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# Phylogenetic position of Malabar Spiny Tree Mouse (*Platacanthomys lasiurus* Blyth, 1859) (Rodentia) and resurrection of the family Typhlomyidae

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## Abstract

The family Platacanthomyidae was established in 1876 to include *Platacanthomys lasiurus* Blyth, 1859 from the Western Ghats. Subsequent studies incorporated the genus *Typhlomys* Milne-Edwards, 1877 into this family. In 1947, Ognev assigned *Typhlomys* to a separate subfamily, Typhlomyinae. Phylogenetic studies aimed at exploring evolutionary relationships within Platacanthomyidae began in 2009 but, without suitable data for *Platacanthomys* due to lack of fresh tissue samples. The present study aims to reassess the taxonomic placement of the genera *Typhlomys* and *Platacanthomys* within Platacanthomyidae with an Integrative Taxonomic Approach (ITA). Based on our phylogenetic analyses and other evidence, we propose elevating the subfamily Typhlomyinae to family status Typhlomyidae for the genus *Typhlomys*. We discuss the phylogenetic positions of Platacanthomyidae and Typhlomyidae within the larger Muroidea tree. Earlier studies indicated the divergence of members of *Typhlomys* in the late Miocene. Our preliminary ultrametric tree indicates that the Western Ghats endemic *Platacanthomys* diverged during Eocene period, exposing this monotypic genus as an ancient relict.

**Key words:** Platacanthomyidae, relict species, refugia, Spiny tree mouse, Typhlomyidae, Western Ghats

## Introduction

The extant superfamily Muroidea comprises six families, Platacanthomyidae (predominantly found in Palearctic and Indo-Malayan regions), Spalacidae (distributed across Palearctic, Afrotropical and Indo-Malayan regions), Calomyscidae (located to the Palearctic region), Nesomyidae (confined to the Afrotropical region), Cricetidae (present in the Holarctic, Neotropical and marginally Indo-Malayan region), and Muridae (worldwide distribution except Antarctica) (Wilson et al., 2017).

The family Platacanthomyidae includes two extant genera (*Platacanthomys* and *Typhlomys*) and seven extant species. The genus *Typhlomys* comprises six of these species (*T. cinereus* Milne-Edwards, 1877, *T. chapensis* Osgood, 1932, *T. daloushanensis* Wang and Li, 1996, *T. nanus* Cheng et al., 2017, T. *huangshanensis* Hu and Zhang, 2021, and *T. fengjiensis* Pu et al., 2022) that are geographically distributed in China and Vietnam (Fig. 1). The genus *Platacanthomys* is monotypic, with *Platacanthomys lasiurus* Blyth, 1859 (Malabar spiny tree mouse) endemic to the montane forests of the Western Ghats, specifically in the southwestern regions of Karnataka, Kerala, and Tamil Nadu states (Giarla, 2017; Hu et al., 2021; Pu et al., 2022) (Fig. 1).

### History of taxonomic placements of Malabar spiny tree mouse, *Platacanthomys lasiurus*

The Malabar spiny tree mouse *Platacanthomys lasiurus* was described by Blyth in 1859 based on the collection by Rev. H. Baker from Mundakyum, Alipi, Southern Malabar (= Mundakyum, Kottayam district), Kerala, India.

