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Phylogenetic and morphological significance of an overlooked flying squirrel (Pteromyini, Rodentia) from the eastern Himalayas with the description of a new genus

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ABSTRACT

The flying squirrels (Pteromyini, Rodentia) are the most diverse and widely distributed group of gliding mammals. Taxonomic boundaries and relationships within flying squirrels remain an area of active research in mammalogy. The discovery of new specimens of *Pteromys (Hylopetes) leonardi*

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Thomas, 1921, previously considered a synonym of

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Hylopetes alboniger, in Yunnan Province, China allowed a morphological and genetic reassessment of the status of this taxon. Phylogenetic reconstruction was implemented using sequences of two mitochondrial (12S ribosomal RNA and 16S ribosomal RNA) and one nuclear (interphotoreceptor retinoid-binding protein) gene fragments. Morphological assessments involved examinations of features preserved on skins, skulls, and penises of museum specimens, supplemented with principal component analysis of craniometric data. Together these assessments revealed that this taxon should be recognized not only as a distinct species, but should also be placed within a new genus, described here as *Priapomys* **gen. nov.**

Keywords: Eastern Himalayas; Flying squirrel; Penis; *Priapomys*; Pteromyini; New genus; Systematics; Taxonomy

INTRODUCTION

Flying squirrels (Pteromyini, Rodentia) are the most diverse lineage of gliding mammals. Extant species range in size from pygmy flying squirrels (*Petaurillus*, 13.5 g) to giant flying squirrels (*Petaurista*, 2 710 g) (Thorington et al., 2012) and occur in forests in Europe, Asia, and North America. Their distribution ranges from tropical lowlands to taiga, even to above the tree-line within the Himalayas (Jackson & Schouten, 2012).

The taxonomic history of flying squirrels is convoluted and unstable, with major taxonomic changes being reviewed by Thorington et al. (2002) and Jackson & Thorington (2012). Current taxonomy tentatively recognizes 56 living species in 15 genera (Arbogast et al., 2017; Jackson & Schouten, 2012; Jackson & Thorington, 2012; Jackson et al., 2021; Koprowski et al., 2016; Li et al., 2019; Thorington et al., 2012) as well as 70 fossil species placed both in extant genera and 19 extinct genera (Jackson & Thorington, 2012; Lu et al., 2013; Qiu, 2019; Tiunov & Gimranov, 2019). Until recently most taxonomic revisions were mainly based on morphological comparisons rather than the phylogenetic analysis of genetic data.

In this paper we review the taxonomic status of a largely overlooked flying squirrel taxon, *Pteromys* (*Hylopetes*) *leonardi*, which was described by Thomas (1921) based on a single specimen collected from Kachin State in northern Myanmar. Subsequently, Pocock (1923) recognized *Hylopetes* as a genus distinct from *Pteromys*, and *leonardi* was recognized as a valid species within *Hylopetes* by Ellerman (1940). This taxon was treated as a subspecies of *H. alboniger* (without critical review or analysis) by Ellerman & Morrison-Scott (1951), Ellerman (1961), Yin (1967), Wang (2003), Smith & Xie (2008) and Thorington et al. (2012), and synonymized entirely with *H. alboniger* by Corbet & Hill (1992), Thorington & Hoffmann (2005), and Jackson & Thorington (2012). The taxon *leonardi* was previously known only by the holotype (lodged at the Natural History Museum,

London, catalogue number 20.8.8.2), which does superficially resemble specimens of *Hylopetes alboniger*, and no morphological and genetic assessments involving the holotype of *leonardi* have since been published.

During field studies conducted between 2014 and 2016 on Mount Gaoligong, in the western part of Yunnan Province, China, five specimens of a flying squirrel morphologically very similar to "*P. (H.) leonardi*" were collected. Subsequently, we also identified another eight specimens similar to "*P. (H.) leonardi*" from northwest Yunnan Province within the collections of the Kunming Institute of Zoology (Chinese Academy of Sciences) and Dali University. Our initial genetic analysis revealed that these "*P. (H.) leonardi*" specimens (Yunnan population, hereafter) were most closely related, albeit with a deep genetic divergence, to species within the Sundaland endemic genus *Iomys*, rather than to species of *Hylopetes*. Therefore, the aims of this study were to: (1) determine whether these Yunnan specimens belong to the same species as the holotype of *leonardi*, (2) undertake a comprehensive morphological and genetic study to clarify the taxonomic status of *leonardi*, and (3) recommend changes to its taxonomic status if appropriate.

MATERIALS AND METHODS

Ethics statement

Methods for all animal research undertaken for this study were approved by the Animal Ethics Committee of the Kunming Institute of Zoology, Chinese Academy of Sciences (approval ID: SMKX2018021).

Morphological techniques

We examined 469 specimens of flying squirrels that included all living species except *Hylopetes winstoni* and *Petaurillus emiliae* (Supplementary Text). Museum collections that were accessed to examine these specimens included the American Museum of Natural History, New York, United States (AMNH); Natural History Museum, London, United Kingdom (BMNH); Dali University, Dali, Yunnan Province, China (DU); Field Museum, Chicago, United States (FMNH); Kunming Natural History Museum of Zoology, Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences (CAS), Kunming, Yunnan Province, China; Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington DC, United States (USNM); Naturalis Museum, Leiden, Netherlands (NML); Zoological Collection of the Faculty of Environmental Sciences, National University of Laos, Vientiane, Lao PDR (NUoL); and Zoological Collection of the Zoological Survey of India, Kolkata (Calcutta), India (ZSI).

Terminology of cheekteeth

Dental abbreviations in the text are: P for premolars, M for molars, superscript (P^x , M^x) for upper premolars and upper molars, subscript (P_x , M_x) for lower premolars and lower molars. Dental observations were made under a light microscope (Keyence digital microscope system VHX-2000C with 50X Kenyence VH-Z00R lens, Japan). Terminology for cheekteeth occlusal morphologies is modified from Zhou et al.

(1975), Kawamura (1988), Tong (2007), Li et al. (2019), Qiu (2019), and Jackson et al. (2021) (Figure 1); equivalents of terms used by other authors are given in Supplementary Table S1.

Craniodental measurements

Craniodental variables were measured with handheld Vernier Calipers (Mitutoyo 500-197, 200 mm, Japan) to the nearest 0.01 mm following a modified version of the measurements recorded by Helgen et al. (2009) and Li et al. (2012) (24 variables, Figure 2).

