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Uncertainties in Systematics of Flying Squirrels (Pteromyini, Rodentia): Implications from a New Record from Vietnam

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Abstract: Taxonomic status of gliding squirrels belonging to the "northern" form of *Petinomys setosus* known from N. Burma and Thailand has been controversial. Earlier it was assigned to a distinct genus *Olisthomys*, however, currently it is synonymized with *P. setosus* s. str. from Sumatra and Borneo Islands, and Malay Peninsula. A squirrel collected in Song Hinh forest (Phu Yen Province, south central Vietnam) was examined genetically using sequence data on three mitochondrial genes (*cytb*, 12S, 16S) and one nuclear (IRBP) gene. The molecular results demonstrated that this squirrel is significantly divergent from the other examined specimens of *Petinomys* and belongs to a separate genetic lineage within the Glaucomyina clade. The obtained phylogenetic pattern supports recognition of *Olisthomys* as a valid genus; however, to confirm this conclusion a comprehensive taxonomic revision of *Petinomys* and related genera is required. The reconsideration of taxonomic position of the "northern" *P. setosus* also raises the question of the conservation status of this taxon.

Keywords: sciuridae; South-East Asia; *Petinomys*; *Olisthomys*

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1. Introduction

The complex history and multiplicity of habitats in tropical Asia ensures the existence of an extremely diverse mammalian fauna, which richness remains underestimated. Research carried out in the last decade in Indochina, and Vietnam in particular, regularly result in the discovery of species new to this region [1–3] or new to science [4–10], as well as a reassessment of the systematic position of already known taxa (e.g., [11]).

Despite the wide distribution and a large number of described taxa [12], flying squirrels (tribe Pteromyini) remain insufficiently studied. The reason for this is the secretive nocturnal lifestyle of these squirrels and the fact that many pteromyine species inhabit the relatively poorly studied areas of the tropical and subtropical forests of Southeast Asia. Recent descriptions of new species [13,14], new genera [15], and remote faunistic findings (e.g., [16]) definitely indicate that the taxonomy and distribution of the tribe require further study.

In Vietnam, about six or seven species of flying squirrels from three genera, namely *Petaurista*, *Hylopetes* and *Belomys* [12,17,18], are known, but there is a reason to expect the presence of unidentified or even undescribed taxa in the local fauna (e.g., [19]), especially in poorly studied mountain forests.

In the first half of 2021, a short-term small animal study was carried out within the framework of biodiversity survey organized by the Joint Vietnamese-Russian Tropical Research and Technological Centre in the Phu Yen Province, Vietnam. During this survey, one individual of a small flying squirrel was captured. The animal was identified in the

field by its size and fur coloration as *Petinomys setosus*, a species with a highly patchy distribution in Indonesia, Malaysia, Brunei, Thailand and Burma [12,20,21], and recently also reported for Laos [16]. The latter represents the only published species record east of Mekong. Vietnam is included on the map published by IUCN Red List, but not mentioned in the corresponding species account [22]. Thus, if the identification is confirmed, our finding will be the first documented record for Vietnam. However, taking into account some inconsistency of the published identification keys and the ambiguity of the existing diagnostic features [15,21,23,24], we considered it necessary to study morphology in more details, including cranial features, and analyze DNA sequences.

2. Materials and Methods

The small mammal survey was carried out in the Song Hinh forest (N 12.83° E 108.00°) situated in the foothills of a small mountain range in the south of the Phu Yen Province, along the right tributaries of the Hinh River (southern Central Vietnam). Despite close proximity to the relatively well-studied Khanh Hoa and Dak Lak provinces, Phu Yen is poorly studied in the context of mammals, and the published information on the fauna of Song Hinh is practically absent. Therefore, the survey was accompanied with the collection of voucher specimens, after the permission from The Department of Forestry, Ministry of Agriculture and Rural Development of Vietnam and from the Forest Protection Departments of the Peoples' Committee of Phu Yen Province, Vietnam (No 2190/UBND-KGVX). Animals were collected following methods approved in the Animal Care and Use Guidelines of the American Society of Mammalogists [25]. The flying squirrel (an adult male) was caught in the late evening of 12 June 2021, in a mist net set for catching bats at the edge of a disturbed primary forest, approximately 4 km from the reservoir on the river Hinh and 22 km to the south-east from the Hai Rieng town (elevation approx. 245 m above sea level). The animal was taken as a voucher (collection ID ZMMU S-207534; Zoological Museum of Moscow M.V. Lomonosov State University) and preserved as a dry skin, carcass in alcohol (70% ethanol) and cleaned skull. Tissue sample for DNA extraction containing small pieces of skeletal muscles was preserved in 96% ethanol.

For further size comparison, standard external measurements were taken in the field with the help of mechanical calipers to the nearest 0.1 mm. Twenty-four cranial measurements employed previously by [16,26] were taken with digital calipers under the laboratory binocular to the nearest 0.01 mm.

Available specimens of flying squirrels from genera *Pteromys*, *Petaurista*, *Glaucomys*, *Belomys*, *Pteromyscus*, *Euglaucomys*, *Petinomys* and *Hylopetes*, stored in collections of the Zoological Museum of Moscow M.V. Lomonosov State University (ZMMU) and Zoological Institute of Russian Academy of Sciences (ZIN), were used for morphological comparison, together with published data on tropical pteromyine species and photographs of the syntype of *Petinomys setosus* from the Naturalis Biodiversity Center, the Netherlands (RMNH.MAM.13316) (see List S1).