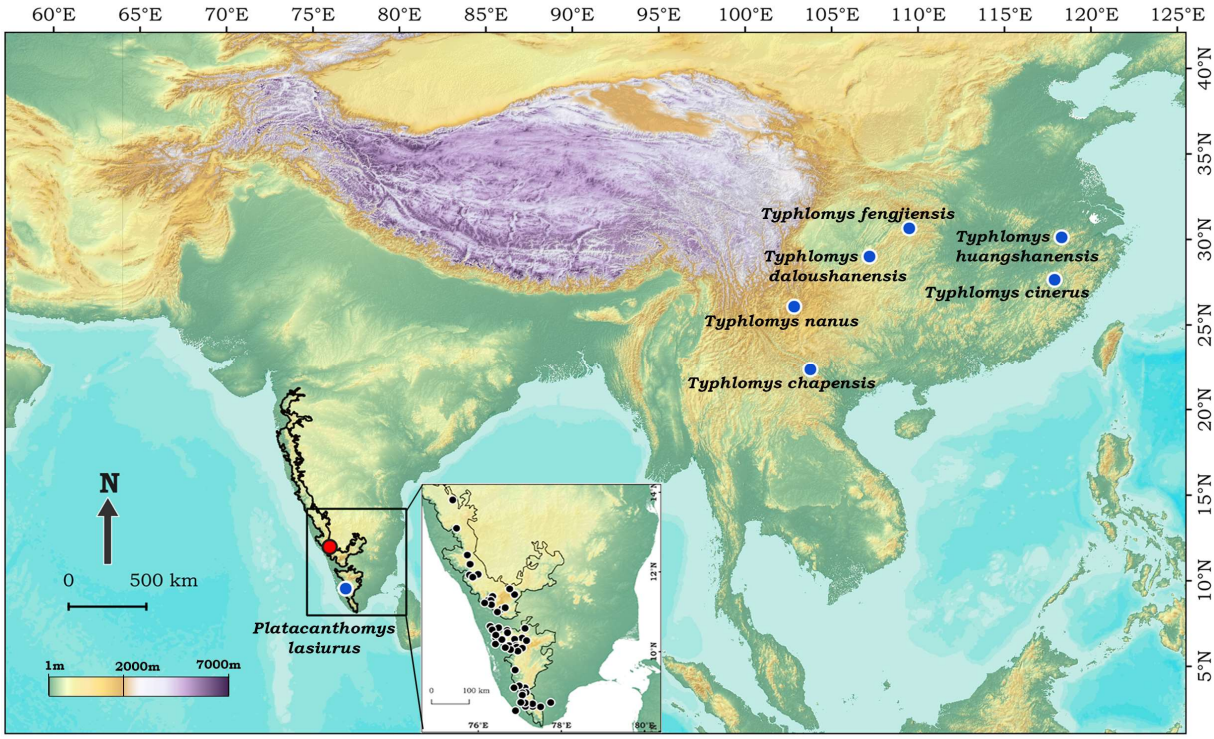


**Figure 1:** Type locality details for the members of the genus *Platacanthomys* and *Typhlomys* (blue circles), and the collection locality of a specimen used in the present study (red circle). The inset map depicts the distribution of *Platacanthomys* based on literature.

Initially the species was placed in the family Myoxidae (= Gliridae) due to its dormouse-like hairy tail. In 1865, Peters described the genus and species in detail, clarifying that *Platacanthomys lasiurus* lacks premolars and has only three pairs of molars in both the upper and lower jaws. Consequently, *Platacanthomys* is not a member of Myoxidae as previously suggested by Blyth (1859) but instead resembles other Murinae genera of tropical India.

Subsequently, Alston (1876) placed the taxon into the family Muridae and proposed a new subfamily Platacanthomyinae for this monotypic genus. Jerdon (1867) had earlier placed the genus in the subfamily Murinae. Following Alston's classification, this taxon was placed in the subfamily Platacanthomyinae of Muridae with key characters "crowns of worn molars with oblique subparallel bands of enamel; tail with long coarse hair" by Blanford (1888–1891).

On the basis of distinguished cheek teeth exhibiting oblique cross-ridged enamel pattern, Miller and Gidley (1918) elevated the rank to a family Platacanthomyidae. In 1947, Ognev placed the genus *Typhlomys* into a separate subfamily Typhlomyinae within the family Platacanthomyidae. Vorontsov (1979) however rejected Ognev's classification and retained both genera within the subfamily Platacanthomyinae.

Ellerman (1940, 1961) and Ellerman and Morrison-Scott (1951) placed the genera *Platacanthomys* and *Typhlomys* in subfamily Platacanthomyinae within Muscardinidae (= Gliridae), but also noted that dental formula is like in Muridae. Simpson (1945) considered Platacanthomyidae (with *Platacanthomys* and *Typhlomys*) to be close to Gliridae, hence placed them under superfamily Gliroidea. Corbet and Hill (1992) and Wilson and Reeder (1993) treated these genera in the subfamily Platacanthomyinae under Muridae; this was followed by Agrawal (2000).

Musser and Carleton (2005) placed *Platacanthomys* within the family Platacanthomyidae of the superfamily Muroidea and suggested the common name 'Malabar Spiny Tree Mouse' as a replacement name to 'Malabar Spiny Dormouse'. This common name was adopted by Giarla (2017), and later on Srinivasulu (2019) recommended further English names 'Long-tailed Spiny Mouse' and 'Pepper Rat'.

The taxonomic placement of *Platacanthomys* has been a subject of debate for over a century, with researchers classifying it under various taxonomic hierarchies. The family Platacanthomyidae was considered enigmatic by researchers due to its morphological peculiarities, disjunct distribution pattern and fossil records (Carleton and Musser, 1984; Jansa et al., 2009). Fossil records are available for the extinct genus *Neocometes* and for the extant genera *Platacanthomys* and *Typhlomys* (Lee and Jacobs, 2010). Palaeontological evidence suggests a closer relationship between the extinct genus *Neocometes* and extant *Typhlomys* than either has to *Platacanthomys* (Giarla, 2017).

Morphology alone was inconclusive in ascertaining the taxonomic position of *Typhlomys* and *Platacanthomys.* In such cases, molecular data serve as a valuable tool for achieving taxonomic clarity. A literature review reveals significant lack of molecular data for *P. lasiurus*, despite extensive morphometric and distribution studies (Ellerman, 1961; Rajgopalan, 1968; Jayson and Christopher, 1995; Prabhakar, 1997; Shanker and Sukumar, 1998; Agrawal, 2000; Meena, 2001; Mudappa et al., 2001; Molur et al., 2005; Jayson and Jayahari, 2009; Molur and Singh, 2009) (Fig. 1).

In this study we provide for the first time a multigene sequence for *Platacanthomys* to address the familial placement of *Typhlomys* and *Platacanthomys* based on the Integrative Taxonomic Approach (ITA).