A Principal Component Analysis (PCA) based on the covariance matrix was used to evaluate variation in 20 of 24 craniodental variables ($LP^3 M^3$ was excluded because *Iomys* spp. have no P^3 ; BP^4 , BM^1 , BM^3 were also excluded because only specimens lodged at KIZ measured these variables) taken from *P. (H.) leonardi* (holotype+4 specimens of the Yunnan population), from similar sized flying squirrels which occur sympatrically or parapatrically with *P. (H.) leonardi* (i.e., *Hylopetes alboniger*, $n=10$; *H. phayrei*, $n=10$; *Belomys pearsonii*, $n=2$), and from flying squirrels most closely related genetically to *P. (H.) leonardi* (*Iomys horsfieldii*, $n=7$; *I. sipora*, $n=2$). Missing data was filled with the average of the species. Raw measurements were log-transformed to standardize

variances and improve normality. All analyses were performed using PAST v.4.02 (Hammer et al., 2001).

Morphological comparison

Qualitative comparisons of craniodental morphological features were made for all available skulls in Supplementary Text, and included: (1) the pattern of internal septae of the auditory bulla (Supplementary Figure S1); (2) the development of the coronoid process; (3) presence or absence of P^3 ; (4) the development of the mesostyle, mesolophule, anterolophule, paraconule, metaconule, metaloph, lingual flexus, hypoconulid, protolophid, and entolophid on the cheekteeth.

Non-cranial morphology that was assessed included checking for the presence of ear tufts (Supplementary Figure S2) and the shape and size of the glans penis. Detailed pelage comparisons were also made between the Yunnan specimens and the holotype of *P. (H.) leonardi*.

Molecular techniques

Most of the sequences used in this study were downloaded from GenBank, especially from the studies of Mercer & Roth (2003) and Li et al. (2020) (Supplementary Table S2). In addition, four new samples (two *P. (H.) leonardi* of the Yunnan population, KIZ034951, KIZ034952; one *Hylopetes alboniger*,

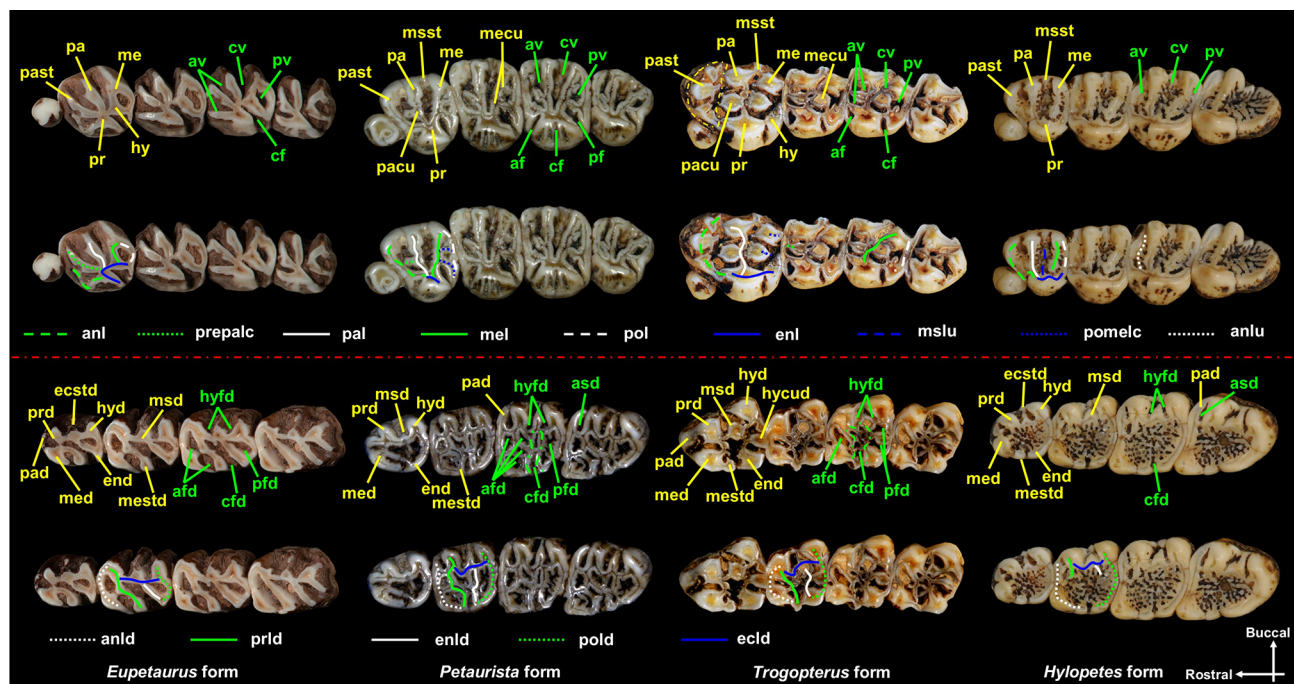


Figure 1 Terminology of four typical kinds of upper cheekteeth (above) and lower cheekteeth (bottom) of living flying squirrels

“*Eupetaurus* form” (*Eupetaurus* only), “*Petaurista* form” (*Petaurista* and *Aeretes*), “*Trogopterus* form” (*Trogopterus*, *Belomys*, and *Pteromyscus*), and “*Hylopetes* form” (*Eoglaucmys*, *Glaucmys*, *Hylopetes*, *Petaurillus*, *Petinomys*, and *Pteromys (Hylopetes) leonardi* (= *Priapomys* gen. nov.); the cheekteeth of *Pteromys* are closest to the *Petaurista* form but simplified; the cheekteeth of *Biswamoyopterus*, *Aeromys*, and *Iomys* are closest to the *Hylopetes* form but with some modification. Abbreviations for upper molars: Paracone (pa), metacone (me), protocone (pr), hypocone (hy), parastyle (past), mesostyle (msst), paraconule (pacu), metaconule (mecu), anteroloph (anl), paraloph (pal), metaloph (mel), posteroloph (pol), endoloph (enl), mesolophule (mslu), anterolophule (anlu), preparaconule crista (prepalc), postmetaconule crista (pomelc), anterior valley (av), central valley (cv), posterior valley (pv), anterior flexus (af), central flexus (cf), posterior flexus (pf). Abbreviations for lower molars: protoconid (prd), hypoconid (hyd), metaconid (med), entoconid (end), mesoconid (msd), paraconid (pad), ectostylid (ecstd), metastylid (mestd), hypoconulid (hycud), anterolophid (anld), protolophid (prld), entolophid (enld), posterolophid (pold), ectolophid (ecl), anterobuccal sinusid (asd), hypoflexid (hyfd), anterior fossettid (afd), central flexid (cfd), posterior fossettid (pfd).