Molecular Studies

Total DNA was extracted from ethanol-fixed muscle using the MiniElute PCR Purification Kit (QIAGEN) including an overnight lysis step at 50 °C following the manufacturer's protocol and recommendations of [27].

We sequenced the complete mitochondrial cytochrome b (*cytb*) gene (1140 bp), fragments of the 12S and 16S mitochondrial genes (822 and 537 bp, respectively), and partial exon of the IRBP nuclear gene (1023 bp). The choice of the markers was motivated by the availability of the comparative data in GenBank.

The primers used for amplification and sequencing are presented in Table 1. All genes were amplified and sequenced using external forward/reverse primer combinations in the double-stranded polymerase chain reaction (PCR) entailed 36 thermal cycles as follows: 30 s denaturation at 94 °C, 1 min annealing at 55 °C (*cytb*) or 62 °C (12S, 16S and IRBP), 1 min extension at 72 °C and a final extension at 72 °C for 6 min. PCR products

were visualized on 1% agarose gel and then purified using Diatom DNA Clean-Up kit (Isogen). Approximately 30 ng of the purified PCR product was used for sequencing with each primer by autosequencing system ABI 3100-Avant using ABI PRISM®BigDyeTM Terminator v. 3.1.

Table 1. The primers used for amplification and sequencing of the analyzed markers.

Primers	Sequence (5′→3′)	Reference
IRBP—interphotoreceptor retinoid-binding protein, exon		
F31a	AGCCATYGAGCAGGCCATGAAGAGT	This study
R1135b	RGC AGCCTCATCCTTGGGYATCTCAG	This study
Cytb*—cytochrome *b		
L7-fw	ACCAATGACATGAAAAATCATCGTT	Montgelard et al., 2002
H6-rev	TCTCCATTTCTGGTTTACAAGAC	Montgelard et al., 2002
***12S* ribosomal RNA**		
12S_L17b	GCAAAGCRCTGAAAATGCTTAGATGAGT	This study
12S_H906a	GGCGGTGTGTGCGTGCTTTATTG	This study
***16S* ribosomal RNA**		
16S_L1930	CCGCCTGTTTACCAAAAACATCACCTCT	This study
16S_H2496	CCGGTCTGAACTCAGATCACGTAGGAC	This study

The sequences were deposited in GenBank at the following accession numbers: *cytb*—OL954524, 12S—OL954526, 16S—OL954525 and IRBP—OL954527.

The numbers of sequences downloaded from GenBank for *cytb*, 12S, 16S, and IRBP were 49, 30, 29, and 20, respectively (Table 2). Sequences of *cytb* and IRBP were aligned by eye in BioEdit version 7.0.9.0 (Bioedit Company, Manchester, UK) [28], sequences of 12S and 16S were aligned with the use of ClustalW accessory application incorporated in BioEdit. Hypervariable loop regions in 12S/16S that cannot be reliably aligned between genera were excluded from the subsequent analyses. The sequences of the two rRNA genes were obtained from the same sample of specimens; therefore, the two alignments were combined for tree reconstructions.

The Maximum Likelihood trees for the three datasets (*cytb*, IRBP, 12S/16S) were reconstructed in IQTREE ver. 1.6 (http://www.iqtree.org/, accessed on 13 June 2022) [29]. In order to determine the optimum partitioning scheme for the protein coding genes and to identify best-fit substitution models for each subset, the ModelFinder routine [30] was used with the Bayesian information criterion (BIC). Clade support was estimated using Ultrafast Bootstrap [31] with 10,000 replicates. Trees were rooted at the branch separating subtribes Pteromyina and Glaucomyina, which were supported as monophyletic by previous molecular studies [32,33]. We also reconstructed the ML tree based on the concatenation of the three datasets. In this analysis, the taxonomic set was reduced by omitting species represented in less than two datasets. Estimations of the genetic *p*-distances were performed in PAUP 4.0b10 [34].

Table 2. Accession numbers of the GenBank sequences analyzed in the current study.

	Cytb	12S	16S	IRBP
Aeretes melanopterus		AY227535	AY227481	AY227593
Aeromys tephromelas		AY227536	AY227482	AY227594
Belomys pearsonii	AB126245 LC006019	AY227537	AY227483	AY227595
Biswamoyopterus biswasi	MK105508 MK105509	MK105526 MK105527	MK105519 MK105520	MK105534 MK105535
Eoglaucomys fimbriatus	AB126246 AB126248	AY227562	AY227485	AY227597
Eupetaurus cinereus		AY227538	AY227484	AY227596
Glaucomys sabrinus	AF359223			
Glaucomys volans	AJ389531	AY227559 MT259089	AY227486 MT259089	AY227598
Hylopetes alboniger	DQ093187 KX710106	KX710106	KX710106	
Hylopetes lepidus	AB126250 AB126251 DQ093188			
Hylopetes nigripes	DQ093190			
Hylopetes phayrei	AB126252 KC447305 KP708707	AY227539 KC447305 KP708707	AY227487 KC447305 KP708707	AY227599
Hylopetes spadiceus	DQ093189			
Iomys horsfieldi		AY227540	AY227488	AY227600
Petaurillus kinlochii		AY227542	AY227490	AY227602
Petaurista albiventer	DQ072109 AB092612			
Petaurista alborufus	AB092613 AB092614	JQ743657	JQ743657	AY227601
Petaurista elegans	JQ928698 MK105516 MK105518			MK105539
Petaurista hainana	DQ072108	JX572159	JX572159	
Petaurista lena	AB092615	AY227541	AY227489	
Petaurista leucogenys	AB092616 AB092617 AB092618 AB092619 AB433219 AB433269			
Petaurista petaurista	AB092608 AB092609 AB092611			
Petaurista philippensis	MK105510 MK105515	MK105528 MK105531 MK105532	MK105521 MK105522 MK105523	MK105536 MK105537 MK105538
Petaurista xanthotis	DQ072111			
Petaurista yunanensis	DQ072110 JQ928701 JQ928702	KX528208	KX528208	
Petinomys fuscocapillus	KP973562	KP973561		
Petinomys setosus	AB030260	AY227544	AY227492	AY227604
Pteromys momonga	AB164675 AB164676			
Pteromys volans	EU919142 KR063240 KR063244	AY227545 JQ230001 MH212330 MT430951	AY227493 JQ230001 MH212330 MT430951	AY227605
Pteromyscus pulverulentus		AY227543	AY227491	AY227603
Trogopterus xanthipes		AY227546	AY227494	AY227606