## Material and Methods

### Field collection and morphometry

A fresh raptor-killed juvenile female Malabar spiny tree mouse was collected from Suryamudi, Kottiyur Wildlife Sanctuary, Kerala (N. 11.54; E. 75.562; Alt. 1279 m.), during small mammal surveys conducted in the Southern Western Ghats (Fig. 2). Tissue was extracted for molecular studies and specimen was deposited in the National Zoological Collection (NZC) of Zoological Survey of India (ZSI), Western Regional Centre (WRC), Pune (ZSI/WRC/M/922). Specimen measurements were recorded and matched with published (Ellerman, 1961; Agrawal, 2000) as well as with those on specimen tags of four adult museum vouchers housed at the ZSI, Pune collection. Microscopic studies were performed using Leica S9i Stereo Microscope, and measurements were taken using Mitutoyo Vernier Callipers to the 0.01 mm precision.

Museum specimens of *Platacanthomys lasiurus* include: 1 female, Suryamudi, Kottiyur Wildlife Sanctuary, Kannur district, Kerala state, India, collected on 23/03/2021 by S.S Talmale and Jafer Palot (ZSI/WRC/M/922); 1 female, Thai Shola Forest (Nilgiries), Tamil Nadu State, India, collected during 1994 by Kartik Shankar (ZSI/WRC/M/761), 1 unsexed, Thai Shola Forest (Nilgiries), Tamil Nadu State, India, collected during February, 1994 by Kartik Shankar (ZSI/WRC/M/762), 1 female, Sengaltheri, Kalakkad Mundanthurai, Tamil Nadu State, India, collected on 24/06/1996 by Divya Mudappa (ZSI/WRC/M/841), 1 male, Sengaltheri, Kalakkad Mundanthurai, Tamil Nadu state, India, collected on 24/06/1996 by Divya Mudappa (ZSI/WRC/M/842).

**Abbreviations used:** HB – length of head and body, TL – length of tail, HF – length of hind foot, E- length of ear, onl – occipitonasal length, cbl - condylobasal length, nas – nasal length, pal – length of palate, mtr – length of maxillary toothrow, dia – length of diastema, apf – length of anterior palatal foramina, zw – zygomatic width, iw – interorbital width, ml – length of mandible.

**Figure 2:** Carcass of juvenile Malabar Spiny Tree Mouse, *Platacanthomys lasiurus* from Suryamudi, Kannur, Kerala, India (ZSI/WRC/M/922) (Photo credit: Dr. Md. Jafer Palot).

### Molecular protocols

Genomic DNA (gDNA) was extracted from liver tissue using DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) as per the manufacturer's instructions. The eluted DNA was quantified with a Qubit 2.0 fluorometer (Invitrogen, Oregon, USA) by dsDNA HS Assay kit. Mitochondrial *Cytochrome Oxidase subunit I* (mt *COI*) gene was amplified using BatL5310: 5'- CCTACTCRGCCATTTTACCTATG-3' and R6036R: 5'- ACTTCT GGGTGTCCAAAGAATCA-3' primers (Robins et al., 2007); and ~1100bp of *Cytochrome b* (*Cyt b*) with primer pair MVZ 05: 5'-CGAAGCTTGATATGAAAAACCATCGTTG-3' and MVZ 14: 5'- GGTCTTCATCTYHGGYTTACAAGAC-3' (Meegaskumbura et al., 2007).

PCR amplification was carried out in 25 µL reaction volume comprised of 12.5µL of 2X Go Taq Hot Start Green Master mix (Promega, Madison, USA), 1µL (10µM) of each primer, 2µL (50-100ng) of gDNA, and nuclease free water up to *Quantum Satis* (*Q.S*). Thermal cycling profile for *COI* and *Cyt b* genes followed Robins et al. (2007) and Meegaskumbura et al. (2007), respectively. PCR products were confirmed on 1% agarose gel by electrophoresis and visualized under UV light via Gelstain Gel Documentation system (Medicare, Tamil Nadu, India). Positive PCRs were purified using Invitrogen's Pure Link PCR Purification Kit followed by bidirectionally sequencing using Sanger's method outsourced to Barcode Biosciences Pvt Ltd. Bangalore.

Acquired sequences were manually verified and submitted to the GenBank (mt *COI*, OM180014.1, OM180015.1; mt *Cyt b*, PP779398.1, PP779399.1). Platacanthomyidae sequences available in the Gen Bank were downloaded for mt *COI* and *Cyt b* genes along with *ND2*, *GHR*, and *IRBP* genes for phylogenetic analyses (Supplementary file Table S2). Sequence alignment, editing and translation checks were performed in MEGA 11 (Tamura et al., 2021). Concatenation was done in Sequence Matrix 1.7.8 software. Partition finder v1.0.1 (Lanfear et al., 2012) was used to estimate the best partition schemes based on genes and codon positions according to Bayesian Information Criterion (BIC) for single gene and concatenated data sets.