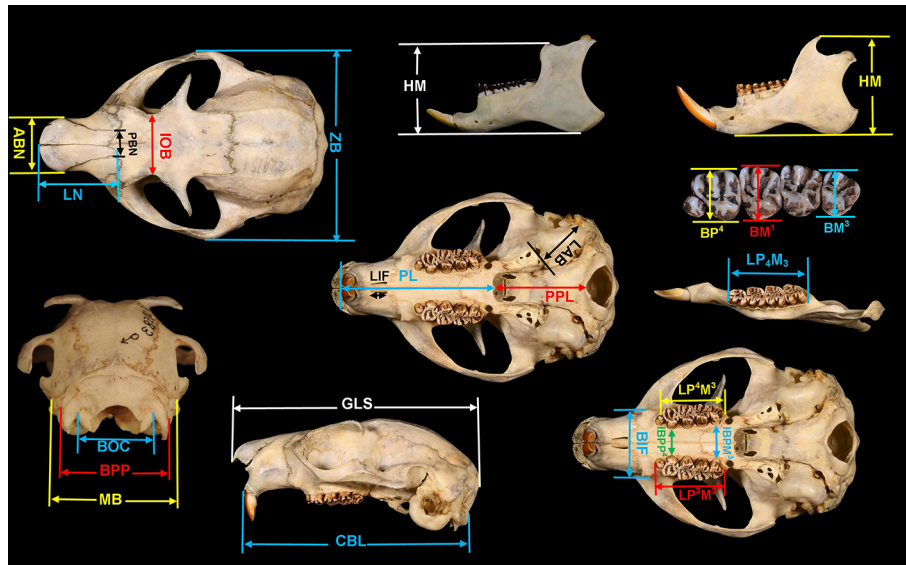


Figure 2 Craniodental measurements taken for this study

Greatest length of skull (GLS), length of nasals (LN), zygomatic breadth (ZB), anterior breadth of nasals (ABN), posterior breadth of nasals (PBN), interorbital breadth (IOB), condylobasal length (CBL), palate length (PL), post palatal length (PPL), length of incisive foramina (LIF), length of auditory bulla (LAB), length from P³ to M³ (LP³ M³), length from P⁴ to M³ (LP⁴ M³), breadth of P⁴ (BP⁴), breadth of M¹ (BM¹), breadth of M³ (BM³), inside breadth of bony palate at P⁴ (IBPP⁴), inside breadth of bony palate at M³ (IBPM³), breadth across infraorbital foramina (BIF), breadth of occipital condyle (BOC), mastoid breadth (MB), breadth across paroccipital process (BPP), length from P₄ to M₃ (LP₄M₃), and height of mandible (HM).

KIZ034942; and one *Petaurista elegans*, KIZ034939) were sequenced. We did not include previously widely used “*Aeretes*” sequences (GenBank accession Nos.: AY227593, AY227535, AY227481) in our analyses, because these come from a misidentified specimen (Roth & Mercer, 2015: 223, Quan Li, personal observation).

DNA extraction and PCR

Total genomic DNA was extracted from muscle tissue of four specimens collected from Mount Gaoligong using the DNeasy Tissue kit (Qiagen, Germany). Two mitochondrial (12S ribosomal RNA (12S), and 16S ribosomal RNA (16S)) and one nuclear (interphotoreceptor retinoid-binding protein (*IRBP*)) gene fragments were amplified with rtaq DNA Polymerase (Takara, Japan) with the primers presented in Supplementary Table S3. PCR products were purified with the QIAquick PCR Purification kit (Qiagen, Germany) and sequenced with the BigDye Terminator Cycle kit v3.1 (USA) using an Applied Biosystems automated sequencer (ABI 3730xl, USA). Sequencing reads were assembled and edited using the DNASTAR Lasergene v7.1 (Burland, 2000).

Phylogenetic analyses, divergence time estimation, and intergeneric genetic differences calculation

All sequences were assembled by Seqman (Burland, 2000) and aligned in MEGA 7.0 (Kumar et al., 2016). MEGA 7.0 was also used to calculate K2P distance between taxa based on the 12S and 16S loci. Sequences of the aplodontiid *Aplodontia rufa*, and the sciurids *Ratufa bicolor*, *Sciurus vulgaris*, and *Tamiasciurus hudsonicus* were employed as outgroups. Three datasets were applied in the phylogenetic analyses: (1) the mtDNA dataset based on 12S and 16S, (2) the *IRBP* dataset,

and (3) the mtDNA+nuDNA concatenated dataset. This study used RAXML (Edler et al., 2021) and Beast 1.8.2 (Drummond et al., 2012) to construct the Maximum Likelihood (ML) and Bayesian (BI) trees respectively. The best evolutionary model for each gene fragment was estimated using the Bayesian Information Criterion (BIC) in PartitionFinder (Lanfear et al., 2012). In ML analyses, this study used GTR+G for each partition and 1 000 replicates for the rapid bootstrapping algorithm, while in BI analyses, 12 models (GTR, GTR+G, HKY, HKY+G, TrN, TrN+G, TrNef, TrNef+G, K80, K80+G, SYM, SYM+G) were provided for substitution model selection of each partition. Each BI analysis was composed of a random starting tree, an uncorrelated lognormal relaxed molecular clock model, and a birth-death tree prior. Two fossil occurrences were applied as calibration points when constructing the BI trees: the oldest fossil squirrel (*Douglassciurus jeffersoni*) which dates to the late Eocene (ca. 36 million years ago (Ma)) (Emry & Thorington, 1984; Goodwin, 2008), and the fossil flying squirrel *Miopetaurista neogrivensis*, dated to ca. 11.6 Ma (Casanovas-Vilar et al., 2018). Each analysis consisted of 3×10⁷ generations sampled every 1 000 generations. Convergence was assessed using Tracer v1.7.1 (Rambaut et al., 2018) and the 1st 15% of the generations were discarded as burn-in. Maximum-likelihood bootstrap proportions (BP)≥70 and Bayesian posterior probability (PP)≥0.95 were considered as strong supports.

RESULTS

PCA

A PCA evaluated morphological variation in 20 craniodental variables among *P. (H.) leonardi* and related species (“similar

sized+sympatric/parapatric” or “genetic similarity”, see Methods section). The 1st component (65.5% of variation) separated samples mainly on the basis of HM, LN, ZB, and PL, the 2nd component (13.25% of variation) on the basis of LIF, LAB, and IBPP⁴, and the 3rd (6.31% of variation) on the basis of PBN, LIF, IBPP⁴, BIF, and LAB (Supplementary Table S4). The bivariate scatter plot of specimen-scores on component 1 clearly distinguished *Hylopetes alboniger* and *H. phayrei* from *P. (H.) leonardi*, *Iomys horsfieldii*, *I. sipora*, and *Belomys pearsonii*. Additionally, component 2 further distinguished *Iomys horsfieldii*, *I. sipora*, and *Belomys pearsonii* from *P. (H.) leonardi* (Figure 3). The holotype of *P. (H.) leonardi* clusters with samples of the Yunnan population (Figure 3). Raw craniodental measurements were given in Supplementary Table S5.