3. Results

3.1. Morphological Comparison

The specimen ZMMU S-207534 from Song Hinh was preliminary identified as *Petinomys setosus* because it fits generally the species diagnosis [20] and, in particular, because it is highly similar to the specimen from Laos, referred to as *P. setosus* [16]. Its external measurements are as follows: head and body 115 mm, tail length 109 mm, ear length 18.1 mm, hind foot (without claws) 26.7 mm, body mass 47 g. This fell within the size variation of *P. setosus* (102–140, 80–136, 14–19, and 18–28 mm, and 29–58 g, respectively: [16,35]; see full list of used measurements and their values for the specimen S-207534 in List S2, Table S1). In head and body size our specimen is quite small within the species size variation, while its hind foot is proportionally large (larger than in "southern" specimens and better fits those captured north from Isthmus of Kra). Fur on the upper side is blackish, strongly tipped with pale buff on head, neck and rump, and whitish-buff on back (Figure 1). Ventral pelage is whitish, with definite yellowish tinges, especially well seen on throat, chest, lower belly, and lower sides of fore limbs. Cheeks are white with yellowish wash. Hairs on

undersides of flying membranes are with gray bases. Yellowish-white coloration protruded upward on the sides on neck, forming half-collar. Eyes are surrounded with blackish rings (or periocular spots) which continue forward into blackish stripes between eye and nose. There are small pale patches on the sides of the nose above these stripes. White ventral fur is protruded behind the edge of the flying membrane, forming narrow white stripe if looking from above. Tail is flat, blackish-grey, with pale zone at base and pure white tip. Ears are with grey tips and margins and not pigmented bases. Ear margins are hairless, but there are long black bristles near the ear bases, in front and behind ear openings, forming something like sparse tufts. On the whole, coloration of our specimen well fits that of northern population of *P. setosus* as described in [36]. Laotian specimen differs only in more brownish hair tips on back, less pronounced yellow tinges on chest and better developed white zone at tail base [16].

