

The first record of *Episoriculus umbrinus* from Vietnam, with notes on the taxonomic composition of *Episoriculus* (Mammalia, Soricidae)

Alexei V. Abramov*, Anna A. Bannikova, Daria M. Chernetskaya, Vladimir S. Lebedev, Viatcheslav V. Rozhnov

ABSTRACT. The mitochondrial cytochrome *b* and nuclear *ApoB* and *RAG2* genes were used to estimate the phylogenetic relationships in Asiatic red-toothed shrews (Soricidae, *Episoriculus*). Based on molecular data, the genus *Episoriculus* seems to consist of at least seven valid species: *E. baileyi*, *E. caudatus*, *E. leucops*, *E. macrurus*, *E. sacratus*, *E. soluensis*, and *E. umbrinus*. Genetic distances among all of them are found to be of 8–16%, with the only low distance (3.4%) being that between *E. baileyi* and *E. leucops*. Taiwanese shrew *E. fumidus* shows high genetic divergence (16–17% for *cytb*) from other species of *Episoriculus*. Based on both genetic and morphological data it should be attributed to a separate new genus *Pseudosoriculus* **gen.n.** *Episoriculus umbrinus* was found in Lao Cai Province, representing a new species record for the fauna of Vietnam; morphology-based diagnosis of this specimen has reliably been confirmed by molecular data.

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Первая находка *Episoriculus umbrinus* во Вьетнаме, с заметками по таксономическому составу *Episoriculus* (Mammalia, Soricidae)

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РЕЗЮМЕ. Митохондриальный (cytochrome *b*) и ядерные (*ApoB* и *RAG2*) маркеры были использованы для оценки филогенетических связей в группе восточно-азиатских бурозубок (Soricidae, *Episoriculus*). По молекулярным данным, род *Episoriculus* включает не менее семи валидных видов: *E. baileyi*, *E. caudatus*, *E. leucops*, *E. macrurus*, *E. sacratus*, *E. soluensis* и *E. umbrinus*. Генетические дистанции между ними составляют 8–16%, за исключением *E. baileyi* и *E. leucops*, дистанция между которыми всего 3.4%. Тайваньская бурозубка *E. fumidus* значительно отличается от остальных видов *Episoriculus* (генетическая дивергенцию по *cytb* 16–17%). На основании генетических и морфологических данных она выделена в отдельный новый род *Pseudosoriculus* **gen.n.** *Episoriculus umbrinus* был обнаружен в провинции Лао Кай и является новым видом для фауны Вьетнама; прежняя морфологическая идентификация этого экземпляра достоверно подтверждена молекулярными данными.

КЛЮЧЕВЫЕ СЛОВА: *Episoriculus umbrinus*, Вьетнам, распространение, таксономия, *Pseudosoriculus* gen.n.

* Corresponding author

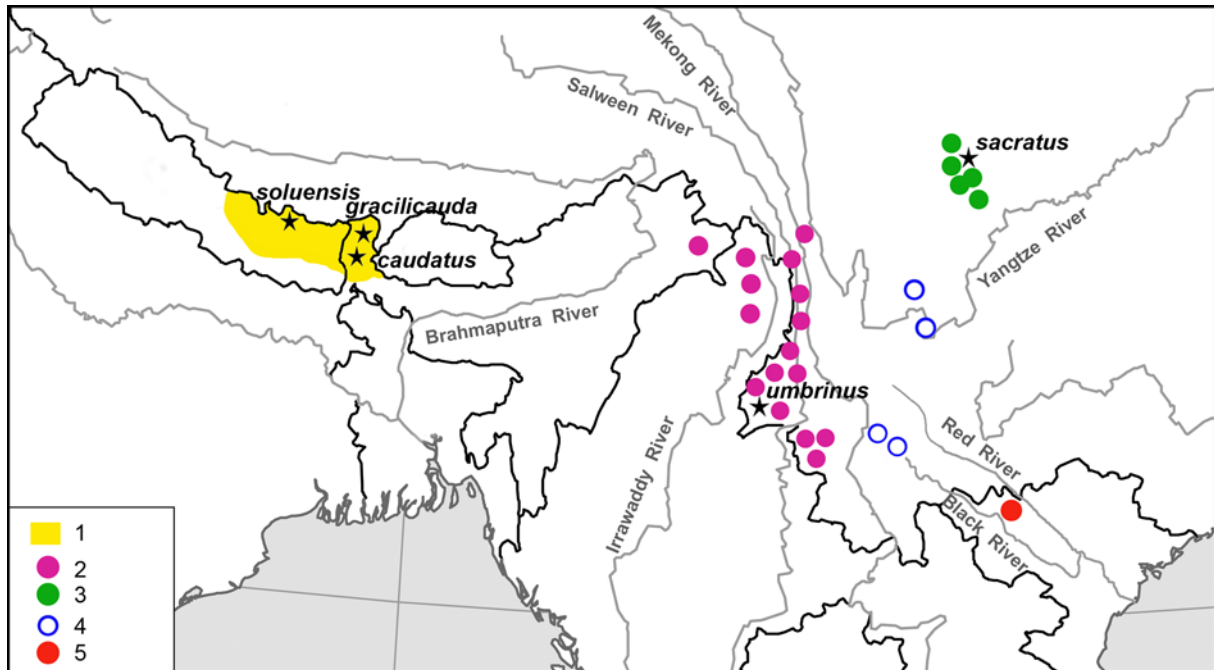


Figure 1. Distribution of *Episoriculus caudatus* s. lato: 1 — *E. caudatus* and *E. soluensis*; 2 — *E. umbrinus*; 3 — *E. sacratus*; 4 — records of “*E. caudatus*” after Hoffmann & Lunde (2008); 5 — specimen ZIN 96263, northern Vietnam. The type localities are indicated as asterisks.