Morphological comparisons

Skins: The specimens of the Yunnan population (mass 150–204 g, head body length 195–210 mm, tail length 194–213 mm, ear length 33–37 mm, hindfoot length 40–45 mm) are slightly larger than the holotype of *P. (H.) leonardi* (Thomas (1921) measured on the skin: head body length 180 mm, tail length 125 mm, hindfoot length 39 mm). The tail of the holotype appears to be notably shorter (Tail length/Head and body length=69% in the holotype, 88%–106% in the Yunnan population) and broader than in the Yunnan population (Figure 4). Except for these aspects, their skins are very similar, especially in overall pelage color, and in having white throat patch and facial patterns (Figure 4). The fur is long and fine, with the general color above being blackish buffy, the hairs having long blackish slaty bases and buffy tips. The venter is overall pinkish buffy, with the chest and axillary regions pure white. The face and the streaks running along the sides of the neck are buff. The ears are naked, prominently black, and larger than most other small-sized

flying squirrels (e.g.: body size: *Hylopetes alboniger*>*P. (H.) leonardi*>*Belomys pearsonii*, ear length: *P. (H.) leonardi*=33–37 mm, *Hylopetes alboniger*=24–35 mm, *Belomys pearsonii*=22–24 mm). Ear tufts are absent. The dorsal surfaces of the hands and feet are blackish, lighter along their inner edges terminally. The tail is flat, very thick and bushy; its wool-hair buffy, its long hairs glossy blackish (Thomas, 1921). The uropatagium (tail membrane or interfemoral membrane) is less developed than in the larger flying squirrels.

Skulls: The skulls of the Yunnan population and the holotype of *P. (H.) leonardi* are similar (Figure 5) and resemble other small sized flying squirrels in overall shape (Supplementary Figure S3A, B, C). However, the auditory bullae are relatively much smaller (Supplementary Figure S3B, C) (length of auditory bulla: *P. (H.) leonardi*=7.46–7.91 mm, *Hylopetes alboniger*=8.65–9.35 mm, *Belomys pearsonii*=9.24–9.45 mm) and the palate is unusually arched between the molars to form a strongly developed posterior palatal spur (Supplementary Figure S3B).

Cheekteeth: The cheekteeth of the Yunnan population and the holotype of *P. (H.) leonardi* are very similar (Figure 5) and generally resemble other small sized flying squirrels, especially *Glaucomys* and *Eoglaucmys* (Supplementary Figure S3D, see Diagnosis). The cheekteeth are relatively small. The enamel is slightly sculpted between and on the sides of the ridges. All major ridges of the upper cheekteeth (anteroloph, paraloph, metaloph, posteroloph, endoloph) are developed normally, except the metaloph is absent on M³. The buccal side of the endoloph usually possesses traces of the anterolophule and mesolophule. Most specimens do not possess a mesostyle, and their mesolophules do not develop into mesolophs extending to the outer exit of the central valley (the single exception is KIZ034952, which possesses a very faint mesoloph and a very small mesostyle). As a result, from

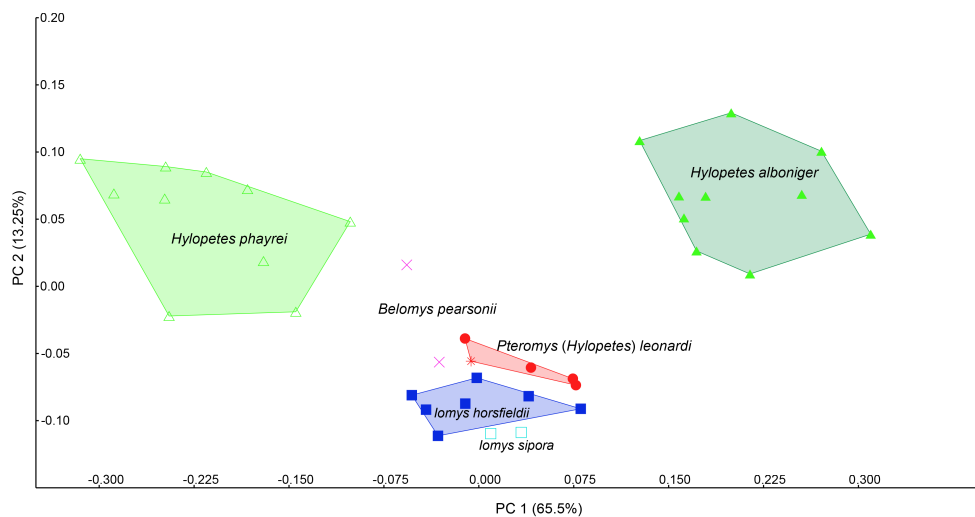


Figure 3 Principal component analysis scatter-plot of the skulls of *Pteromys (Hylopetes) leonardi* (=Priapomys leonardi) and related species (“similar sized+sympatric/parapatric” or “genetic similarity”)

Red dots: Yunnan population of *Pteromys (Hylopetes) leonardi*; Red star: Holotype of *Pteromys (Hylopetes) leonardi*; Blue filled squares: *Iomys horsfieldii*; Blue open squares: *Iomys sipora*; Green open triangle: *Hylopetes phayrei*; Green filled triangle: *Hylopetes alboniger*; and Purple X: *Belomys pearsonii*.



Figure 4 Skin comparison of *Pteromys (Hylopetes) leonardi* (= *Priapomys leonardi*) and related species (“similar sized+sympatric” or “genetic similarity”)

From top to bottom: *Pteromys (Hylopetes) leonardi* (holotype, BMNH20.8.8.2), *Pteromys (Hylopetes) leonardi* (Yunnan population, KIZ034951), *Iomys horsfieldii* (USNM153684), *Hylopetes alboniger* (KIZ034942), and *Belomys pearsonii* (KIZ034940).

the buccal side of the upper cheekteeth, only three cusps can be seen in *P. (H.) leonardi*, rather than four cusps in most species of *Hylopetes* and *Petinomys* (Supplementary Figure S4). The endoloph does not develop a distinct hypocone and there is not any distinct lingual fold. The paraconule is absent and the metaconule is small but recognizable on P⁴, M¹, and M². The lower cheekteeth also resemble those of other small sized flying squirrels, with the protolophid and entolophid less developed, the paraconid does not merge with the protoconid, and the anterobuccal sinusid present.