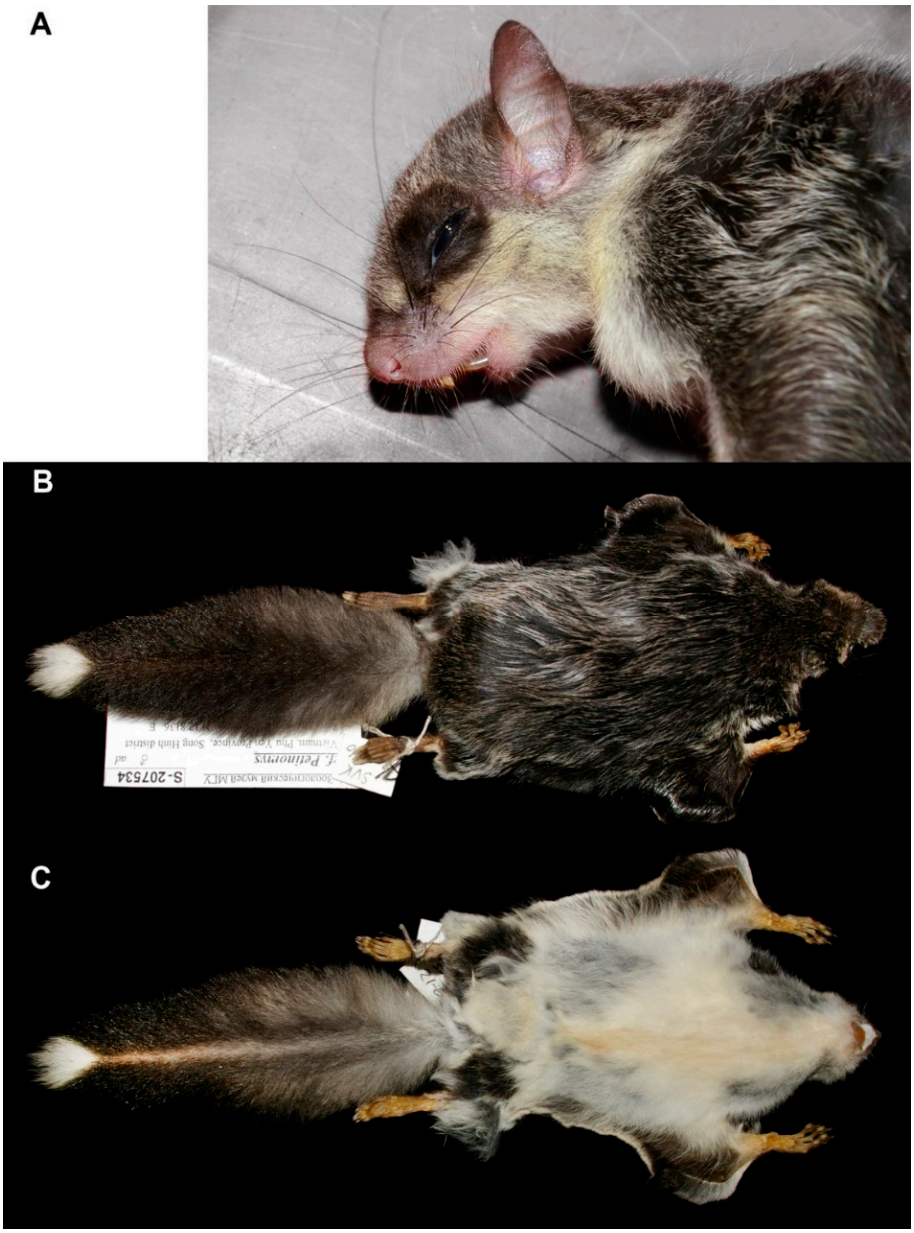

Figure 1. External appearance of the specimen ZMMU S-207534 from Phu Yen Province: head, showing characteristic fur coloration and ear shape (**A**) and the study skin from above (**B**) and below (**C**).

In cranial measurements, the specimen ZMMU S-207534 (TL = 31.7 mm, P3 − M3 = 5.66 mm) is smaller than all flying squirrels known for Vietnam, and more or less resembles *Petinomys setosus*, *P. vordermanni* and *Hylopetes lepidus* [24]. Skull has proportionally short rostrum and wide and high braincase. Frontal region in lateral view is almost straight, without any concavity (Figure 2). Eye sockets are large. Postorbital processes are thin and delicate, curved backward; postorbital width is distinctly wider than the interorbital constriction. Auditory bullae are large (especially in ventral view), but not remarkably inflated. Mastoid part of temporal region is not inflated. In auditory bulla, six septa could be seen: two larger in anterior third and in the middle of the bulla and four smaller in the bulla's posterior third. Noteworthy, that the bulla walls are thick enough to obscure the position of septa in ordinary light. Position of septa could be seen through the auditory opening with the use of binocular microscope, or into the light through, with intense illumination also through the auditory opening (as is done by [15]). Posterior edge of the bony palate protruded on 1.2 mm beyond posterior teeth and the anterior border of the mesopterygoid fossa has a small medial process. On the mandible, coronoid process is thin, slightly higher than the articular process. Angular process is large, wide, somewhat rectangular in shape (as in *Iomys* and *Petinomys*). The teeth are relatively simple (Figure 3). Only the enamel ridges on P4 are somewhat scalloped; the ridges on the molars are almost straight. There are no additional enamel folds. There is a small but distinct mesostyle on M1-2. P3 is small, slightly larger than the P4 parastyle, lingually displaced. On the lower molars, the protoconid, metaconid, and hypoconid are well developed, the mesoconid is very poorly developed, and the central flexid is very thin, but clearly visible at least on m1-2. Most of the chewing surface of the lower molars represents a cup-like concavity without any folds. In general, the teeth structure is most similar to that of *Glaucomys*. Judging by the wear of the metacone, protoconid, and hypoconid, the animal was adult.

Compared with the syntype of *P. setosus* the specimen ZMMU S-207534, besides some difference in coloration (which could be attributed to geographic variation or discoloration of the stuffed skin), differs significantly in several cranial features. In particular.

- the nasofrontal suture is W-shaped (Figure 4) in the type of *P. setosus* while being nearly transverse (or slightly M-shaped) in the Song Hinh specimen.
- the coronal suture is markedly V-shaped in the type of *P. setosus* but is transverse in the Song Hinh specimen.
- in the type of *P. setosus* the number of visible septa in bulla tympani is five, however the position of septae is different from the Song Hinh specimen with the second septa placed more anteriorly in the former; additionally, bullae appear more inflated in the Song Hinh specimen.
- the ratio of interorbital width to postorbital width is 0.77 (6.9/8.9 mm) in the type of *P. setosus* compared to 0.64 (7.0/11.0 mm) in the Song Hinh specimen (this ratio is 0.61/0.69 in *P. setosus* specimens studied by [35]).
- the rostrum is relatively wider in the type of *P. setosus*, with the maximum width of nasals reaching 5.0 mm (versus 4.59 mm in the Song Hinh specimen); the ratio of nasal length to nasal width in the type is 1.25, which is smaller than in the Song Hinh specimen (1.51) or in the sample examined by [16] (1.58–1.73) It should be noted that, in the Laotian specimen [16], the shape of sutures and cranial proportions are similar to those in the Song Hinh specimen. Meantime, it is worth mentioning that the auditory bullae septa pattern in Laotian specimen was reported as a "honeycomb", which contradicts both our specimen and the characteristics of *Petinomys setosus* as a whole (see [23,24,35]). We only may suggest that the "honeycombs" observed in the Laotian animal represents some artifact of the bullae wall and do not reflect the actual number of septa.

Figure 2. Upper, lower and lateral view of the skull and mandible of the specimen ZMMU S-207534 from Phu Yen Province. Scale bar 5 mm.

Figure 3. Right upper (to the left) and left lower (to the right) tooth rows of the specimen S-207534 from Phu Yen Province. Scale bar 2 mm.