Introduction

Asian red-toothed shrews of the *Soriculus* group are among of the poorly studied taxa of the tribe Nectogalini Anderson, 1879 (Lipotylphla, Soricidae). Shrews of this group are widely distributed in Asia — from northern China, southward to northern Vietnam and Myanmar, and from Kashmir to Taiwan (Hoffmann, 1986). Earlier, *Soriculus* Blyth, 1854 was treated in a broad sense and also included *Episoriculus* Ellerman et Morrison-Scott, 1966 and *Chodsigoa* Kastchenko, 1907 as the subgenera/synonyms (Hoffmann, 1986; Corbet & Hill, 1992; Motokawa & Lin, 2005). Only recently these taxa were given a full generic rank (Hutterer, 2005; Motokawa *et al.*, 2008, 2009; He *et al.*, 2010). The distinctions between these genera involve differences in the shape of articular facets of the mandible, the amount of brownish dental pigmentation, the number of upper unicuspid teeth, and the relative proportions of teeth, forefeet and tail (see Hoffmann, 1986). Phylogenetic relationships between genera of the *Soriculus* s. lato, as inferred by previous genetic studies, remain somewhat ambiguous, and the genus *Episoriculus* was found to be polyphyletic (Ohdachi *et al.*, 2006; Dubey *et al.*, 2007; He *et al.*, 2010). *Soriculus* consists of one species, *S. nigrescens* (Gray, 1842), whereas the taxonomic content of *Episoriculus* and *Chodsigoa* vary in different checklists. According to Hutterer (2005), there are eight species in *Chodsigoa* and four in *Episoriculus*.

Based on the review by Hoffmann (1986), four species are recognized in *Episoriculus*: *E. caudatus* (Horsfield, 1851) distributed from Kashmir to northern

Myanmar and south-western China; *E. leucops* (Horsfield, 1855) distributed from central Nepal, Sikkim and Assam to southern China, northern Myanmar and northern Vietnam; *E. macrurus* (Blanford, 1888) distributed from central Nepal to western and southern China and to northern Myanmar and Vietnam; *E. fumidus* (Thomas, 1913) endemic to Taiwan. *Episoriculus caudatus* includes three subspecies (*caudatus*, *sacratus* and *umbrinus*) and *E. leucops* includes two subspecies (*leucops* and *baileyi*) (see Hoffmann, 1986; Hutterer, 2005).

Based on external and cranial characters, Motokawa & Lin (2005) considered *Episoriculus baileyi* (Thomas, 1914) as a valid species. According to their data, *E. baileyi* is known from Sikkim and Assam in India, Myanmar and Vietnam, whereas *E. leucops* is restricted to Nepal. Further karyological studies revealed large differences in the karyotypes of *E. caudatus* s. lato (Motokawa *et al.*, 2008, 2009). Shrews from Sichuan Province of China with $2n=58$, $FN=108$ were treated as a distinct species *E. sacratus* (Thomas, 1911), the smaller form from Nepal with $2n=74$, $FN=126$ — as *E. soluensis* Gruber, 1969 and the large form from Nepal with $2n=60$, $FN=118$ — as *E. caudatus*. The fourth taxon, *E. umbrinus* (Allen, 1923), has not been karyotyped yet, but it differs from others in its skull measurements (Motokawa & Lin, 2005; see also Motokawa *et al.*, 2009). According to Motokawa *et al.* (2009), *E. sacratus* occurs in Sichuan Province of China; *E. umbrinus* is distributed in Assam, Myanmar, and Yunnan Province of China; *E. soluensis* occurs in Nepal and Sikkim, and *E. caudatus* is known from Nepal only (Fig. 1).

According to all recent reviews (Hoffmann, 1986; Corbet & Hill, 1992; Hutterer, 2005; Motokawa & Lin, 2005; Motokawa *et al.*, 2009), there are no shrews of the *E. caudatus* s. lato in Vietnam. However, in 2005, a specimen of red-toothed shrew, which undoubtedly belongs to this group, was collected from northern Vietnam (see Abramov *et al.*, 2013).

Recent genetic studies (Ohdachi *et al.*, 2006; Dubey *et al.*, 2007; He *et al.*, 2010) produced a multitude of *cytb* sequences of the *Soriculus/Episoriculus* in GenBank. However, it is not uncommon that sequences submitted to GenBank are assigned to species names without proper taxonomic verification. GenBank data is known to be error-ridden (Harris, 2003) and often lacks reference to the actual specimens examined (Ruedas *et al.*, 2000), thus rendering molecular diagnostics unreliable. This disturbing trend was first noted 10 years ago and colloquially referred to as the “taxonomic impediment” (Carvalho *et al.*, 2007). Quite often, the situation can be clarified only with the help of information on geographic origin of the specimen.

In this paper we try to use all the available data on distribution of the examined taxa of *Episoriculus* with the aim to evaluate the taxonomic position of the Vietnamese specimen, to elucidate the taxonomic affiliation of the sequences from GenBank, and to examine the phylogenetic relationships and taxonomic composition of the genus, focusing on the *E. caudatus* s. lato.

Material and methods

The specimen of *Episoriculus* cf. *caudatus* was collected in northern Vietnam, Lao Cai Province, near Tram Ton Station of Hoang Lien National Park, c. 6 km W of Sa Pa Town (22°21'N, 103°46'E) in December 2005. The collecting locality is shown in Fig. 1. This specimen (ZIN 96263) is deposited in the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia. Other original material includes two specimens of *Chodsigoa* spp. and three specimens of genus *Neomys* Kaup, 1829.

A total of 65 sequences of *cytb*, 41 sequences of *ApoB* and 40 sequences of *RAG2*, which are available from GenBank and attributed to several sources published earlier (Ohdachi *et al.*, 2006; He *et al.*, 2010; Abramov *et al.*, 2017; Sheftel *et al.*, 2017), was used in phylogenetic analyses (Appendix 1).

The complete mitochondrial *cytb* gene (1140 bp) and fragments of apolipoprotein B (*ApoB*) exon 26 and recombination-activating gene 2 (*RAG2*) exon 2 were amplified by PCR with the primer combination and conditions for amplification as in our previous studies (Bannikova *et al.*, 2011; Abramov *et al.*, 2017). The sequencing with each primer was performed by the ABI 3100-Avant autosequencing system using ABI PRISM®BigDyeTM Terminator v.3.1. *Cytb* gene sequences were aligned by eye using BioEdit v.7.0.5.3 (Hall, 1999).