Glans penis: The glans penis of the holotype of *P. (H.) leonardi*, although male, is missing. The male Yunnan specimens possess a bony, slim, ultralong (17% of head and body length), and “S” shaped glans with two faint smooth crests on the right side (Supplementary Figure S5). Due to the

rarity of well-preserved penile specimens, we only examined the glans of species of 11 living genera, of which the glans of *Iomys* was damaged (tip missing, only the base was left); the glans of *Aeretes*, *Aeromys*, *Petaurillus*, *Petinomys* are still unreported. The glans of most flying squirrels we examined were usually stouter, shorter (2%–7% of head and body length), and with more developed crest(s) than the Yunnan specimens (Supplementary Figure S5 and Table S6), whereas *Glaucomys volans* and *Iomys horsfieldii* possess a slightly similar glans. The glans of *Glaucomys volans* is ultralong (16% of head and body length), straight, and the baculum was half the length of the glans. In contrast, the glans of the Yunnan population was “S” shaped, and the baculum was as long as the glans. The only available glans sample of *Iomys* is a broken glans base (AMNH185169), which was as slim as

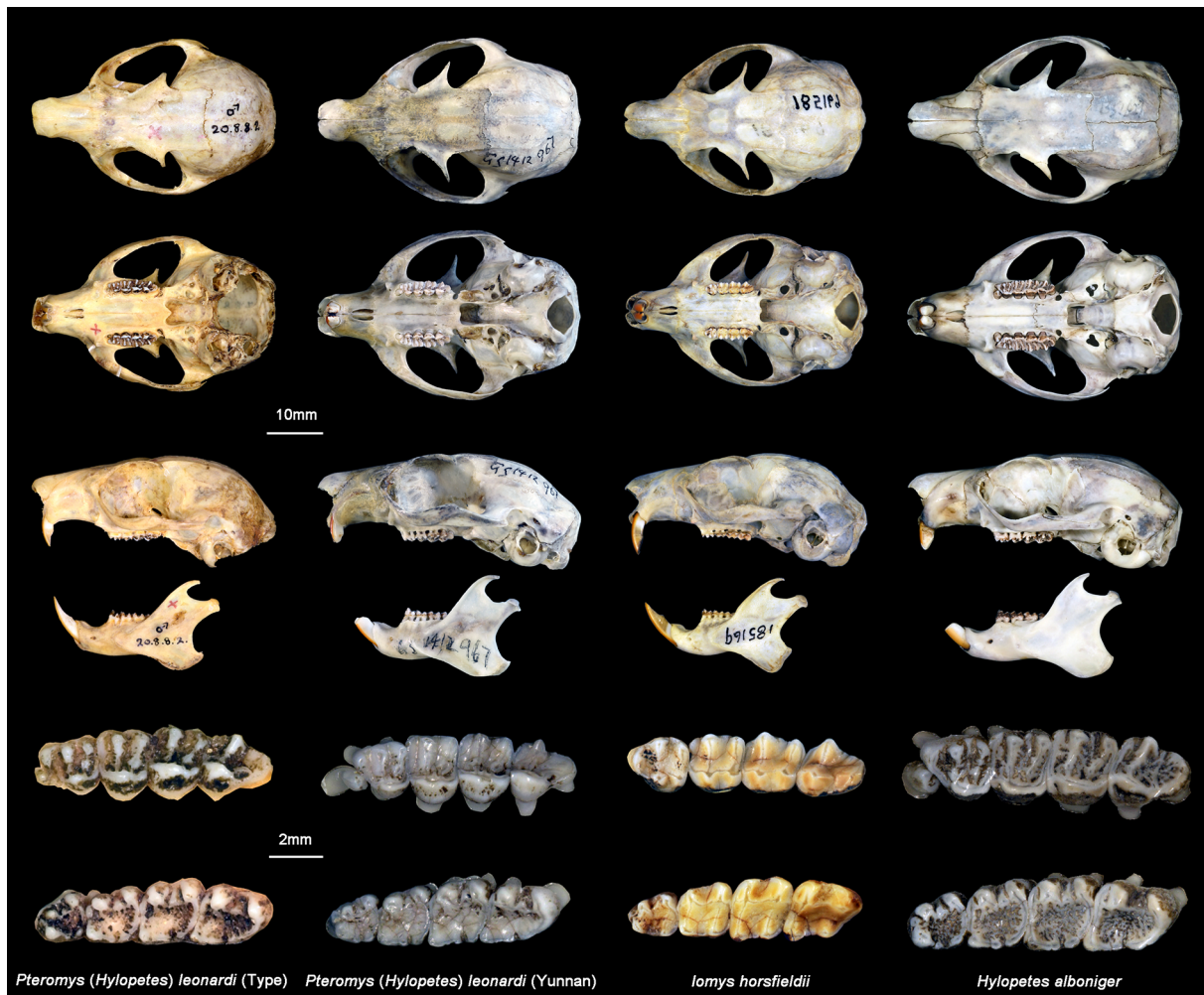


Figure 5 Skull and dentition comparison of *Pteromys (Hylopetes) leonardi* (= *Priapomys leonardi*) and related species (“similar sized+sympatric” or “genetic similarity”)

From left to right: *Pteromys (Hylopetes) leonardi* (holotype, BMNH20.8.8.2), *Pteromys (Hylopetes) leonardi* (Yunnan population, KIZ034951), *Iomys horsfieldii* (AMNH185169), and *Hylopetes albioniger* (KIZ034942).

the glans of the Yunnan population. However, because the tip is missing, we cannot tell if *Iomys* shares a similarly elongated glans with the Yunnan population (Supplementary Figure S5). More details of the morphological comparisons are shown in Supplementary Table S6.

Phylogeny

The phylogenetic reconstructions used three different datasets and showed similar topologies with both BI and ML approaches (Figure 6; Supplementary Figure S6). In all trees, the samples of the Yunnan population clustered in a monophyletic clade and showed a sister relationship with *Iomys*, with strong support (PP=1, BP=83–99).

Divergence time

Estimated flying squirrel intergeneric (14 genera excluding the genus *Aeretes* and the Yunnan population) divergence times from the mtDNA+nuDNA concatenated dataset range from 4.56 to 23.9 Ma. The Yunnan population splitting with its sister lineage, the genus *Iomys*, is estimated to have occurred in the late Miocene (11.27 Ma, 95% CI=6.19–12.07) (much younger

than the divergence time between the Yunnan population and *Hylopetes*: 16.61 Ma, 95% CI=9.94–15.99). This is older than the divergence time for many accepted sister genus pairs, 6.64 Ma (95% CI=4.44–9.05) for *Aeromys* vs. *Biswamoyopterus* and 4.56 Ma (95% CI=3.32–6.8) for *Trogopterus* vs. *Belomys*) (Figure 6).

Intergeneric genetic differences

For mitochondrial 12S ribosomal RNA sequences, the range of intergeneric (14 genera excluding the genus *Aeretes* and the Yunnan population) divergences were 5.4%–15.2% (Supplementary Table S7A). The genetic distances between the Yunnan population and other genera ranged from 6.9 to 14.2%, which is greater than 5.4% for *Trogopterus* and *Belomys*.