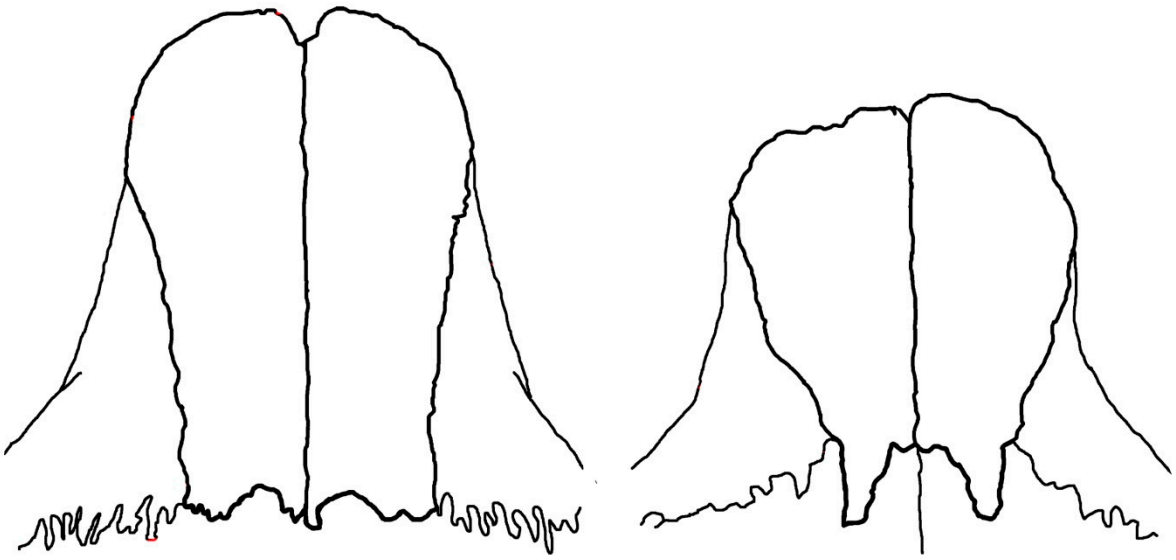

Figure 4. The schematic drawings of the rostra (viewed from above), showing shape of the nasofrontal suture in the specimen S-207534 (to the **left**) and the syntype of *Petinomys setosus* (to the **right**).

3.2. Molecular Phylogeny

In the mitochondrial *cytb* gene tree the sequence of the Song Hinh specimen is placed as the sister group to a clade containing all available *Hylopetes* and *Petinomys* sequences and, thus, it does not form a monophyletic group with GenBank sequences of *Petinomys setosus* and *Petinomys fuscocapillus* (Figure 5). Its mean distance from *Hylopetes* + *Petinomys* is 16.3% and from the other *Petinomys* specimens—15.0 and 16.4%, which corresponds to the generic level of difference (e.g., 16.6% between *Eupetaurus* and *Biswamoyopterus*). The distance between the GenBank sequences of *Petinomys setosus* and *Petinomys fuscocapillus* is 5.2%. It is necessary to mention that in this phylogenetic reconstruction *Hylopetes* is paraphyletic against *Petinomys* as the latter genus groups with *H. alboniger* and *H. phayeri* to the exclusion of *H. spadiceus* + *H. lepidus* and *H. nigripes*.