Bayesian analysis was executed in MrBayes v 3.2 for mt *COI* and *Cyt b* and all sequences of *Typhlomys*. The analysis was run for $1 \times 10^6$ generations, sampled every 1,000 generations. Convergence was assessed using Tracer v1.5, the first 25% of the generations were discarded as burn-in, and the output tree was visualised in FigTree v1.4 using *Jaculus* as outgroup (Cheng et al., 2017). Maximum Likelihood (ML) analysis was performed for subfamilies of Muroidea using IQ tree web server with default parameters (Supplementary file Fig. S4, Table S1) to assess the *Platacanthomys* relationship with other muroids.

An ultra-metric species phylogeny was estimated by *BEAST model in BEAST v2.4.8 software (Bouckaert et al., 2014) using molecular parameters and fossil calibration as specified by Cheng et al. (2017) (Fig. 5). Geographic distribution map was prepared using QGIS 3.24 software (Figs. 1, 6).

## Results

### Morphological studies

Ranges for morphometric measurements (in mm; n= 4) are as follows: HB 85–115, TL 80–95, HF 20.8–22.4, E 20.8–23.1, onl 27.7–31.6, cbl 25.9–29.1, nas 8.8–12.9, pal 9.2–11.1, mtr 5.1–5.3, dia 7.3–9.4, bl 3.0–4.6, apf 1.5–2.0, zw 16.4–18.7, iw 6.4–6.9, ml 15.0–17.

*Platacanthomys* and *Typhlomys* exhibit similar morphological characters such as pale ventrum, large naked ears, a bushy tail, and molars with flat crowns and obliquely arranged cusps (Fig. 3). However, *Platacanthomys lasiurus* has shorter tail, white-tipped flattened spines on dorsum (Fig. 3A), two pairs of mammae, and lacks a caecum. In contrast, *Typhlomys* possess soft dorsal fur without spines, four pairs of mammae, and it possesses a caecum. Based on morphology, Giarla (2017) suggested that both genera belong to the same evolutionary lineage. In our view, their unique morphological characters (Table 1) justify separation of families Platacanthomyidae and Typhlomyidae. Additionally, the distributions of these families are allopatric, with members of Platacanthomyidae found in the Western Ghats of India, while members of Typhlomyidae are distributed in China and Vietnam (Figs. 1 and 6).

**Table 1:** Morphological comparison between the extant representatives of the families Platacanthomyidae and Typhlomyidae.

| Details | Family: Platacanthomyidae Alston, 1876 | Family: Typhlomyidae Ognev, 1947 |
|---|---|---|
| Type genus | *Platacanthomys* Blyth, 1859 | *Typhlomys* Milne-Edwards, 1877 |
| Type species | *Platacanthomys lasiurus* Blyth, 1859 | *Typhlomys cinereus* Milne-Edwards, 1877 |
| Type locality | Mundakyum, Alipi, Malabar (present day Mundakayam, Kottayam district), Kerala, India | W. Fujian, China |
| Body size* | Large sized, range for length of head and body is 118–140 mm | Small sized, range for length of head and body is 71–76 mm |
| Tail* | Shorter (76–106 mm) than head and body length, tail tip bushy | Longer (96–102 mm) than head and body length, tail short-haired at base, tufted in distal half |
| Dorsal pelage | White tipped flattened spines present on dorsum | Soft dorsal fur without spines |
| Venter | Creamy color | Greyish white color |
| Number of Mammae | Two pairs | Four pairs |
| Caecum in the intestinal tract | absent | present |
| Skull: Supra-orbital ridges | Prominent | Weak or absent |
| Skull: Post-palatal foramina (between molars) | Single, large sized | Multiple, small sized |
| Distribution | The Western Ghats, India | China, Vietnam |

*Measurements of *Platacanthomys lasiurus* and *Typhlomys cinereus* (following Giarla, 2017).