For mitochondrial 16S ribosomal RNA sequences, the range of intergeneric (14 genera excluding the genus *Aeretes* and the Yunnan population) divergences were 5.2%–14.7% (Supplementary Table S7B). The genetic distances between the Yunnan population and other genera ranged from 5.6 to

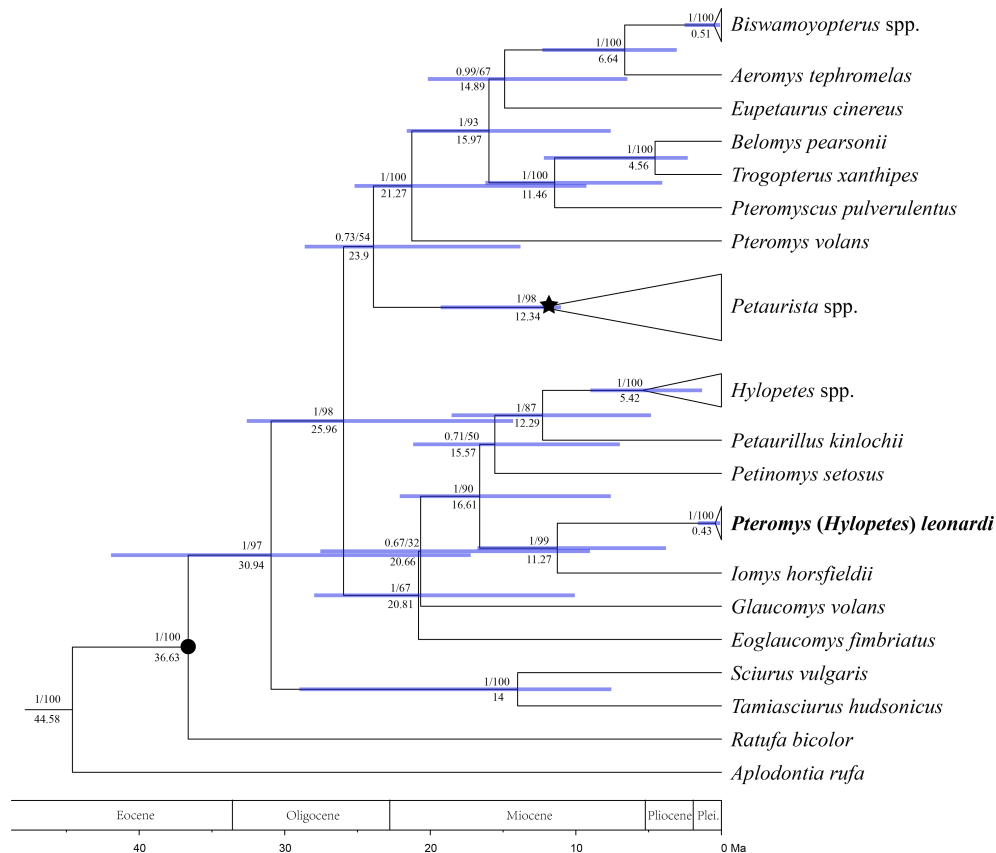


Figure 6 Flying squirrel phylogeny (includes all genera except *Aeretes*) and node dating estimates based on Bayesian and Maximum likelihood approaches utilizing the mtDNA+nuDNA concatenated dataset

Numbers of the branches are Bayesian posterior probabilities (top left), likelihood bootstrap values (top right), and node dating estimate values (bottom). Dot is the fossil occurrence of *Douglassciurus jeffersoni* and star is the fossil occurrence of *Miopetaurista neogrivensis*.

13.3%, which is greater than some intergeneric variations, such as 5.2% for *Aeromys* and *Biswamoyopterus*, and 5.5% for *Trogopterus* and *Belomys*.

DISCUSSION

The Yunnan population and the holotype of *P. (H.) leonardi* are slightly different in body size and tail length and shape (see Results). However, as there was only one specimen available (holotype) from the type locality (northern Myanmar), we do not know if these differences are consistent or statistically significant. There is a distance of only ca. 100 km between the type locality (N28°5', E97°25'; Thomas, 1921) and the nearest sampling point of the Yunnan population. However, the Irrawaddy River runs between them (Figure 7), which may contribute to geographical variation between these populations. Based on the PCA (Figure 3) and the qualitative morphological comparisons (see Results), we found that the Yunnan population is very similar to the holotype in most respects. We consider that the Yunnan population and the holotype are the same species and thus that our morphological and genetic analysis using the samples of the Yunnan population represent the taxon *leonardi*.

Based on the PCA (Figure 3), skins (Figure 4), skulls/teeth (Figure 5), glans (Supplementary Figure S5), and genetic analyses (Figure 6), it is clear that *leonardi* is a distinct

species from *H. alboniger*, with which it has previously been confused or allied (see Introduction). These analyses also indicate that *leonardi* has a sister relationship with *Iomys*, albeit with a deep, intergeneric-level divergence. In considering whether *leonardi* should be allocated to the genus *Iomys*, or described as the type species of new genus sister to *Iomys*, we considered three criteria for defining a new genus (Dong et al., 2010; Liu et al., 2012): (1) generic monophyly; (2) reasonable compactness as defined by consistent levels of intergeneric divergence across flying squirrel systematics; and (3) ecological, morphological, or biogeographical distinctness.

Morphological differences evident between *leonardi* and *Iomys* included: (1) P³ absent in *Iomys* vs. present in *leonardi*; (2) hypocone present in *Iomys* vs. absent in *leonardi*; (3) paraloph, metaloph, protolophid, entolophid much more developed in *Iomys* than in *leonardi*; and (4) quadricuspidate molars in *Iomys* vs. non-quadricuspidate molars in *leonardi*. Hunter & Jernvall (1995) proposed that the hypocone is a key innovation that has allowed invasion of, and diversification within, herbivorous adaptive zones. We speculate that possession of a hypocone by *Iomys* suggests a more herbivorous diet, while lack of a hypocone in *leonardi* suggests an overall more omnivorous diet.