Phylogenetic reconstructions were performed with (1) the alignment of *cytb* sequences and (2) each of two nuclear genes separately. We did not combine nuclear and mitochondrial sequences in the same analyses because of the lack of nuclear data for most of *Episoriculus* lineages. We determined the best partitioning strategy for nuclear genes using the program Partition Finder (Lanfear *et al.*, 2012). The *cytb* data set was partitioned into three codon positions. Phylogenetic trees were inferred in maximum likelihood (ML) with TreeFinder (October 2008 version) (Jobb, 2008) and maximum parsimony (MP) with PAUP v.4.0b (Swofford, 1998). To assess clade support, 1000 bootstrap pseudoreplicates were analyzed.

Genetic distances were calculated through MEGA5 (Tamura *et al.*, 2011). To define natural groups based on mtDNA data we employed the Automatic Barcode Gap Discovery (ABGD) method (Puillandre *et al.*, 2012). The automatic identification of the ‘barcode gap’ was performed using the ABGD application (available at <http://www.abi.snv.jussieu.fr/public/abgd/abgdweb.html>) under the following parameters: Pmin (prior minimal distance) = 0.01, Pmax (prior maximal distance) = 0.1, X (relative gap width) = 1.0. A matrix of uncorrected *p*-distances was taken as input.

Results

The final alignments have included 1140 bp of the *cytb*, 518 bp of *ApoB* and 730 bp of *RAG2*. The optimum partitioning scheme for the nuclear genes identified by Partition Finder under the BIC criterion has corresponded to the scheme of three subsets per gene. The best-fit substitution models employed for each of the subsets are given in the Appendix 2.

The ML analysis of the *cytb* data has revealed six clades within *Episoriculus* with a genetic distance of 8–17% among them (Fig. 2, Table 1). These clades correspond to different species or groups of species: *E. fumidus*, *E. macrurus*, *E. soluensis*, *E. caudatus*, *E. umbrinus*, *E. baileyi* + *E. leucops*. Yet, the phylogenetic analysis of mitochondrial gene data by means of the ML and MP methods has failed to support the monophyly of the genus *Episoriculus*, because of the isolated position of the Taiwanese taxon *E. fumidus* outside the cluster of the rest of *Episoriculus* species. In the *cytb* tree it appears as sister to all Nectogalini, however with only moderate support in ML and without any support in MP. The genetic uncorrected *p*-distance between *E. fumidus* and other *Episoriculus* was found to be not less than 17%. Besides *E. fumidus*, the most distant position on the mitochondrial tree is occupied by *E. macrurus*, which forms the basal branch in the cluster of *Episoriculus* s. stricto. The clade *E. baileyi* + *E. leucops* is found to be a sister taxon to the remaining *Episoriculus* species, with the genetic distance of not less than 12%. Specimens from Yunnan (*E. baileyi*) and from Nepal (*E. leucops*) are rather close (3.4%). The monophyly of the grouping *E. caudatus/E. umbrinus* is highly sup-

Table 1. The interspecific genetic *p*-distances within *Episoriculus* s. lato for *cytb*.

	" <i>E.</i> <i>fumidus</i> "	<i>E. macrurus</i>	<i>E. baileyi</i>	<i>E. leucops</i>	<i>E. umbrinus</i>	<i>E. caudatus</i>
" <i>E.</i> <i>fumidus</i> "						
<i>E. macrurus</i>	16.0±0.9					
<i>E. baileyi</i>	17.2±1.0	15.1±0.9				
<i>E. leucops</i>	17.6±0.0	16.2±0.0	3.4±0.0			
<i>E. umbrinus</i>	16.9±0.9	15.5±0.8	11.3±0.8	12.3±0.8		
<i>E. caudatus</i>	16.4±0.9	15.0±0.8	10.4±0.8	11.4±0.9	7.8±0.6	
<i>E. soluensis</i>	16.1±1.0	16.1±0.9	13.5±0.9	13.1±0.9	12.4±0.9	11.8±0.8

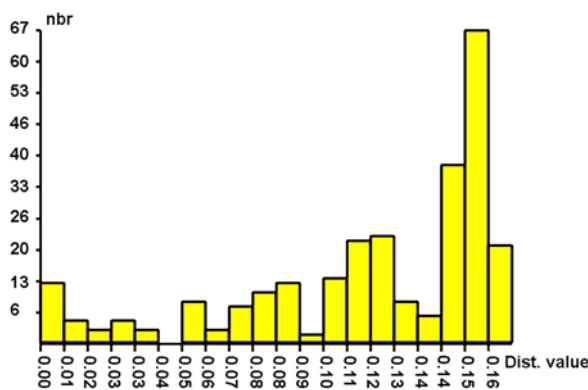


Figure 3. Distribution of the *p*-distances between haplotypes of *cytb* within *Episoriculus*.

ported. All the studied specimens of *E. umbrinus* from Yunnan form two lineages (*p*-distance of 4%). Our specimen ZIN 96263 from northern Vietnam falls into one of these groups and differs from Chinese specimens by 3.5%, which is within the limits of intraspecies variability of *E. umbrinus*. Position of *E. soluensis* on the tree has a low support and thus remains unresolved with a tendency to join with *E. caudatus*/*E. umbrinus* group (~10%).

The distribution of genetic *p*-distances between haplotypes (Fig. 3) shows the most evident gap between 4 and 5%. In the ABGD species delimitation method (Puillandre *et al.*, 2012) with the exclusion of *E. fumidus*, eight groups have been found for primary partitions (prior maximal distance *p* below 0.016): five of them correspond to *E. leucops/baileyi*, *E. caudatus*, *E. umbrinus*, *E. soluensis* and three groups are formed by splitting *macrurus* in three clusters. Thus, the result does not support *baileyi* as a distinct species that is separate from *E. leucops*.

The GenBank nuclear data of *Episoriculus* are very scarce, thus an efficient nuclear phylogenetic analysis is not possible yet. However, it is evident from our *ApoB* and *RAG2* data that *E. fumidus* is very distant from other species of the genus (Figs 4A, B). It is placed as the sister branch to all *Chodsigoa* in the *ApoB* gene tree with moderate support in ML and MP analyses. In the ML analysis of *RAG2* it is branching off after *Neomys*, but with the low bootstrap support. Within

Episoriculus s. stricto, *E. macrurus* is clearly separated from *E. umbrinus* and *E. leucops/baileyi*.

