120	0.111	0.113	0.139	0.126	0.132	0.141	0.145	0.129	0.153	0.160	0.131	0.092	0.008	0.009
L5c	0.105	0.082	0.087	0.077	0.105	0.082	0.088	0.084	0.105	0.087	0.106	0.113	0.100	0.069	0.065	0.058

Two subspecies have been described for the mainland Sumatra taxon of *L. sabanus* complex (Chasen 1940), viz. *ululans* from Daras, Kerinci (Robinson & Kloss 1916) and *tapanulius* from Tapanuli (Lyon, 1916). If these taxa are conspecific, the name *usulans* has priority as it was published in July 1916 (as *Epimys ululans*) while the name *tapanulius* was published in September 1916 (as *Rattus vociferans tapanulius*).

Three *Leopoldamys* species occurred in the Sundaland region. *Leopoldamys sabanus* (lineage L5a and L5c) is a semi-arboreal species and found in the lowland forest. A study by Balakirev, Abramov and Rozhnov (2013) has proposed that only individuals from Borneo (lineage L5a) are considered the ‘true’ *L. sabanus* while individuals from Sumatra (lineage 5c) are regarded as insular forms. *Leopoldamys vociferans* (lineage L5b) inhabits the lowland forest of Malay Peninsula, while *L. ciliatus* (lineage labelled as * in Figure 3) occupies the highland forest (elevation above 1075 metres) in Peninsular Malaysia and Sumatra. As Sundaic species, they might be influenced by the Pleistocene event that involved climatic fluctuations and affected their future distributions. Past studies

(Gorog, Sinaga & Engstrom 2004; Latinne et al. 2015) have shown the vicariance of *L. sabanus* (including *L. vociferans* in this study) on Sunda Islands and Malay Peninsula during the Pleistocene. Gorog, Sinaga and Engstrom (2004) and Balakirev, Abramov and Rozhnov (2013) observed the same trichotomy as in this study and that their divergence pre-dated the event. As there are no past studies pertaining to *L. ciliatus*, the exact scenario of this species during the Pleistocene could not be determined. Our speculation is that the species might be speciated from *L. herberti* (lineage L1) since they are closely related and that the Indochina *L. herberti* was suggested to expand towards southern China during the Pleistocene event (Latinne et al. 2015). However, more studies are needed to confirm this speculation. The ancient event that took place until 10,000 years ago (Cannon, Morley & Bush 2009) impacted every species differently, depending on their forest habitat conditions and dispersal capabilities (Cros et al. 2020; Lim et al. 2020; Mason, Helgen & Murphy 2019). Thus, their conservation is highly recommended as they possess unique genetic structures that are directly related to their survivality and adaptation to the climate change.

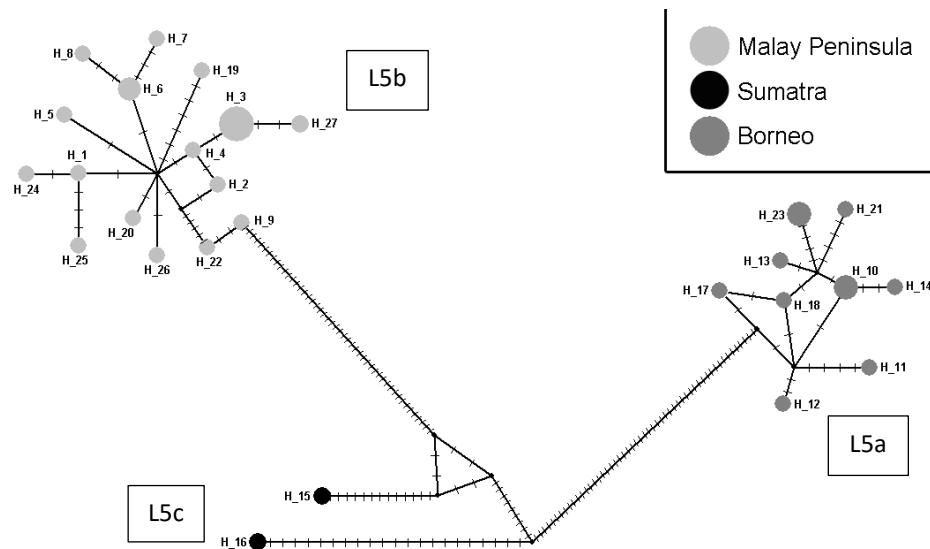


FIGURE 4. Minimum spanning network of *Leopoldamys vociferans* (Malay Peninsula) and *L. sabanus* (Borneo and Sumatra) across the three regions inferred from mtDNA *cyt b* haplotypes. Circle sizes resemble the number of individuals per haplotype, while the perpendicular lines on the branches correspond to the number of base pair changes between haplotypes. Letters in the box represent their clades (also lineages) in Figure 3