The species of *Iomys* inhabit a variety of tropical forests in Sundaland (Jackson & Schouten, 2012). Conversely, *leonardi*

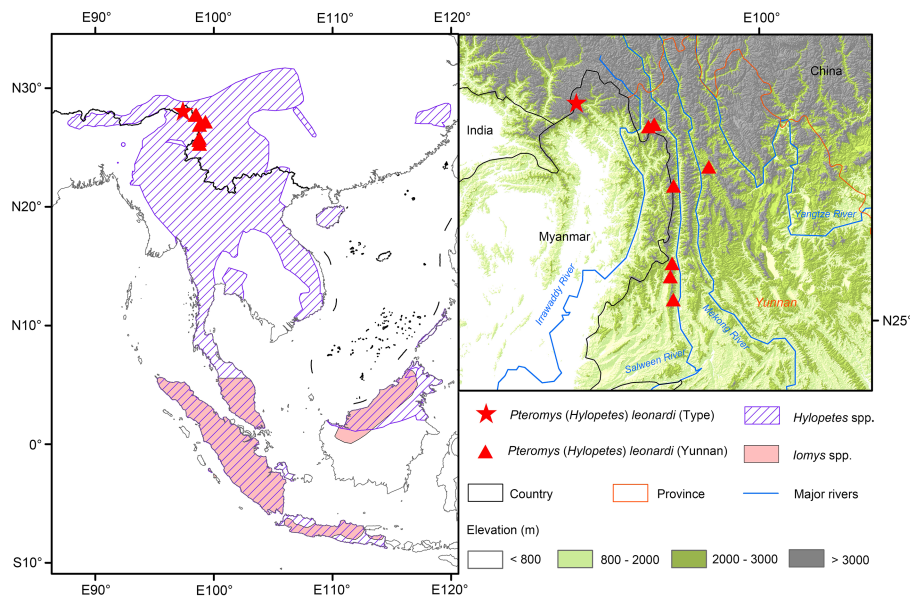


Figure 7 Currently hypothesized distribution of *Pteromys (Hylopetes) leonardi* (= *Priapomys leonardi*) and two other flying squirrel genera “*Iomys* spp.” include all species of *Iomys*, which is the sister lineage of *Pteromys (Hylopetes) leonardi*; and “*Hylopetes* spp.” include all species of *Hylopetes*, with which *Pteromys (Hylopetes) leonardi* has previously been confused taxonomically. Data from IUCN.

lives in subtropical evergreen broad-leaved forest and temperate mixed coniferous and broad-leaved forest of the eastern Himalayas (Quan Li, personal observation). There is a large gap between the distributions of *leonardi* and *Iomys* (Figure 7). Various other sister genus/species pairs show a similar disjunct East Himalaya/Annamite and Sundaic distribution, such as the crested arguses *Rheinardia*, colugos *Galeopterus*, banded civets *Hemigalus* and *Chrotogale*, and striped rabbits *Nesolagus*. This general biogeographic pattern may result from several large-scale marine transgressions (Woodruff, 2003) and the gradual aridification and seasonality of the Indochina Peninsula during the Late Cenozoic (Morley, 2018). Given major morphological differences between *leonardi* and *Iomys*, their different biogeographic occurrences, respective monophyly of the genus *Iomys* and the taxon *leonardi*, and comparative intergeneric level genetic difference between *leonardi* and *Iomys*, here we describe a new genus for the taxon *leonardi*, which represents an overlooked major phylogenetic lineage within the Pteromyini.

Taxonomy

Class Mammalia Linnaeus, 1758
 Order Rodentia Bowdich, 1821
 Family Sciuridae Fischer de Waldheim, 1817
 Subfamily Sciurinae Fischer, 1817
 Tribe Pteromyini Brandt, 1855
 Subtribe Glaucomyina Thorington and Hoffmann, 2005

Priapomys gen. nov.

Type species: *Pteromys (Hylopetes) leonardi* Thomas, 1921.

Included species: *Priapomys leonardi* (Thomas, 1921) (李氏小飞鼠).

Referred specimens: BMNH20.8.8.2 (holotype), adult male, skin, skull, collected from Kachin State (N28.083°, E97.417°, 2 438 m a.s.l.), northern Myanmar. Collected 11 January 1917, by P.

M. Leonard.

KIZ034951 (adult female, Genbank accession Nos. MW929354, MW929358, MW929361), KIZ034954 (adult female), skin, skull, collected from Qiqi (其期, N27.715°, E98.571°, 2 171 m a.s.l.), Mt. Gaoligong, Gongshan, Yunnan Province, China. Collected 15–16 December 2014, by Q. Li.

KIZ034952 (adult male, Genbank accession Nos.: MW929355, MW929359, MW929362), KIZ034953 (juvenile female), skin, skull, collected from Jidu (基独, N27.715°, E98.516°, 2 601 m a.s.l.), Mt. Gaoligong, Gongshan, Yunnan Province, China. Collected 17 October 2016, by Q. Li.

KIZ035090 (adult male), whole body preserved in ethanol, collection information as for KIZ034952 and KIZ034953.

KIZ034971 (juvenile female), skull, collected from Zhiziluo (知子罗, N26.544°, E98.973°, 2 649 m a.s.l.), Mt. Biluo, Fugong, Yunnan Province, China. Collected 2 November 2011, by C.Z. Pu.

KIZ0410099 (adult female), skin, skull, collected from Maku (马库, N27.694°, E98.291°, 1 416 m a.s.l.), Mt. Gaoligong, Dulongjiang, Yunnan Province, China. Collected 5 November 2004, by X.L. Jiang.

DUE110001, DUE110002, DUE110003, DUE110005, DUE110006, DUE110007, skins; from the upper Mekong river valley (unknown whether these were collected from the east or the west bank), Weixi, Yunnan Province, China, by staff of Dali University; sex, maturity, and dates of collection not recorded.

Etymology: The specific name is derived from Priapus (the Greek god of fertility), and mys, Greek for mouse (and mouse-like animals). *Priapomys* is masculine. The ultralong glans of penis of the type species inspired the name.

Suggested English name: Himalayan Large-eared Flying Squirrel (喜山大耳飞鼠属).

Diagnosis: External morphology (less developed uropatagium, flat tail) and overall shape of skull generally

resemble other small-sized flying squirrel genera (Figure 4; Supplementary Figure S3A, B, C). The external ear is larger than most other small-sized flying squirrels, while the auditory bulla is very small; there are no ear tufts.

Cheekteeth are generally similar to other genera of Glaucomyina, but the combination of characteristics can distinguish *Priapomys* from other extant flying squirrel genera (Figure 5; Supplementary Figure S3D). The endoloph does not develop a distinct hypocone, no central notch/flexus (endoloph develops a distinct hypocone to form a central notch/flexus in *Aeromys*, *Belomys*, *Biswamoyopterus*, *Eupetaurus*, *Iomys*, *Pteromyscus*, and *Trogopterus*). Posterior flexus absent (present in *Aeretes* and *Petaurista*). Mesolophule usually obsolete, not extending to the outer exit of the central valley, and mesostyle absent (mesolophule connect to the well-developed mesostyle to form a distinct “mesoloph” in most species of *Petinomys* and *Hylopetes*). Metaloph complete and metaconule less developed (metaloph deeply notched to cut off a separate metaconule in *Pteromys*). Anteroloph, posteroloph, and paraconid distinct (much reduced in *Petaurillus*). Thus, *Priapomys* can be easily distinguished from most living flying squirrel genera by dentition, except *Eoglaucmys* and *Glaucmys*.