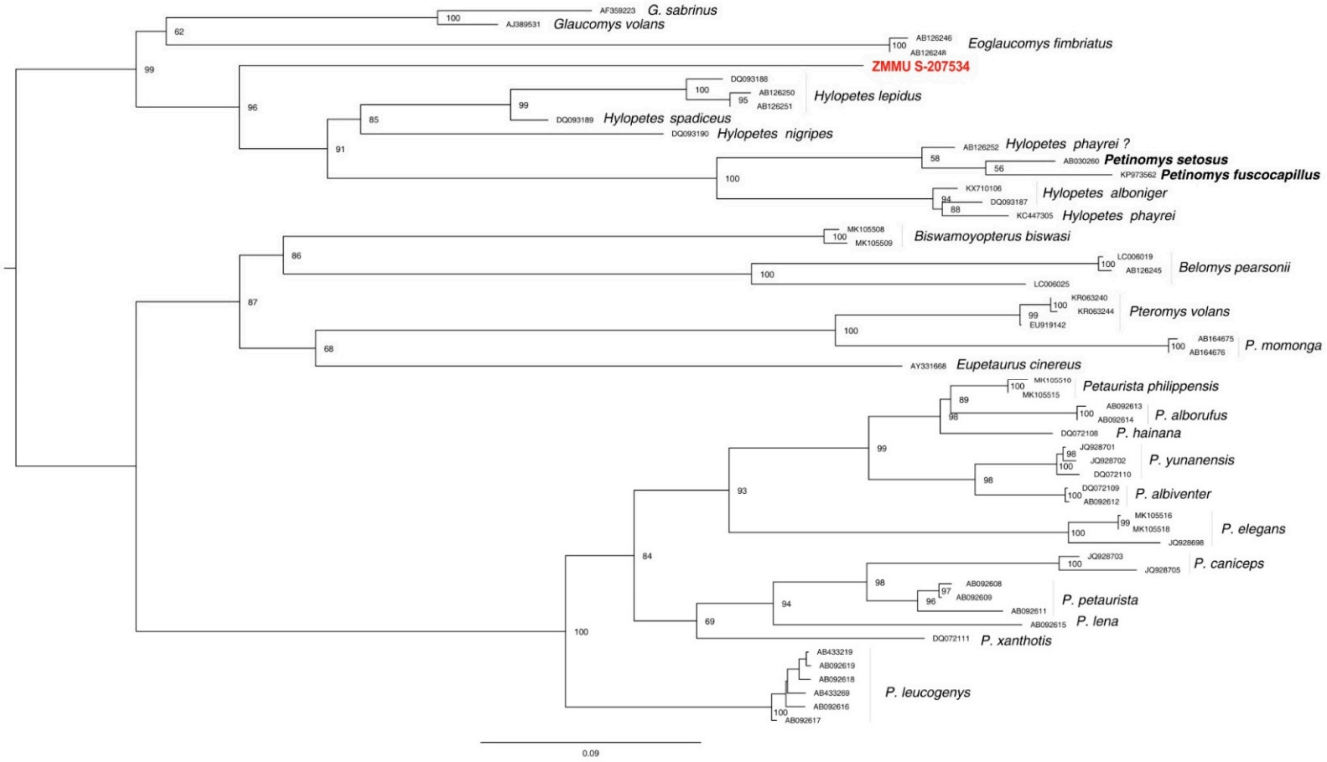

Figure 5. Phylogenetic ML tree for the Pteromyini tribe reconstructed from alignment of the mitochondrial gene *cytb*. Numbers on tree nodes indicate bootstrap values.

In the 12S/16S tree (Figure 6), the specimen ZMMU S-207534 is placed as the sister group to *Petinomys setosus* + *Petinomys fuscocapillus*, however, the distance between these two lineages is relatively high (5.0%) being comparable to distances between *Pteromyscus* and *Belomys* + *Trogopterus* (5.0%) or between *Glaucomys* and *Eoglaucomys* (4.3%). The distance between *Petinomys setosus* and *Petinomys fuscocapillus* is 1.7%. In contrast to the *cytb* tree, *Hylopetes* represented by *H. alboniger* and *H. phayeri* clustered not with *Petinomys* but with *Petaurillus*.

In the phylogenetic tree reconstructed from the nuclear IRBP gene (Figure 7), the specimen ZMMU S-207534 takes a sister position to the *Petinomys setosus* from Malaysia (which is the same specimen as in the 12S/16S dataset). The distance between these two sequences is 1.56%, which is, again, similar to the distances between each two of the recognized genera *Belomys*, *Pteromyscus* and *Trogopterus* + *Aeretes* (1.35–1.45%) or between *Biswamoyopterus* and *Aeromys* (1.54%).

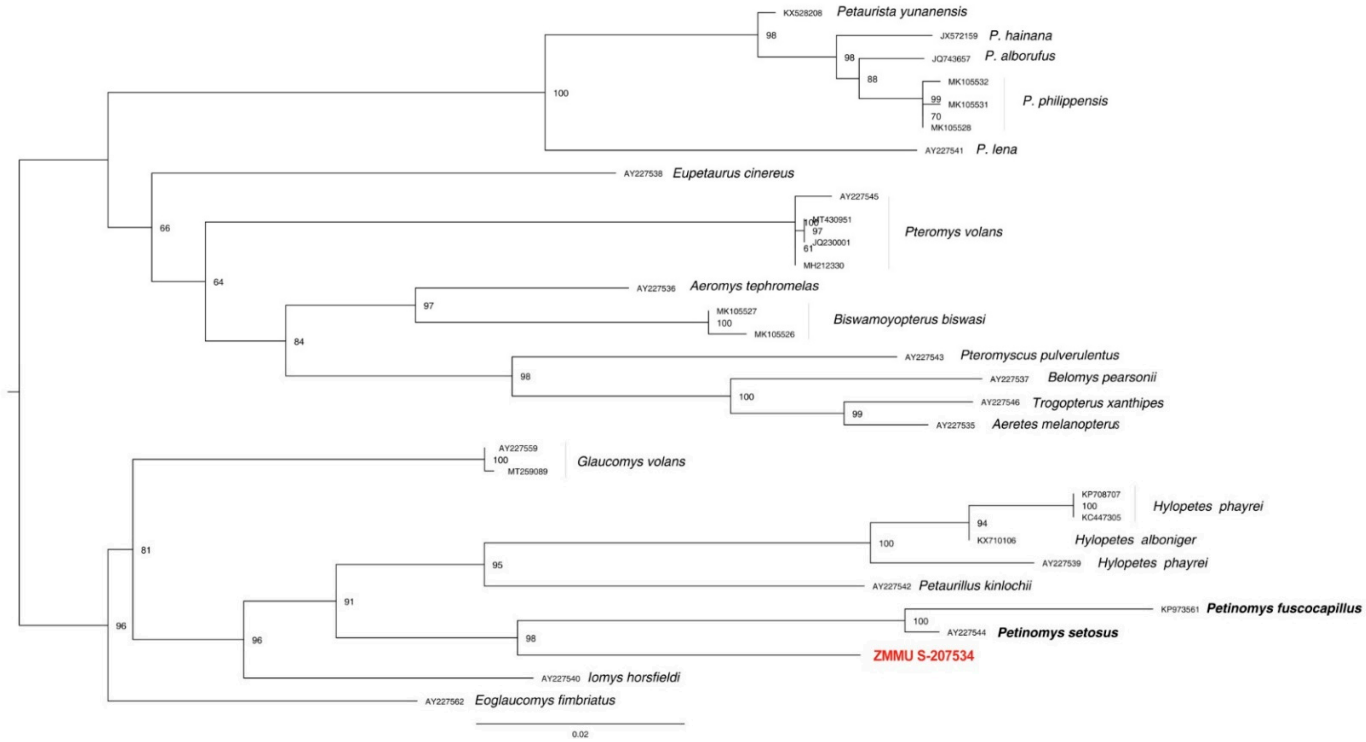

Figure 6. Phylogenetic ML tree for the Pteromyini tribe reconstructed from alignment of the 12S/16S mitochondrial genes. Numbers on tree nodes indicate bootstrap values.