CONCLUSION

This study shows that: (1) *L. ciliatus* from Peninsular Malaysia is distinctly different from *L. edwardsi* and

is closer related to *L. revertens* and *L. herberti*; (2) *L. revertens*, *L. herberti* and *L. neilli* are valid species; (3) *L. edwardsi* as presently constituted consists of a complex of

several species; (4) *L. neilli* complex consists of several sibling species; (5) there are three distinct groups of the *L. sabanus* complex – *L. sabanus* in Borneo (Sabah, Sarawak and Kalimantan), *L. vociferans* in Peninsular Malaysia and South Thailand, and the Sumatra taxon. A more extensive taxon sampling from various regions, particularly from Sumatra and other regions of Indonesia, as well as the use of morphological and molecular (mitogenomes or multiple genes) data sets are needed to provide a robust phylogeny and systematics.

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TABLE S1. Mitochondrial *cyt b* sequences of *Leopoldamys* and outgroup taxa used in this study, including their localities, country, Genbank accession numbers and publications. The emended species names are in parenthesis and lineages referred to the phylogenetic tree constructed in Figure 3

Lineages	Taxa	Localities	Country	Accession number	Publication
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Dong Nai	Vietnam	GU457019	Balakirev & Rozhnov (2010)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Tay Ninh	Vietnam	JQ755905	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Tay Ninh	Vietnam	JQ755906	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Tay Ninh	Vietnam	JQ755907	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Tay Ninh	Vietnam	JQ755908	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Tay Ninh	Vietnam	JQ755909	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Dong Nai	Vietnam	JQ755910	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Dong Nai	Vietnam	JQ755911	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Dong Nai	Vietnam	JQ755898	Balakirev et al. (2012)
L1a	<i>L. sabanus</i> (<i>L. revertens</i>)	Binh Phuoc	Vietnam	JQ755913	Balakirev et al. (2012)
L1b	<i>Leopoldamys</i> sp. (<i>L. herberti</i>)	Phrae	Thailand	KF577948	Latinne et al. (2013a)
L1b	<i>Leopoldamys</i> sp. (<i>L. herberti</i>)	Loei	Thailand	KF577949	Latinne et al. (2013a)
L1b	<i>Leopoldamys</i> sp. (<i>L. herberti</i>)	Loei	Thailand	KF577950	Latinne et al. (2013a)
L1b	<i>Leopoldamys</i> sp. (<i>L. herberti</i>)	Nan	Thailand	KF577951	Latinne et al. (2013a)
L1b	<i>Leopoldamys</i> sp. (<i>L. herberti</i>)	Nan	Thailand	KF577952	Latinne et al. (2013a)
L1b	<i>L. sabanus</i> (<i>L. revertens</i>)	Khammouan	Lao PDR	JX173163	Balakirev, Abramov & Rozhnov (2013)

Supplementary data. (Continued)