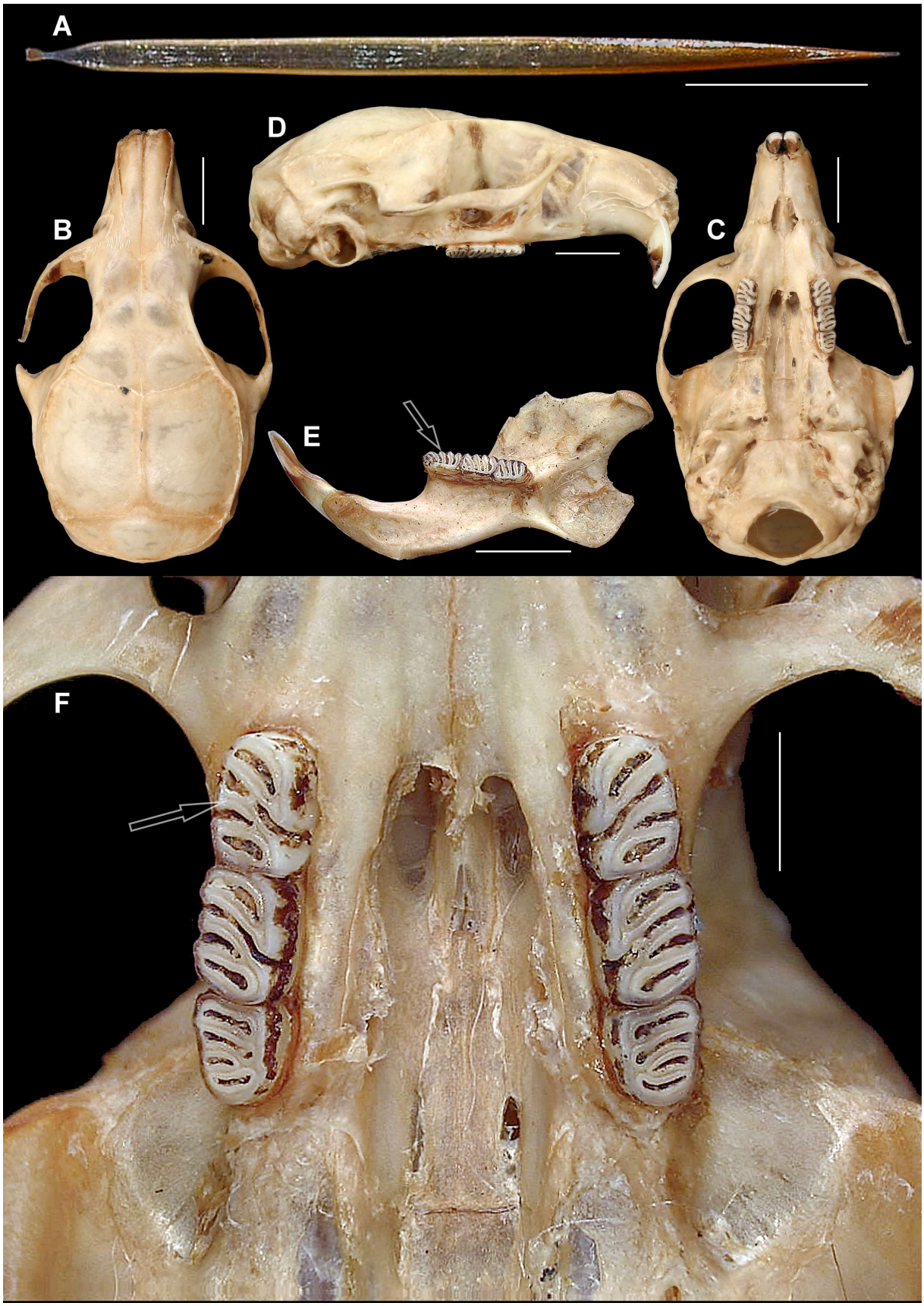


**Figure 3:** Morphological details for the Malabar Spiny Tree Mouse, *Platacanthomys lasiurus* (ZSI/WRC/M/761): (A) Flat spine from dorsal pelage (which is absent in *Typhlomys*); Skull in dorsal (B), ventral (C) and lateral view (D). (E) Mandible in lingual view; arrow points on lower molars. (F) Grinding surface of upper molars (with diagonal laminae) (Arrow marked). Scale Bar: A and F: 2 mm; B, C, D and E: 5 mm.

**Phylogenetic analysis**

Our study, along with the results of Cheng et al. (2017) and Pu et al. (2022) placed *Platacanthomys* and *Typhlomys* in distinct clades in both single gene and multigene phylogenies (Figs. 4 and 5). Genetic divergence between *Typhlomys* and *Platacanthomys* was 26.1% to 29.5% for mt *COI* sequences and 27.5% to 31.6% for *Cyt b gene*. All four single-gene and multi-gene Bayesian analyses produced similar tree topologies (Supplementary data Fig. S1-S3), indicating monophyly of lineages with strong bootstrap support. The species tree Fig. 5) was concordant with the single gene trees (Supplementary data Fig. S1-S2).

**Molecular dating analysis**

Incorporating our genetic data with Cheng et al.'s (2017) for molecular dating, the divergence period for the *Platacanthomys* node was estimated to be around 39 mya (Eocene epoch) (Fig. 5). However, our study agrees with earlier studies for the divergence period for the ancestral *Typhlomys* node to be during Miocene (Fabre et al., 2012; Cheng et al., 2017). Using thousands of nuclear UCEs, Swanson et al. (2019) estimated the divergence of these genera at 42 million years ago, closely agreeing with our mitochondrial estimate.

The *Platacanthomys lasiurus* clade presumably emerged within the Eocene geological era, concurring with Fabre et al.'s (2012) studies, with a single extant species at present. While the divergence of *Typhlomys* ancestors from other muroids took place in Eocene, the most recent common ancestor (mrca) of *Typhlomys* occurred during Miocene (Fabre et al., 2012; Cheng et al., 2017). Molecular dating analysis indicates that the *Platacanthomys* lineage is archaic compared to TMRCA of *Typhlomys*. The genus *Platacanthomys* exhibits closer phylogenetic relationship to other muroid lineages than to *Typhlomys,* (Supplementary file, Fig. S4). The Divergence data between *Platacanthomys* and *Typhlomys* suggests that *Typhlomys* diverged from other muroid lineages earlier in the Eocene epoch (~45 mya), compared to *Platacanthomys.* The present *Platacanthomys* lineage could be a relict taking refugium in the hill ranges of the Western Ghats whose ancestors might have gone extinct due to various geological events in the past. The two genera are not monophyletic on the phylogenetic tree which supports separate familial placement for them.