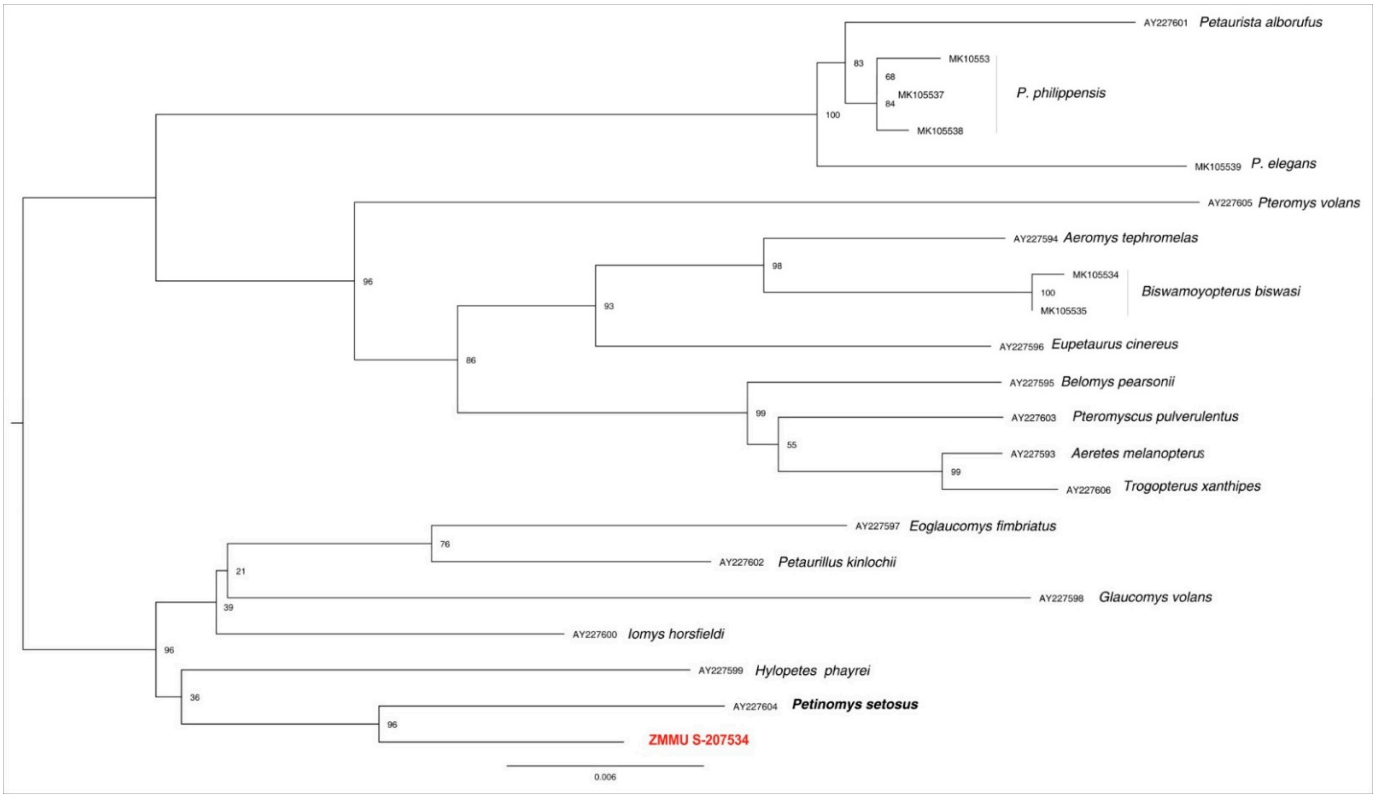

Figure 7. Phylogenetic ML tree for the Pteromyini tribe reconstructed from alignment of the nuclear gene IRBP. Numbers on tree nodes indicate bootstrap values.

In the concatenated tree, the specimen ZMMU S-207534 was placed as the sister group to the *Hylopetes* + *Petinomys* clade; however, the support for this branching pattern was low (Figure S1).

4. Discussion

The specimen ZMMU S-207534 from the Phu Yen Province clearly belongs to a species of flying squirrel that is not previously recorded in Vietnam. However, its generic and specific determination is controversial, due to the lack of an up-to-date revision of the genus *Petionomys* as well of other genera of SE Asian Pteromyini.

Relatively complicated structure of the auditory bullae excludes belonging of the specimen ZMMU S-207534 to the genus *Hylopetes* (which members have more simple bullae). Morphologically, this animal fits well in the description of the so called "northern" *Petinomys setosus*, which is known from N. Burma, N. Thailand [35,36] and likely from Laos [16]. Externally, this form differs from the "southern" *P. setosus* by larger size and details of the coloration (e.g., white-tipped tail). Following the revision by [35] "southern" populations distributed in peninsular Malaysia south of Kra and N. Borneo are attributed to the nominotypical subspecies (type locality in N. Sumatra), while the "northern" Temminck's flying squirrel is treated as a subspecies *Petinomys setosus morrisi* (Carter, 1942) (terra typica in N. Burma, [37]).