Lineages	Taxa	Localities	Country	Accession number	Publication
L1b	<i>L. edwardsi</i>	-	Thailand	KY464179	Camacho-Sanchez et al. (2017)
*	<i>L. ciliatus</i>	Genting Highlands, Pahang	Pen. Malaysia	MZ221531	This study
*	<i>L. ciliatus</i>	Genting Highlands, Pahang	Pen. Malaysia	MZ221532	This study
*	<i>L. ciliatus</i>	Genting Highlands, Pahang	Pen. Malaysia	MZ221533	This study
*	<i>L. ciliatus</i>	Genting Highlands, Pahang	Pen. Malaysia	MZ221534	This study
*	<i>L. ciliatus</i>	Genting Highlands, Pahang	Pen. Malaysia	MZ221535	This study
L2a	<i>L. neilli</i> (<i>L. herberti</i>)	Phrae	Thailand	HM217459	Pages et al. (2010)
L2a	<i>L. neilli</i> (<i>L. herberti</i>)	Phrae	Thailand	HM217460	Pages et al. (2010)
L2a	<i>L. neilli</i> (<i>L. herberti</i>)	Loei	Thailand	HM217462	Pages et al. (2010)
L2a	<i>L. neilli</i> (<i>L. herberti</i>)	Loei	Thailand	HM217463	Pages et al. (2010)
L2a	<i>L. neilli</i>	Nan	Thailand	HM219597	Latinne et al. (2013)
L2a	<i>L. neilli</i>	Nan	Thailand	HM219598	Latinne et al. (2013)
L2a	<i>L. neilli</i>	Saraburi	Thailand	HM219600	Latinne et al. (2013)
L2a	<i>L. neilli</i>	Saraburi	Thailand	HM219601	Latinne et al. (2013)
L2d	<i>L. neilli</i>	Kanchanaburi	Thailand	HM219606	Latinne et al. (2013)
L2d	<i>L. neilli</i>	Kanchanaburi	Thailand	HM219607	Latinne et al. (2013)
L2e	<i>L. sabanus</i> (<i>L. herberti</i>)	Ha Tinh, Huang Son Camp	Vietnam	HQ877106	Gorog, Sinaga & Engstrom (2004)
L2e	<i>L. sabanus</i> (<i>L. herberti</i>)	Ha Tinh, Huang Son Camp	Vietnam	HQ877107	Gorog, Sinaga & Engstrom (2004)
L2e	<i>L. edwardsi</i> (<i>L. herberti</i>)	Son La	Vietnam	JQ755902	Balakirev et al. (2012)
L2e	<i>L. edwardsi</i> (<i>L. herberti</i>)	Son La	Vietnam	JQ755903	Balakirev et al. (2012)
L2f	<i>L. neilli</i> (<i>L. herberti</i>)	Khammouan	Lao PDR	JX173162	Balakirev et al. (2013)
L2f	<i>L. neilli</i> (<i>L. herberti</i>)	Khammouan	Lao PDR	JX173164	Balakirev et al. (2013)
L3a	<i>L. edwardsi</i>	Cat Ba Island	Vietnam	JQ755869	Balakirev et al. (2012)
L3a	<i>L. edwardsi</i>	Cat Ba Island	Vietnam	JQ755870	Balakirev et al. (2012)
L3a	<i>L. edwardsi</i>	Son La	Vietnam	JQ755895	Balakirev et al. (2012)
L3b	<i>L. edwardsi</i>	Tuyen Quang	Vietnam	HQ877101	Gorog, Sinaga & Engstrom (2004)
L3b	<i>L. edwardsi</i>	Tam Dao, Vinh Phu	Vietnam	KY754013	Steppan & Schenk (2017)

Supplementary data. (Continued)					
Lineages	Taxa	Localities	Country	Accession number	Publication
Northern	<i>L. edwardsi</i>	Yongshun, Hunan	China	KP992502	Li et al. (2019)
Northern	<i>L. edwardsi</i>	Yongshun, Hunan	China	KP992503	Li et al. (2019)
Northern	<i>L. edwardsi</i>	Kuatun, Fujian	China	KP992500	Li et al. (2019)
Northern	<i>L. edwardsi</i>	Kuatun, Fujian	China	MK123078	Li et al. (2019)
Northern	<i>L. edwardsi</i>	-	China	KM434322	Zhu et al. (2016)
Southern	<i>L. edwardsi</i>	Jinggangshan, Jiangxi	China	MK123063	Li et al. (2019)
Southern	<i>L. edwardsi</i>	Jinggangshan, Jiangxi	China	KP992496	Li et al. (2019)
Southern	<i>L. edwardsi</i>	Ruyuan, Guangdong	China	KP992494	Li et al. (2019)
Southern	<i>L. edwardsi</i>	Beiliu, Guangxi	China	KP992486	Li et al. (2019)
Southern	<i>L. edwardsi</i>	Wuming, Guangxi	China	KP992487	Li et al. (2019)
Hainan	<i>L. edwardsi</i> (<i>L. hainanensis</i>)	Ledong, Hainan	China	MK123054	Li et al. (2019)
Hainan	<i>L. edwardsi</i> (<i>L. hainanensis</i>)	Ledong, Hainan	China	MK123055	Li et al. (2019)
Hainan	<i>L. edwardsi</i> (<i>L. hainanensis</i>)	Ledong, Hainan	China	MK123056	Li et al. (2019)
Hainan	<i>L. edwardsi</i> (<i>L. hainanensis</i>)	Baoting, Hainan	China	MK123057	Li et al. (2019)
Hainan	<i>L. edwardsi</i>	Jianfengling, Hainan	China	KY068766	Zhang et al. (2016)
L4	<i>L. milleti</i>	Hon Ba Nature Reserve	Vietnam	JQ755931	Balakirev et al. (2012)
L4	<i>L. milleti</i>	Chu Yang Sin National Park	Vietnam	JX173158	Balakirev et al. (2013)
L4	<i>L. milleti</i>	Chu Yang Sin National Park	Vietnam	JX173159	Balakirev et al. (2013)
L5a	<i>L. sabanus</i>	West Kalimantan	Indonesia (Borneo)	HQ877104	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	Lanjak Entimau Wildlife Sanctuary, Sarawak	E. Malaysia (Borneo)	HQ877109	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	West Kalimantan	Indonesia (Borneo)	HQ877110	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	West Kalimantan	Indonesia (Borneo)	HQ877111	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	East Kalimantan	Indonesia (Borneo)	HQ877114	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	East Kalimantan	Indonesia (Borneo)	HQ877115	Gorog, Sinaga & Engstrom (2004)
L5a	<i>L. sabanus</i>	Sabah	E. Malaysia (Borneo)	KM262606	Latinne et al. (2015)
L5a	<i>L. sabanus</i>	Sabah	E. Malaysia (Borneo)	KM262607	Latinne et al. (2015)