Discussion

Taxonomic position of the Vietnamese "*E. caudatus*"

The majority of researchers listed only two *Episoriculus* species, *E. leucops* (including *baileyi*) and *E. macrurus*, for Vietnam (Hoffmann, 1986; Corbet & Hill, 1992; Hutterer, 2005; Hoffmann & Lunde, 2008). However, many recent checklists of Vietnamese mammals also added *E. caudatus* to the species list (Dang *et al.*, 1994, 2007, 2008; Kuznetsov, 2006). These "records" were based on the incorrect synonymy of "*caudatus*" and "*baileyi*" (see also Hoffmann, 1986), and in fact should be referred to *E. baileyi* (sensu Motokawa & Lin, 2005). Hoffmann (1986: 468) stressed upon the fact that *E. caudatus* does not occur in Vietnam.

According to the initial description (Horsfield, 1855) and based on the examination of type specimen, *E. baileyi* is a large dark brown shrew with a tail only slightly longer than its body (see also Hoffmann, 1986). *E. baileyi* from Assam resembled this form in size and color, being just slightly smaller. Large red-toothed shrews from Northern Vietnam recorded in above-mentioned papers undoubtedly belong to *E. leucops-baileyi* group. Typical *E. caudatus* described from Darjeeling has smaller skull and body size, the shorter tail being equal to or less than head and body length.

Based on external and cranial characters, the specimen ZIN 96263 from Lao Cai Province was identified as *E. caudatus* s. lato (Abramov *et al.*, 2013). New genetic data have confirmed this identification and placed it in *E. umbrinus*. All the studied specimens of *E. umbrinus* form two lineages (*p*-distance for *cytb* 3.8±0.4%) which probably represent distinct geographic populations. Allen (1923) described *Soriculus caudatus umbrinus* from Mucheng in western Yunnan (Fig. 1). Perhaps, the populations located eastward of Salween River (eastern and southern parts of Yunnan Province and northern Vietnam), may correspond to distinct taxa of the subspecies rank. An additional study of samples from Yunnan is required to clarify the taxonomic status of these lineages.

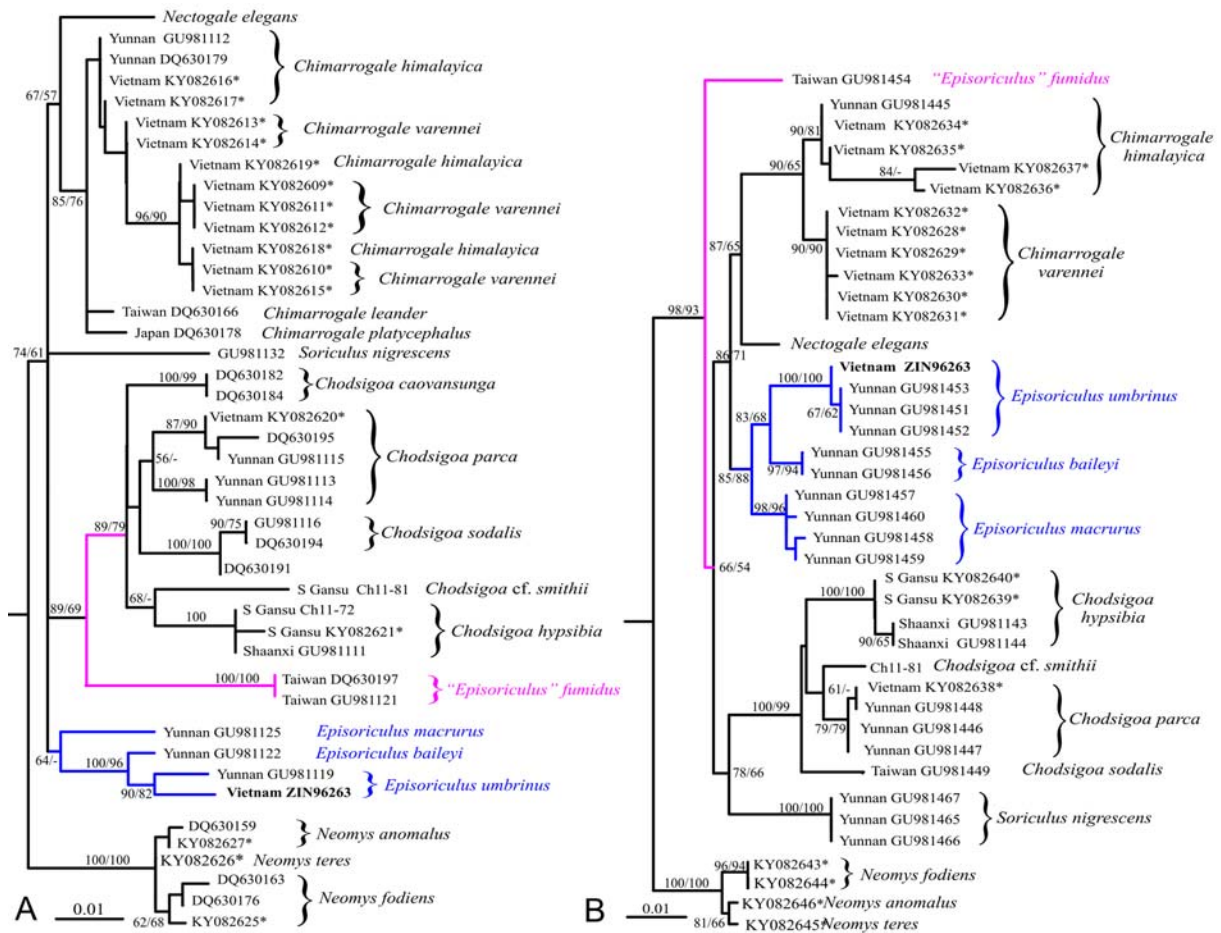


Figure 4. The ML trees of Nectogalini as inferred from the exons of *ApoB* (A) and *RAG2* (B). Sequences used from our previous studies (Abramov *et al.*, 2017; Sheftel *et al.*, 2017) are marked by asterisks.