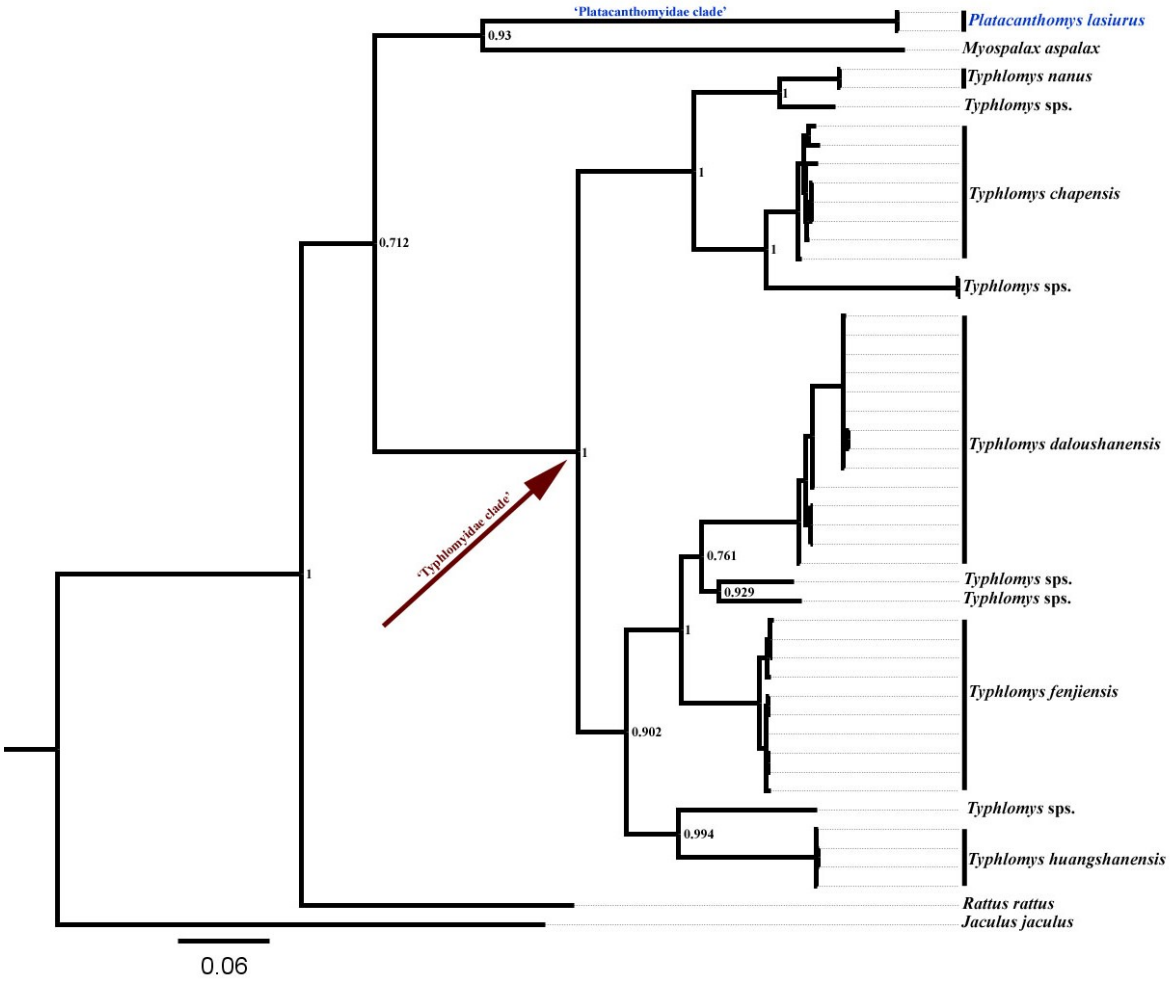


**Figure 4:** Bayesian phylogenetic tree for the Platacanthomyidae based on 1690 bp of mitochondrial concatenated (*COI* + *Cyt b*) gene dataset. Tree is rooted with *Rattus rattus* and *Jaculus jaculus* as outgroups.