The cheekteeth of *Priapomys* have more pitted enamel than *Eoglaucmys* and *Glaucmys*, and a more well-developed paraconid (Supplementary Figure S3D). Moreover, the auditory bulla of *Priapomys* is much smaller than *Eoglaucmys* and *Glaucmys*, and the postorbital processes are more developed than in *Glaucmys* (Supplementary Figure S3A, B, C). The glans penis of *Priapomys* also differs from *Eoglaucmys* and *Glaucmys* (Supplementary Figure S5 and Table S6).

Distribution: *Priapomys leonardi* is known to occur in northern Myanmar (Kachin State), at Mount Gaoligong (the watershed of the Ayeyarwady (=Irrawaddy) River and the Nu (=Salween) River), and in the upper Mekong River Valley (Weixi, Yunnan Province, China). Therefore, we suspect that *Priapomys leonardi* may occur more broadly in suitable habitat of eastern Himalayas, especially north of the known localities. No specimens have been collected south of Baoshan, China (N25°; Figure 7).

Natural history: Very little is yet known about the natural history of *Priapomys leonardi*. The Yunnan population inhabits evergreen broad leaf forests and coniferous broad leaf mixed forests at an elevation of 1400–2700 m a.s.l., and populations in Myanmar presumably inhabit similar environments (holotype collected from 8000 feet (=2438 m a.s.l.), Thomas (1921)). *Hylopetes alboniger*, *Belomys pearsonii*, *Petaurista yunanensis*, *Petaurista elegans*, and *Biswamoyopterus gaoligongensis* occur sympatrically with *Priapomys leonardi* at Mount Gaoligong.

Conservation: Little is currently known about the conservation status of *Priapomys leonardi*. Due to its small body size, it is not a major target for hunting and poaching, but it is captured by indiscriminate traps set for hunting meat by herb collectors who visit its range. During 2014 to 2016, Q. Li observed this species being sold at game markets on northern Mount Gaoligong where it is abundant. While the known extent of occurrence is relatively small, ca. 25 000 km² based

on the known localities (Figure 7), it does not qualify for the IUCN ranking of Vulnerable (extent of occurrence < 20 000 km²). Therefore, we recommend an IUCN Red List classification of Near Threatened (NT) for this species, based on our current understanding of threats to the species, and its distribution.

Key to the genera of living flying squirrels:

- 1) (a) endoloph does not develop a distinct hypocone, central notch/flexus indistinct..... **2**
- (b) endoloph develops a distinct hypocone, central notch/flexus distinct..... **3**
- 2) (a) coronoid process much reduce; metaloph deeply notched to cut off a separate metaconule..... **Pteromys**
- (b) coronoid process normal, higher than condylar process; metaloph does not deeply notch to cut off a separate metaconule..... **4**
- 3) (a) P³ always absent, chewing surface of molars is quadricuspidate..... **Iomys**
- (b) P³ usually present, chewing surface of molars is not quadricuspidate..... **5**
- 4) (a) posterior flexus distinct..... **6**
- (b) posterior flexus indistinct..... **7**
- 5) (a) metacone and metaloph completely absent on M³..... **8**
- (b) metacone and metaloph present or at least recognizable on M³..... **9**
- 6) (a) incisor grooved..... **Aeretes**
- (b) incisor ungrooved..... **Petaurista**
- 7) (a) auditory bulla septae complex, arachnoid (cobweb-like) ..
..... **Petinomys**[#]
- (b) auditory bulla septae < 4..... **10**
- 8) (a) ear tufts present, auditory bulla septae complex, honeycomb..... **Biswamoyopterus**
- (b) ear tufts absent, auditory bulla septae < 4..... **Aeromys**
- 9) (a) mesostyle absent, paraconule, metaconule indistinct...
..... **Eupetaurus**
- (b) mesostyle present, paraconule, metaconule distinct.... **11**
- 10) (a) mesolophule connects to the well-developed mesostyle to form a distinct “mesoloph”, four cusps can be seen from the buccal side of the upper cheekteeth..... **Hylopetes**^{*}
- (b) mesostyle and mesolophule absent or obsolete, three cusps can be seen from the buccal side of the upper cheekteeth..... **12**
- 11) (a) ear tufts absent, auditory bulla septae ca. 5.....
..... **Pteromyscus**
- (b) ear tufts present, auditory bulla septae complex, honeycomb..... **13**
- 12) (a) body size very small (<50 g), cheekteeth simplified, anteroloph, posteroloph and small cusps reduced.. **Petaurillus**
- (b) body size not very small (>50 g), cheekteeth normal, anteroloph, posteroloph and small cusps distinct..... **14**
- 13) (a) P⁴>>M¹..... **Trogopterus**
- (b) P⁴≥M¹..... **Belomys**
- 14) (a) auditory bulla large, postorbital process reduced.....
..... **Glaucmys**
- (b) auditory bulla normal or very small, postorbital process normal..... **15**
- 15) (a) auditory bulla normal, enamel smooth, paraconid of P₄ reduced, glans short, stout, and glove-like..... **Eoglaucmys**

(b) auditory bulla very small, enamel slightly pitted, paraconid of P₄ normal, glans slim and ultralong.....

..... **Priapomys gen. nov.**
*: *Hylopetes nigripes* (endemic to Palawan) and *Hylopetes bartelsi* (endemic to Java) lack the distinct mesoloph and mesostyle which most species of *Hylopetes* possess; #: The internal septae of the auditory bulla of *Petinomys setosus* is honeycomb.

NOMENCLATURAL ACTS REGISTRATION

The electronic version of this article in portable document format will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone (see Articles 8.5–8.6 of the Code). This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>.

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SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission for field surveys in Gongshan County was granted by the Gongshan Management Bureau of Gaoligongshan National Nature Reserve.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Q.L. designed the study, contributed to the collection and identification of the specimens, interpreted the data, and drafted the manuscript. F.C. performed the genetic analyses. S.M.J. revised the manuscript and provided the specimen photos from European museums. K.M.H. reviewed the taxonomic and morphological data and analysis and revised the manuscript. S.Y.L. supervised the study of penis morphology. F.L. provided extensive field observations and photographs. D.S. and S.L. provided important samples. W.Y.S. and H.J.W. input data and performed partial molecular experiments. Y.X. and J.S. organized the whole field expedition. X.L.J. supervised the whole process of the study. All authors read and approved the final version of the manuscript.

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