Taxonomic content of *Episoriculus*

All the taxa belonging to *Episoriculus s. stricto* (i.e., *E. baileyi*, *E. caudatus*, *E. leucops*, *E. macrurus*, *E. soluensis*, and *E. umbrinus*) form highly or moderately supported clades in the ML and MP analyses with genetic distances (*cytb*) among them of approximately 8–16%. These data have confirmed the previous morphological and karyological data (Motokawa & Lin, 2005; Motokawa *et al.*, 2008, 2009) and testified the species rank of most studied taxa. However, the distance between *E. baileyi* and *E. leucops* was low, just 3.4%, that contradicts the morphological findings by Motokawa & Lin (2005). According to the current genetic species concept (Baker & Bradley, 2006) the value of more than 5% of divergence in the *cytb* gene is indicative of species rather than subspecies rank and values of <5% have a high probability of being indicative of conspecific populations, however merit additional study concerning specific status. Thus, an additional study is needed to evaluate the taxonomic rank of these two forms.

For one of species from this group, *E. sacratus* from Sichuan, genetic data are still absent. However, mor-

phological and karyological data confirm that it belongs to *Episoriculus s. stricto* (Motokawa & Lin, 2005; Motokawa *et al.*, 2008, 2009).

Taxonomic position of *"Episoriculus" fumidus*

Episoriculus fumidus was described from central Taiwan (Thomas, 1913) and is currently classified as a member of the genus *Episoriculus* based on its morphological characters, including the dental formula (Hoffmann, 1986; Corbet & Hill, 1992; Hutterer, 2005; Lin & Motokawa, 2010).

Molecular data have supported the position of the Taiwanese *E. fumidus* as a monotypic clade within the tribe Nectogalini. This separate branch lies outside of *Episoriculus*, with the large genetic distance (~17%, *cytb*) between *E. fumidus* and the other clades of *Soriculus s. lato* (Fig. 2) as demonstrated by the analyses of both the mitochondrial *cytb* gene and two nuclear loci. Other molecular phylogenetic studies have repeatedly showed the paraphyletic status of *Episoriculus* when *E. fumidus* is included (Ohdachi *et al.*, 2006; Dubey *et al.*, 2007; He *et al.*, 2010). In our work, as in the early

studies (He *et al.*, 2010), gene trees obtained from individual loci (including *BRCA1* which is absent in the present study) show different topologies. However, this does not imply that the conflict among genes is significant because the levels of support for each rival topology are just moderate or low. The uncertainty of the position of *E. fumidus* makes it difficult to provide a clear interpretation of its relationships with other Nectogalini. Taking into consideration all the genetic data available for the tribe by now, it is possible to conclude only that *E. fumidus* belongs to a subclade that includes all genera except *Neomys*, and that the Taiwanese red-toothed shrew indisputably represents a lineage separate from the genus *Episoriculus*. As inferred in He *et al.* (2010), the time of divergence between *E. fumidus* and its sister taxa (~5.04 Mya, Early Pliocene) is comparable to or even higher than those among such distinct genera as *Chimarrogale*, *Episoriculus* s. stricto, *Chodsigoa* and *Nectogale*.

Despite the similar dental formula, *E. fumidus* is clearly distinct from other *Episoriculus* taxa by the external and cranial characters (Jameson & Jones, 1977; Hoffmann, 1986; see below). Considering that *E. fumidus* demonstrates a unique combination of external, craniodental and genetic characteristics and belongs to a distinct phylogenetic lineage, it should not be included in the genus *Episoriculus* s. stricto. Retention of *E. fumidus* in *Episoriculus*, most probably, renders the latter paraphyletic, which violates the major principle of phylogenetic taxonomy. In our opinion, the Taiwanese red-toothed shrew should be assigned to a new genus *Pseudosoriculus* **gen.n.**, of which the description follows.

Systematic part

Family: Soricidae Fischer, 1817

Subfamily: Soricinae Fischer, 1817

Pseudosoriculus Abramov, Bannikova, Chernetskaya, Lebedev et Rozhnov, **gen.n.**

Type species: *Soriculus fumidus* Thomas, 1913

Distribution: Endemic of Taiwan. Widespread in the mountains of main island of Taiwan, between 1,000 and 3,600 m above sea level (Lin & Motokawa, 2010).

Contents: The type species only.

Etymology: The name of the new genus is derived from the Greek word “*pseudēs*” (false) and the generic name *Soriculus* previously attributed to this taxon. Gender is masculine.

Diagnosis: A medium-sized shrew. Fur covering head and body blackish brown, under surface slightly lighter than upper. Tail shorter than head and body, dark brown, little lighter below. The skull with short, narrow rostrum. Angular process quite long and curved; coronoid process high, with converging sides. Upper tooth-row with four antemolars (A1–A4); fourth antemolar very small, and tightly wedged between A3 and

P4. Posterior margin of fourth premolar, first and second molars not strongly concave. The lower incisor relatively long. The dental formula is 1.4.1.3/1.1.1.3, total 30. Teeth are red-tipped. The karyotype has 2n=64, FN=116 (Motokawa *et al.*, 1998).

Comparisons: Teeth of *Pseudosoriculus* **gen.n.** are red-tipped in contrast to white-toothed *Nectogale* and *Chimarrogale*. New genus has four antemolars in upper tooth-row instead of three antemolars in *Chodsigoa*. It differs from *Soriculus* in small body size and relatively long tail (at average 75% of head and body length in contrast to 50% in latter). It is clearly distinct from *Episoriculus* by the relatively short tail, the narrow and shortened rostral part of the skull and the mandible with long angular and coronoid processes.

New genus represents a distinct phylogenetic lineage of Nectogalini, with the large genetic distance (~17%, *cytb*) between it and the other clades of *Soriculus* s. lato.