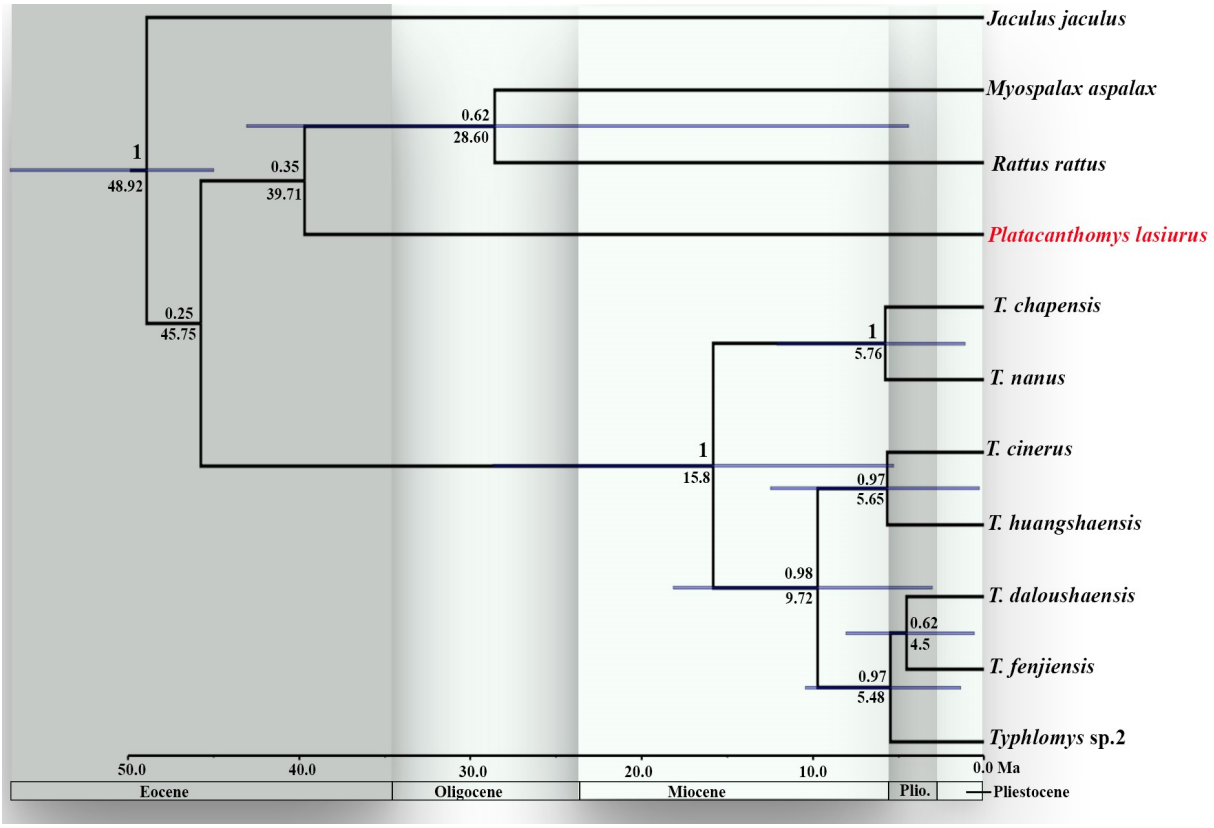


**Figure 5:** Coalescent-based species tree estimated using the *BEAST model in BEAST v 1.8. using 4490 bp of concatenated dataset. Branch lengths represent time and node bars indicate the 95% CI for the clade age. Node numbers are posterior probabilities (upper) and the median ages of the divergence times (lower).