However, the specimen ZMMU S-207534 is well divergent from the two species of *Petinomys* (*fuscocapillis* and *setosus*) in all genes examined and does not form a clade with the *Petinomys* species in the *cytb* tree. It is also distant genetically from all other known flying squirrels. At the same time, the monophyly of *Petinomys* including the specimen ZMMU S-207534 is not rejected by the IRBP tree. Unfortunately, the morphological material for the two specimens of *P. setosus* examined in previous genetic studies is unavailable to us; one of these specimens (for which the IRBP, 12S and 16S sequences were produced) was collected in Malaysia (C. Francis, pers. com.) i.e., within the range of the "southern" *P. setosus*, while the origin of the second specimen (with known *cytb*) is obscure (see [38,39]). However, since in all trees the two *Petinomys* species are clustering together, this therefore suggests that at the generic level they were identified correctly. If so, it appears likely that gliding squirrels known as "northern *setosus*" do not belong to the genus *Petinomys*. Obviously, this preliminary conclusion should be validated based on genetic data for the type species of *Petinomys* (*P. lugens*), which is currently unavailable.

This hypothesis resonates with the fact that, at times, *morrisi* (="northern *setosus*") was considered a member of distinct genus or subgenus. Describing *morrisi* as a new species, Carter [37] placed it into the new taxon *Olisthomys*, which he regarded as a subgenus of *Pteromys*, "most closely related to *Hylopetes* but without any sculpturing on the teeth and with the low spreading bullae of *Petinomys*". Subsequently, Ellerman and Morrison-Scott [40] synonymized *Olisthomys* with *Petinomys* (now recognized as a genus) but at the same retained *P. morrisi* as a full species separate from *P. setosus*. In contrast to that, McKenna [41] clearly separated *Olisthomys* from *Petinomys* placing the former into the *Glaucomys* group, which was erected based on a simple molar pattern with little or no crenulation and lack of mesoloph as opposed to highly crenulated molar crowns with distinct mesoloph in the *Petinomys* group. Another important distinguishing feature is the internal structure of bullae, which have multiple complex honeycomb/cobweb septa in *Petinomys* but only about six simple septa in *Olisthomys*. The latter condition can be viewed as intermediate between those of true *Petinomys* and *Hylopetes* (as illustrated in [15]: Figure S1). However, despite all the differences [42] and subsequently [36,43] preferred not to retain *Olisthomys* as a valid genus subsuming it into *Petinomys*. Here, we suggest that, given the genetic evidence, the status of *Olisthomys* should be reconsidered as it is likely the proper name for the newly discovered genus-level genetic lineage.

Another issue is the relationship of "northern *setosus*" with *P. setosus* proper. According to the revision by [35] the "northern" and "southern" forms appear to be similar in respect to their bullae and dental morphology, however, this account was not supported by a

statistical analysis of cranial traits and, thus, their conclusion of conspecificity is largely based on details of coloration. The type specimen of *P. setosus*, like *Olisthomys*, was found to have just few septa in its bullae, which highlights the fact that *P. setosus* is different from other *Petinomys*. However, other details such as suture shape, position of septa and cranial proportions indicate that the type of *P. setosus* and the Vietnamese specimen can hardly belong to the same species. Considering possible explanations for the observed evidence two major hypotheses should be discussed. First, it may be supposed that the two taxa are just superficially similar, true *Petinomys setosus* is phylogenetically distant from "northern *setosus*", so their bullar similarity is a plesiomorphy or a result of convergence. Alternatively, the two forms are in fact related and should be regarded as members of the same genus *Olisthomys*, which, however, means that both specimens of *P. setosus* with sequences in Genbank were misidentified and must represent some other small size species of *Petinomys*. In the latter scenario, the species status of "northern" and "southern" forms still remains a plausible option. Therefore, in both cases, *Olisthomys* should be resurrected as a valid name, and *O. morrisi* could be implied as a proper name for the species under discussion.

The current conservation status of "*Petinomys setosus*" is assessed as "Vulnerable" due to a suspected population decline, likely as a result of rapid habitat loss [22]. However, considering that the northern form likely belongs to a separate species, its status warrants re-assessment; one can reasonably expect that it will be included into one of the threatened categories.

In addition, it should be noted that the phylogenetic pattern generated from molecular data conflicts with the monophyly of *Hylopetes* indicating closer relationships between *Petinomys* and *H. phayeri*/*H. alboniger* clade. At this stage, it is impossible to check whether the position of *H. alboniger* and *H. phayeri* is an artifact of the *cytb* gene, since for most other genes there is no representative sample for this genus. In a recent work [15] the rank of the taxon *leonardi* was raised to an independent genus (as *Priapomys leonardi*), while this form was previously considered a subspecies of *H. alboniger* [43], even not a species. However, the type species of *Hylopetes* (*H. spadiceus*) was not included in the latter study. Anyway, it is evident that the taxonomy of both *Hylopetes* and *Petinomys* requires thorough revision.

5. Conclusions

Our genetic data suggest that "northern" *Petinomys setosus* is, in fact, a separate taxon that is well divergent from other studied representatives of *Petinomys*. This result is consistent with the view of McKenna [41] who argued that the "northern" *setosus* should be assigned to a separate genus *Olisthomys* (Carter, 1942). Additional molecular studies are needed to confirm the validity of this genus and to clarify its taxonomic content, as well as taxonomic boundaries of some other flying squirrel genera like *Hylopetes*.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14080610/s1, List S1: List of Pteromyini specimens used for the qualitative morphological comparison, List S2: List of the external and cranial measurements used in the study, Table S1: Selected external and cranial measurements of the specimen S-207534 compared with Petinomys setosus (after [16]), Figure S1: Phylogenetic ML tree for the Pteromyini tribe reconstructed from alignment of the concatenated *cytb*, 12S, 16S and NADH genes. Numbers on tree nodes indicate bootstrap values.

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