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References

- Abramov A.V., Bannikova A.A., Lebedev V.S. & Rozhnov V.V. 2017. Revision of *Chimarrogale* (Lipotyphla: Soricidae) from Vietnam with comments on taxonomy and biogeography of Asiatic water shrews // *Zootaxa*. Vol.4232. No.2. P.216–230.
- Abramov A.V., Can D.N., Hai B.T. & Son N.T. 2013. An annotated checklist of the insectivores (Mammalia, Lipotyphla) of Vietnam // *Russian Journal of Theriology*. Vol.12. No.2. P.57–70.
- Allen G.M. 1923. New Chinese insectivores // *American Museum Novitates*. No.100. P.1–11.
- Bannikova A.A., Abramov A.V., Borisenko A.V., Lebedev V.S. & Rozhnov V.V. 2011. Mitochondrial diversity of the white-toothed shrews (Mammalia, Eulipotyphla, *Crocidura*) in Vietnam // *Zootaxa*. No.2812. P.1–20.
- Baker R.J. & Bradley R.D. 2006. Speciation in mammals and the genetic species concept // *Journal of Mammalogy*. Vol.87. No.4. P.643–662.
- Carvalho M.R., Bockmann F.A., Amorim D.S., Brand C.R.F., Vivo M., Figueiredo J.L., Britski H.A., Pinna M.C.C., Menezes N.A., Marques F.P.L., Papavero N., Cancellato E.M., Crisci J.V., McEachran J.D., Schelly R.C., Lund-

- berg J.G., Gill A.C., Britz R., Wheeler Q.D., Stiassny M.L.J., Parenti L.R., Page L.M., Wheeler W.C., Faivovich J., Vari R.P., Grande L., Humphries C.J., DeSalle R., Ebach M.C. & Nelson G.J. 2007. Taxonomic impediment or impediment to taxonomy? A commentary on systematics and the Cybertaxonomic-Automation Paradigm // *Evolutionary Biology*. Vol.34. P.140–143.
- Castiglia R., Annesi F., Aloise G. & Amori G. 2007. Mitochondrial DNA reveals different phylogeographic structures in the water shrews *Neomys anomalus* and *N. fodiens* (Insectivora: Soricidae) in Europe // *Journal of Zoological Systematics and Evolutionary Research*. Vol.45. No.3. P.255–262.
- Corbet G.B. & Hill J.E. 1992. *The Mammals of the Indomalayan Region: A Systematic Review*. Oxford: Oxford University Press. 488 p.
- Dang H.H., Dao V.T., Cao V.S., Pham T.A. & Hoang M.K. 1994. [Checklist of Mammals in Vietnam]. Hanoi: Publishing House “Science and Technics”. 168 p. [in Vietnamese].
- Dang H.H., Hoang M.K., Le X.C., Nguyen X.D., Vu D.T. & Dang H.P. 2007. [Mammals of Vietnam. Morphology, Biology and Ecology of Some Species]. Vol.1. Hanoi: Science and Technics Publishing House. 232 p. [in Vietnamese].
- Dang N.C., Endo H., Nguyen T.S., Oshida T., Le X.C., Dang H.P., Lunde D.P., Kawada S.-I., Hayashida A. & Sasaki M. 2008. [Checklist of Wild Mammal Species of Vietnam]. Hanoi: Primate Research Institute, Inuyama, Japan & Institute of Ecology and Biological Resources. 400. p. [in Vietnamese].
- Dubey S., Salamin N., Ohdachi S.D., Barriere P. & Vogel P. 2007. Molecular phylogenetics of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations // *Molecular Phylogenetics and Evolution*. Vol.44. P.126–137.
- Hall T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT // *Nucleic Acids Symposium Series*. Vol.41. P.95–98.
- Harris D.J. 2003. Can you bank on GenBank? // *Trends in Ecology & Evolution*. Vol.18. P.317–319.
- He K., Li Y.J., Brandley M.C., Lin L.-K., Wang Y.X., Zhang Y.P. & Jiang X.L. 2010. A multi-locus phylogeny of Nectogalini shrews and influences of the paleoclimate on speciation and evolution // *Molecular Phylogenetics and Evolution*. Vol.56. No.2. P.734–746.
- Hoffmann R.S. 1986. A review of the genus *Soriculus* (Mammalia: Insectivora) // *Journal of the Bombay Natural History Society*. Vol.82. No.3. P.459–481.
- Hoffmann R.S. & Lunde D. 2008. Order Erinaceomorpha, Order Soricomorpha // Smith A.T. & Xie Y. (eds.). *A Guide to the Mammals of China*. Princeton: Princeton University Press. P.292–327.
- Horsfield T. 1855. Brief notices of several new or little-known species of Mammalia, lately discovered and collected in Nepal, by Brian Houghton Hodgson, Esq. // *Annals and Magazine of Natural History*. Ser.2. No.16. P.101–114.
- Hutterer R. 2005. Order Erinaceomorpha, Order Soricomorpha // Wilson D.E. & Reeder D.M. (eds.). *Mammal Species of the World. A Taxonomic and Geographic Reference*. Third edition. Baltimore: Johns Hopkins Press. P.212–311.
- Jameson E.W. & Jones G.S. 1977. The Soricidae of Taiwan // *Proceedings of the Biological Society of Washington*. Vol.90. P.459–482.
- Jobb G. 2008. TREEFINDER, version of October 2008. Munich, Germany. Distributed by the author. Available from: <http://www.treefinder.de> (accessed 17 January 2017).
- Kuznetsov G.V. 2006. [Mammals of Vietnam]. Moscow: KMK Scientific Press. 428 p. [in Russian].
- Lanfear R., Calcott B., Ho S.Y.W. & Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses // *Molecular Biology and Evolution*. Vol.29. P.1695–1701.
- Lin L.-K. & Motokawa M. 2010. *Mammals of Taiwan*. Vol.1. Soricomorpha. 89 p. <http://mammal.biota.biodiv.tw/>
- Motokawa M. & Lin L.-K. 2005. Taxonomic status of *Soriculus baileyi* (Insectivora, Soricidae) // *Mammal Study*. Vol.30. P.117–124.
- Motokawa M., Harada M., Lin L.-K., Cheng H.C. & Koyasu K. 1998. Karyological differentiation between two *Soriculus* (Insectivora: Soricidae) from Taiwan // *Mammalia*. Vol.62. P.541–547.
- Motokawa M., Harada M., Mekada K. & Shrestha K.C. 2008. Karyotypes of three shrew species (*Soriculus nigrescens*, *Episoriculus caudatus* and *Episoriculus sac-ratus*) from Nepal // *Integrative Zoology*. Vol.3. P.180–185.
- Motokawa M., Wu Y. & Harada M. 2009. Karyotypes of six soricomorph species from Emei Shan, Sichuan Province, China // *Zoological Science*. Vol.26. P.791–797.
- Ohdachi S.D., Hasegawa M., Iwasa M.A., Vogel P., Oshida T., Lin L.-K. & Abe H. 2006. Molecular phylogenetics of soricid shrews (Mammalia) based on mitochondrial cytochrome *b* gene sequences: with special reference to the Soricinae // *Journal of Zoology*. Vol.270. P.177–191.
- Puillandre N., Lambert A., Brouillet S. & Achaz G. 2012. ABGD, automatic barcode gap discovery for primary species delimitation // *Molecular Ecology*. Vol.21. P.1864–1877.
- Ruedas L.A., Salazar-Bravo J., Dragoo J.W. & Yates T.L. 2000. The importance of being earnest: what if anything constitutes a «specimen examined?» // *Molecular Phylogenetics and Evolution*. Vol.17. P.129–32.
- Sheftel B.I., Bannikova A.A., Fang Y., Demidova T.B., Alexandrov D.Yu., Lebedev V.S. & Sun Y.-H. 2017. [Notes on the fauna, systematics and ecology of small mammals in Southern Gansu, China] // *Zoologicheskii Zhurnal*. Vol.96. No.2. P.232–248 [in Russian with English summary].
- Swofford D.L. 1998. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sunderland, MA: Sinauer Associates.
- Tamura K., Peterson D., Peterson N., Stecher G., Nei M. & Kumar S. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods // *Molecular Biology and Evolution*. Vol.28. P.2731–2739.
- Thomas O. 1913. Four new shrews // *Annals and Magazine of Natural History*. Ser.8. No.11. P.214–218.