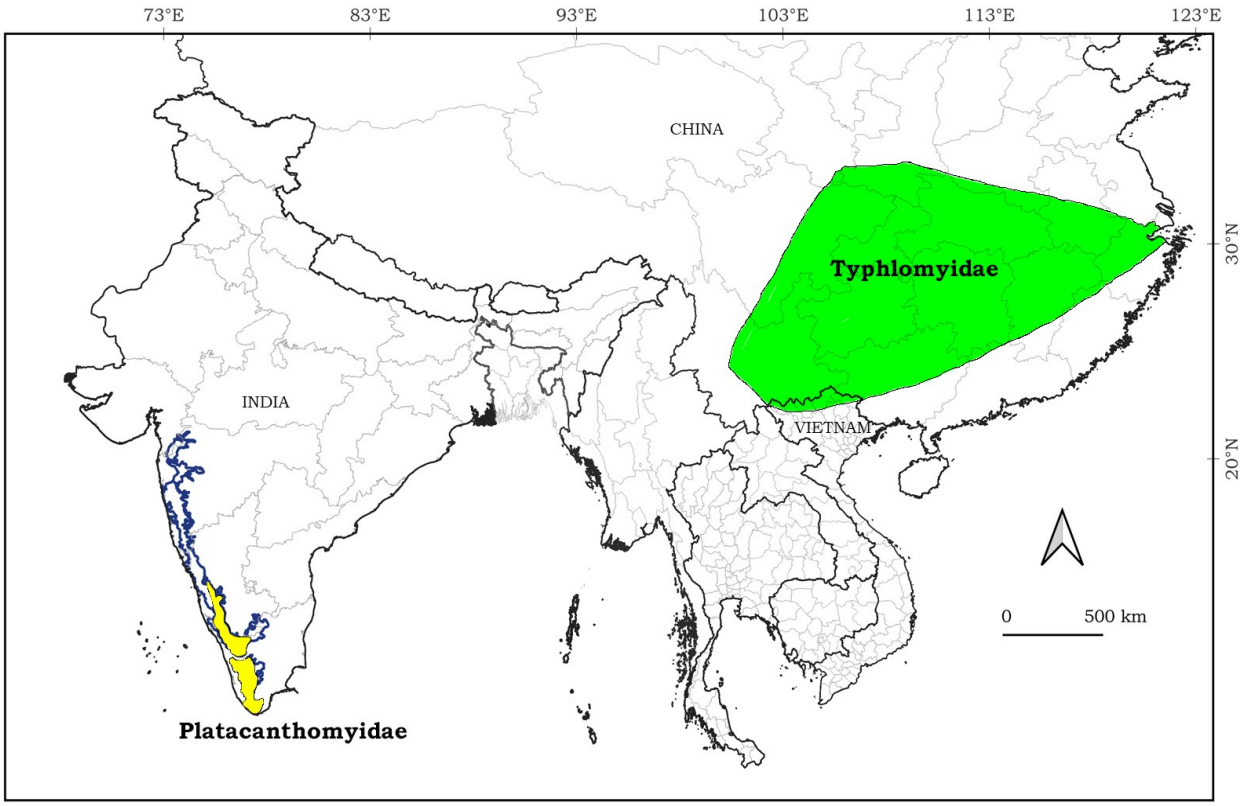


**Figure 6:** Map showing distribution ranges of Platacanthomyidae in the Western Ghats and Typhlomyidae in China and Vietnam.

## Discussion

Jansa et al. (2009) provided the first phylogenetic assessment of the family Platacanthomyidae and explored its evolutionary relationships with other muroids. They acknowledged morphological differences between *Platacanthomys* and *Typhlomys* genera and expressed doubts about whether they are more closely related to each other than to other rodents. Regarding fossil evidence, Jansa et al. noted that no "platacanthomyid" fossil have been found in northern China and that they are unknown outside the Eurasia. Earlier, unidentified "platacanthomyid'' fossils dating to 17 mya are known from the Siwalik deposits in Pakistan (Flynn, 2003), and the modern genera *Platacanthomys* and *Typhlomys* appear in the late Miocene deposits of Yuanmou and Shihuiba in southern China (Ni and Qiu, 2002; Qui and Li, 2003).

Jansa et al. (2009) concluded that in the early Miocene, platacanthomyids were widespread throughout Eurasia and might have gone extinct in Europe in the mid-Miocene. The present-day populations of these genera could be disjunct relicts of western India (*Platacanthomys*) and southern mainland Asia (*Typhlomys*). In 2017, in their phylogenetic and systematic revision of the genus *Typhlomys*, Cheng et al. suggested the diversification of the genus during the late Miocene and Pliocene.

A review of literature retrieved unstable classification of platacanthomyids based on the morphology, anatomy and osteology (Jansa et al., 2009). Only with the aid of genetic data are the higher-level systematics now being resolved, which also is especially useful for relic groups like *Platacanthomys*. We hypothesize that *P. lasiurus* could be a younger species and a relic from Gondwana, whose ancestors, once widespread, are now extinct. Further sampling, as well as studies of nuclear genes and fossil material, is warranted in the future.

Earlier studies by Ellerman (1940, 1949) noted similarities in molar tooth morphology between the Western Ghats genus *Platacanthomys* and rodent subfamily Nesomyinae from Africa and Madagascar. This could be due to convergence or a common Gondwanan origin of these groups and can only be resolved through comprehensive studies. Understanding the limitations of mitochondrial data in higher-level systematics, we advocate for multigene studies (both mitochondrial and nuclear) to clarify the familial placements of the two families on the larger phylogenetic tree.

We recognize two families, Platacanthomyidae and Typhlomyidae, based on genetic distance as retrieved in our phylogenetic study (Supplementary figures Figs. S1, S2), evolutionary divergence at different geological time scales (Fig. 5), morphological characters (Table 1, Figs. 2-3) and geographical isolation (Figs. 1 and 6). Hence, we propose family rank for the subfamily Typhlomyinae Ognev, 1947, with *Typhlomys* Milne-Edwards, 1877 as the type genus as opposed to family Platacanthomyidae Alston, 1876, with *Platacanthomys* as the type genus. We propose to include the extinct genus *Neocometes* under Typhlomyidae due to similarities in their fossil records (Giarla, 2017).

The family Typhlomyidae Ognev, 1947 is distributed in China and Vietnam, while Platacanthomyidae Alston, 1876 is restricted to the Western Ghats, India, and there is no overlap between their distributional ranges. Both genera are geographically separated by at least 5000 km of distance with no species found between the Western Ghats and China.

Current insights revealed distribution range of *Platacanthomys* in the central and southern Western Ghats, across the Palghat Gap (Natural history notes in Supplementary file). Our genetic data come from the central Western Ghats which is to the north of the Palghat Gap. Therefore, further genetic studies from south of the Palghat gap may provide insightful understanding on genetic diversity (gene flow pattern) and variability within the Western Ghats.

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## Author contributions

All authors conceptualised the study. SST, MJP and KAS did the field survey and collected the specimen and ecological notes. SST performed morphometry and morphological studies. AS performed molecular wet lab. KPD and AS performed the Phylogenetic and molecular Dating Analysis. KPD performed data interpretation. AS prepared the maps. All authors contributed to manuscript writing, editing, and proof reading.

## Conflict of interest

The authors declare that there are no conflicting issues related to this research article.

## Supplementary data

https://jad.lu.ac.ir/article_725040.html

## Research ethics

Field study permits were taken from the Kerala state Forest Department with Permit No. KFDHQ-2898/2019-CWW/WL10 dated 20.07.2019 for the period of three years.

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