Supplementary data. (Continued)

Lineages	Taxa	Localities	Country	Accession Number	Publication
L5a	<i>L. sabanus</i>	Kinabalu National Park, Sabah	E. Malaysia (Borneo)	MW209723	Forcina et al. (2021)
L5a	<i>L. sabanus</i>	-	-	NC035819	Salleh et al. (2017)
L5a	<i>L. sabanus</i>	-	Malaysia	KY117551	Salleh et al. (2017)
**L5b	<i>L. vociferans</i>	Lubuk Yu, Pahang	Pen. Malaysia	MZ221536	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221537	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221538	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221539	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221540	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221541	This study
**L5b	<i>L. vociferans</i>	Tioman Island, Pahang	Pen. Malaysia	MZ221542	This study
**L5b	<i>L. vociferans</i>	Fraser's Hill, Pahang	Pen. Malaysia	MZ221543	This study
**L5b	<i>L. vociferans</i>	Fraser's Hill, Pahang	Pen. Malaysia	MZ221544	This study
**L5b	<i>L. vociferans</i>	Fraser's Hill, Pahang	Pen. Malaysia	MZ221545	This study
**L5b	<i>L. sabanus (L. vociferans)</i>	Selangor	Pen. Malaysia	MT241668	Jahari et al. (2021)
**L5b	<i>L. sabanus (L. vociferans)</i>	Selangor	Pen. Malaysia	MT259591	Jahari et al. (2021)
**L5b	<i>L. sabanus (L. vociferans)</i>	Surat Thani	Thailand	HQ877108	Gorog, Sinaga & Engstrom (2004)
**L5b	<i>L. sabanus (L. vociferans)</i>	Endau Rompin National Park	Pen. Malaysia	HQ877112	Gorog, Sinaga & Engstrom (2004)
**L5b	<i>L. sabanus (L. vociferans)</i>	Endau Rompin National Park	Pen. Malaysia	HQ877113	Gorog, Sinaga & Engstrom (2004)
**L5b	<i>L. sabanus</i>	-	Thailand	MN964122	Nicolas et al. (2020)
**L5b	<i>L. sabanus</i>	Mount Telapak Buruk, Negeri Sembilan	Pen. Malaysia	KY117552	Salleh et al. (2017)
**L5b	<i>L. sabanus</i>	Teluk Segadas, Pulau Pangkor, Perak	Pen. Malaysia	KY117553	Salleh et al. (2017)
**L5b	<i>L. sabanus</i>	Temenggor Forest Reserve, Gerik, Perak	Pen. Malaysia	KY117554	Salleh et al. (2017)
**L5b	<i>L. sabanus</i>	Hutan Simpan Lenggong, Kluang, Johor	Pen. Malaysia	KY117555	Salleh et al. (2017)

Supplementary data. (Continued)					
Lineages	Taxa	Localities	Country	Accession Number	Publication
L5c	<i>L. sabanus</i>	Lampung Province	Indonesia (Sumatra)	HQ877105	Gorog, Sinaga & Engstrom (2004)
L5c	<i>L. sabanus</i>	Gunung Leuser National Park	Indonesia (Sumatra)	HQ877102	Gorog, Sinaga & Engstrom (2004)
-	<i>Maxomys ochraceiventer</i>	Kinabalu National Park, Sabah	E. Malaysia (Borneo)	MW209720	Forcina et al. (2021)
-	<i>M. surifer</i>	-	Thailand	NC_036732	Chamacho-Sanchez et al. (2017)
-	<i>Sundamys muelleri</i>	Ketambe Research Station, Sumatra	Indonesia	KY754160	Steppan & Schenk (2017)