APPENDIX 1. List of GenBank and original sequences* used in the study.

Genus	Species**	Locality	cyt b	ApoB	RAG2	Source
<i>Chimarrogale</i>	<i>himalayica</i>	Nepal	AB175092	-	-	Ohdachi <i>et al.</i> , 2006
<i>Chimarrogale</i>	<i>himalayica</i>	China, Yunnan	GU981263	-	-	He <i>et al.</i> , 2010
<i>Chimarrogale</i>	<i>himalayica</i>	China, Yunnan	GU981264	GU981112	GU981445	He <i>et al.</i> , 2010
<i>Chimarrogale</i>	<i>himalayica</i>	China, Yunnan	-	DQ630179	-	Dubey <i>et al.</i> , 2007
<i>Chimarrogale</i>	<i>himalayica</i>	Vietnam	AB175094	-	-	Ohdachi <i>et al.</i> , 2006
<i>Chimarrogale</i>	<i>himalayica</i>	Vietnam	-	KY082616*	KY082634*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>himalayica</i>	Vietnam	-	KY082617*	KY082635*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>himalayica</i>	Vietnam	-	KY082619*	KY082637*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>himalayica</i>	Vietnam	-	KY082618*	KY082636*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>leander</i>	China, Taiwan	AB107875	-	-	Ohdachi <i>et al.</i> , 2006
<i>Chimarrogale</i>	<i>leander</i>	China, Taiwan	-	DQ630166	-	Dubey <i>et al.</i> , 2007
<i>Chimarrogale</i>	<i>platycephalus</i>	Japan	AB108705	-	-	Ohdachi <i>et al.</i> , 2006
<i>Chimarrogale</i>	<i>platycephalus</i>	Japan	AB108703	-	-	Ohdachi <i>et al.</i> , 2006
<i>Chimarrogale</i>	<i>platycephalus</i>	Japan	-	DQ630178	-	Dubey <i>et al.</i> , 2007
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082609*	KY082628*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082614*	-	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082615*	KY082633*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082610*	KY082629*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082611*	KY082630*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082612*	KY082631*	Abramov <i>et al.</i> , 2017
<i>Chimarrogale</i>	<i>varennei</i>	Vietnam	-	KY082613*	KY082632*	Abramov <i>et al.</i> , 2017
<i>Soriculus</i>	<i>nigrescens</i>	China, Yunnan	GU981297	-	-	He <i>et al.</i> , 2010
<i>Soriculus</i>	<i>nigrescens</i>	China, Yunnan	GU981298	GU981132	GU981465	He <i>et al.</i> , 2010
<i>Soriculus</i>	<i>nigrescens</i>	China, Yunnan	GU981299	-	GU981466	He <i>et al.</i> , 2010
<i>Soriculus</i>	<i>nigrescens</i>	China, Yunnan	GU981300	-	-	He <i>et al.</i> , 2010
<i>Soriculus</i>	<i>nigrescens</i>	China, Yunnan	GU981301	-	GU981467	He <i>et al.</i> , 2010

Genus	Species**	Locality	<i>cyt b</i>	<i>ApoB</i>	RAG2	Source
<i>Chodsigoa</i>	<i>sodalis</i>	China, Taiwan	GU981270	GU981116	GU981449	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>sodalis</i>	China, Taiwan	GU981269	–	–	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>sodalis</i>	China, Taiwan	–	DQ981449	–	Dubey <i>et al.</i> , 2007
<i>Chodsigoa</i>	<i>sodalis</i>	China, Taiwan	AB175102	–	–	Ohdachi <i>et al.</i> , 2006
<i>Chodsigoa</i>	<i>sodalis</i>	China, Taiwan, Chiay	AB127978	–	–	Ohdachi <i>et al.</i> , unpublished
<i>Chodsigoa</i>	<i>caovansunga</i>	Vietnam, Ha Giang	AB175104	DQ630182	–	Ohdachi <i>et al.</i> , 2006
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, Shaanxi	GU981260	GU981111	GU981443	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, Shaanxi	GU981261	–	–	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, Shaanxi	GU981262	–	GU981444	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, S Gansu	KX354165*	–	–	Sheftel <i>et al.</i> , 2017
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, S Gansu	KX354166*	KY082621*	KY082639*	Sheftel <i>et al.</i> , 2017; Abramov <i>et al.</i> , 2017
<i>Chodsigoa</i>	<i>hypsiibia</i>	China, S Gansu	KX354167*	MF577031	KY082640*	Sheftel <i>et al.</i> , 2017; Abramov <i>et al.</i> , 2017; this study
<i>Chodsigoa</i>	<i>parca</i>	Vietnam, Ha Giang	AB175105	–	–	Ohdachi <i>et al.</i> , 2006
<i>Chodsigoa</i>	<i>parca</i>	Vietnam, Ha Giang	AB175106	DQ630195	–	Ohdachi <i>et al.</i> , 2006
<i>Chodsigoa</i>	<i>parca</i>	China, Yunnan	GU981265	–	–	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>parca</i>	China, Yunnan	GU981266	GU981113	GU981446	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>parca</i>	China, Yunnan	GU981267	GU981114	GU981447	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>parca</i>	China, Yunnan	GU981268	GU981115	GU981448	He <i>et al.</i> , 2010
<i>Chodsigoa</i>	<i>parca</i>	Vietnam, Lao Cai	–	KY082620*	KY082638*	Abramov <i>et al.</i> , 2017
<i>Chodsigoa</i>	<i>cf. smithii</i>	China, S Gansu	KX354168*	MF577032	MF577033	Sheftel <i>et al.</i> , 2017; this study
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan, Nantou	AB175107	–	–	Ohdachi <i>et al.</i> , 2006
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan, Chiay	AB175108	–	–	Ohdachi <i>et al.</i> , 2006
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan	GU981278	GU981121	GU981454	He <i>et al.</i> , 2010
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan	GU981279	–	–	He <i>et al.</i> , 2010
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan	GU981280	–	–	He <i>et al.</i> , 2010

Genus	Species**	Locality	cyt b	ApoB	RAG2	Source
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan	AY033086	-	-	He <i>et al.</i> , 2010
<i>Pseudosoriculus</i>	<i>fumidus</i>	China, Taiwan	-	DQ630197	-	Dubey <i>et al.</i> , 2007
<i>Episoriculus</i>	<i>macrurus</i>	Nepal, Pokhara	AB175109	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>macrurus</i>	Nepal, Syabru	AB175110	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981285	-	GU981457	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981286	GU981125	GU981458	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981287	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981288	-	GU981459	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981289	-	GU981460	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>macrurus</i>	China, Yunnan	GU981290	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>leucops</i>	Nepal, Syng Gomba	AB175111	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>baileyi</i>	China, Yunnan	GU981281	GU981122	GU981455	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>baileyi</i>	China, Yunnan	GU981282	-	GU981456	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>baileyi</i>	China, Yunnan	GU981283	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>baileyi</i>	China, Yunnan	GU981284	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>soluensis</i>	Nepal, Gosainkund	AB175112	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>soluensis</i>	Nepal, Gosainkund	AB175113	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>caudatus</i>	Nepal, Phulchauki	AB175114	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>caudatus</i>	Nepal, Kurumsan	AB175115	-	-	Ohdachi <i>et al.</i> , 2006
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981272	-	GU981451	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981273	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981274	GU981119	GU981452	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981275	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981276	-	GU981453	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	China, Yunnan	GU981277	-	-	He <i>et al.</i> , 2010
<i>Episoriculus</i>	<i>umbrinus</i>	Vietnam, Lao Cai	MF577030	KY082622*	KY082641*	Abramov <i>et al.</i> , 2017; this study
<i>Neomys</i>	<i>fodiens</i>	Germany	GU981295	-	-	He <i>et al.</i> , 2010

Genus	Species**	Locality	<i>cyt b</i>	<i>ApoB</i>	<i>RAG2</i>	Source
<i>Neomys</i>	<i>fodiens</i>	Italy	DQ991062	–	–	Castiglia <i>et al.</i> , 2007
<i>Neomys</i>	<i>fodiens</i>	Russia, Bryansk	–	KY082624*	KY082643*	Abramov <i>et al.</i> , 2017
<i>Neomys</i>	<i>fodiens</i>	Mongolia	–	KY082625*	KY082644*	Abramov <i>et al.</i> , 2017
<i>Neomys</i>	<i>teres</i>	Armenia	HQ621858	–	–	Gajewska <i>et al.</i> , unpubl.
<i>Neomys</i>	<i>teres</i>	Russia, Adygea	–	KY082626*	KY082645*	Abramov <i>et al.</i> , 2017
<i>Neomys</i>	<i>anomalous</i>	Spain	DQ991055	–	–	Castiglia <i>et al.</i> , 2007
<i>Neomys</i>	<i>anomalous</i>	Russia, Belgorod	–	KY082627*	KY082646*	Abramov <i>et al.</i> , 2017
<i>Neomys</i>	<i>anomalous</i>	Switzerland	–	DQ630159	–	Dubey <i>et al.</i> , 2007
<i>Neomys</i>	<i>milleri</i>	Italy	DQ991051	–	–	Castiglia <i>et al.</i> , 2007
<i>Nectogale</i>	<i>elegans</i>	China, Yunnan	–	GU981128	–	He <i>et al.</i> , 2010
<i>Anourosorex</i>	<i>yamashinai</i>	China, Taiwan	–	GU981257	GU981461	He <i>et al.</i> , 2010

Notes:

* sequences used from our previous studies are marked by *, sequences obtained in the present study are marked in bold.

** species of *Episoriculus* were allocated based on geographic origin of specimens (according to Motokawa & Lin, 2005; Motokawa *et al.*, 2008, 2009).

APPENDIX 2. Models for the mitochondrial *cyt b* gene and *ApoB* and *RAG2* exons employed in maximum likelihood analysis.

	1 st codon positions	2 nd codon position	3 rd codon position
<i>cyt b</i>	TN+G	TVM +G	J1+G
<i>ApoB</i>	HKY	TN+G	J3
<i>RAG2</i>	HKY+G	HKY+G	HKY+G