

## Phylogenetic Relationships of the Endemic Sri Lankan Shrew Genera: *Solisorex* and *Feroculus*

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### ABSTRACT

Sri Lanka has a rich diversity of shrews: ten species in four genera, with two genera and five species endemic to the island. In the current study we use complete cytochrome-*b* mitochondrial gene sequences to infer the relationships of two Sri Lankan monotypic genera *Solisorex* and *Feroculus*. Maximum likelihood and maximum parsimony phylogenetic analyses revealed that *Solisorex* is an old lineage that forms the sister group to all other crocidurines. In contrast, *Feroculus* is nested within *Suncus*.

**Keywords:** *Feroculus feroculus*, phylogeny, phylogeography, *Solisorex pearsoni*, shrews, Sri Lanka

### INTRODUCTION

With 376 described species in 26 genera, shrews are among the most speciose families of mammals, representing about seven percent of the class Mammalia (Hutterer, 2005). Extant shrews are divided into three main subfamilies: Soricinae, Crocidurinae and Myosoricinae (Hutterer, 2005). The Myosoricinae were earlier included in the Crocidurinae (Repenning, 1967; Hutterer, 1993), but subsequent studies showed them to be a monophyletic group separate from the Crocidurinae and recognized at subfamilial rank by Querouil *et al.* (2001) and Dubey *et al.* (2007). Soricinae are widespread in the Holarctic region and Crocidurinae are distributed across Eurasia and Africa, while Myosoricinae are confined to Africa. Fossil evidence suggests that the soricine shrews originated in Europe (Rzebik-Kowalska, 1998). Butler *et al.* (1989) suggested that the Crocidurinae evolved from a Eurasian ancestor that then colonized African forests. The Myosoricinae and Crocidurinae are thought then to have diversified in Africa, with the latter dispersing into and diversifying in Eurasia (Dubey *et al.*, 2007).

With ten species representing four genera (*Suncus*, *Crociodura*, *Solisorex* and *Feroculus*), the Sri Lankan Crocidurinae are remarkably diverse (Hutterer, 2005; Meegaskumbura *et al.*, 2007). Of these, two genera (*Solisorex* Thomas, 1913; *Feroculus* Kelaart, 1850) and five species (*Crociodura miya*, *C. hikmiya*, *Suncus fellowesgordoni*, *S. zeylanicus* and *S. montanus*) are endemic to the island (Hutterer, 2005; Meegaskumbura *et al.*, 2007; Meegaskumbura and

Schneider, 2008; Meegaskumbura *et al.*, 2012a; Meegaskumbura *et al.*, 2012b). *Suncus*, comprising 18 species, and *Crociodura*, with 182 species, are widely distributed in Europe, Africa and Asia. In Sri Lanka, *Solisorex pearsoni* and *F. feroculus* are confined to the highlands (Phillips, 1980). The latter species was also reported from South India (Pradan *et al.*, 1997, Blanford, 1888), but without a preserved voucher material to confirm these records. Pradan *et al.* (1997) reported the Indian '*Feroculus*' to have smaller bodies and longer tails than the specimens of Sri Lanka, adding further doubt to his identification.

The Crocidurinae includes five genera absent from Sri Lanka: *Paracrociodura*, *Sylvisorex*, *Ruwenzorisorex*, *Scutisorex*, and *Diplomesodon* (Hutterer, 2005). The first four of these are confined to the African continent whereas *Diplomesodon* is from Central Asia (Kazakhstan, Uzbekistan and Turkmenistan). The phylogenetic relationships of all crocidurine genera, except *Diplomesodon*, *Feroculus* and *Solisorex*, have been studied using partial mitochondrial 16S rRNA gene sequences (Querouil *et al.*, 2001) partial cytochrome-*b* gene sequences and at least one nuclear gene (Stanley *et al.*, 2013). Molecular systematic analyses to date suggest that *Paracrociodura* falls within the *Crociodura* clade, while the others show close affinities to various *Suncus* species. *Diplomesodon* was shown to fall within the clade of *Crociodura* by Dubey *et al.* (2008). The phylogenetic positions of *Solisorex* and *Feroculus* in the phylogeny of shrews remain untested using molecular data but are important for understanding the evolutionary and biogeographic history of shrews. In this study we attempt to

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determine the phylogenetic placement of their constituent species in the context of the other lineages of Old World crocidurine shrews using sequence data from the mitochondrial cytochrome-*b* gene.

## MATERIALS AND METHODS

### Sampling

All the species of shrews from Sri Lanka, except *Suncus zeylanicus*, were included in the study (Table 1). Voucher specimens of shrews originally deposited in the collection of the Wildlife Heritage Trust (WHT) are now in the collection of the Department of Zoology, University of Peradeniya, Sri Lanka. Tissue samples of the following specimens were obtained from museum collections (Museum of Vertebrate Zoology [MVZ], University of California Berkeley and Field Museum of Natural History [FMNH], Chicago): *Crocidura attenuata*, *C. fuliginosa* and *Euroscaptor longirostris* (as an outgroup for the phylogenetic analysis) from Vietnam; *Sorex araneus* (Soricinae) from Switzerland; and two *Myosorex* species (Myosoricinae) from Tanzania. Several additional sequences were obtained from GenBank (Table 1). All the sequences extracted from the GenBank were complete cytochrome-*b* gene, except sequences from Stanley *et al.*, 2013 and Demos *et al.*, 2014, which were 684 bp and 1116 bp fragments, respectively.

### DNA extraction, amplification, and sequencing

DNA was extracted from ethanol-preserved tissues using Qiagen tissue-extraction kits following manufacturer's protocols. DNA of *F. feroculus* was extracted from dried skin. The complete mitochondrial Cytochrome-*b* gene was sequenced for all the available tissue samples. This particular mitochondrial gene was selected to facilitate analysis of the new data in the context of previously published molecular data (Motokawa, 2000; Dubey *et al.*, 2007; Stanley *et al.*, 2013).

DNA was amplified by PCR in 25 µl reactions containing c. 50 nanograms of DNA template, 1.25 µl of each primer (10 µM), 2.5 µl of 10 mM dNTP, 2.5 µl of 25 mM MgCl<sub>2</sub>, 2.5 µl of 10x PCR buffer, and 0.625 U of Taq DNA Polymerase. The thermal cycling for the cytochrome-*b* fragment was as follows: 35 cycles of denaturation at 94 °C for 30 s, annealing at 45 °C for 30 s, and extension at 72 °C for 60 s, with a final extension of 72 °C for 5 min. The following primers were used for PCR: Forward primer MVZ 05 (CGA AGC TTG ATA

TGA AAA ACC ATC GTTG) and reverse primer MVZ 14 (GGT CTT CAT CTY HGG YTT ACA AGAC) (Smith and Patton, 1993).

### Phylogenetic analysis

Phylogenetic and molecular evolutionary analyses were conducted under the maximum likelihood (ML) criterion using MEGA version 6 (Tamura *et al.*, 2013). The ML analysis was based on the General Time Reversible model, Gamma Distributed (G) rate among sites and Nearest-Neighbor-Interchange (NNI) tree inference option.

The data were also analyzed under maximum parsimony (MP) criterion in PAUP\*v.4.0b10 (Swofford, 2000) with all characters unordered and weighted equally. Cytochrome-*b* sequences were aligned using the translated amino acid sequence. Three species of moles (*Euroscaptor longirostris*, *Talpa altaica* and *T. europaea*) were used as the outgroup because Talpidae is suggested to be proximal to shrews (Stanhope *et al.*, 1998; Asher, 1999). A bootstrap analysis was also carried out in both ML and MP criteria to determine the node support.

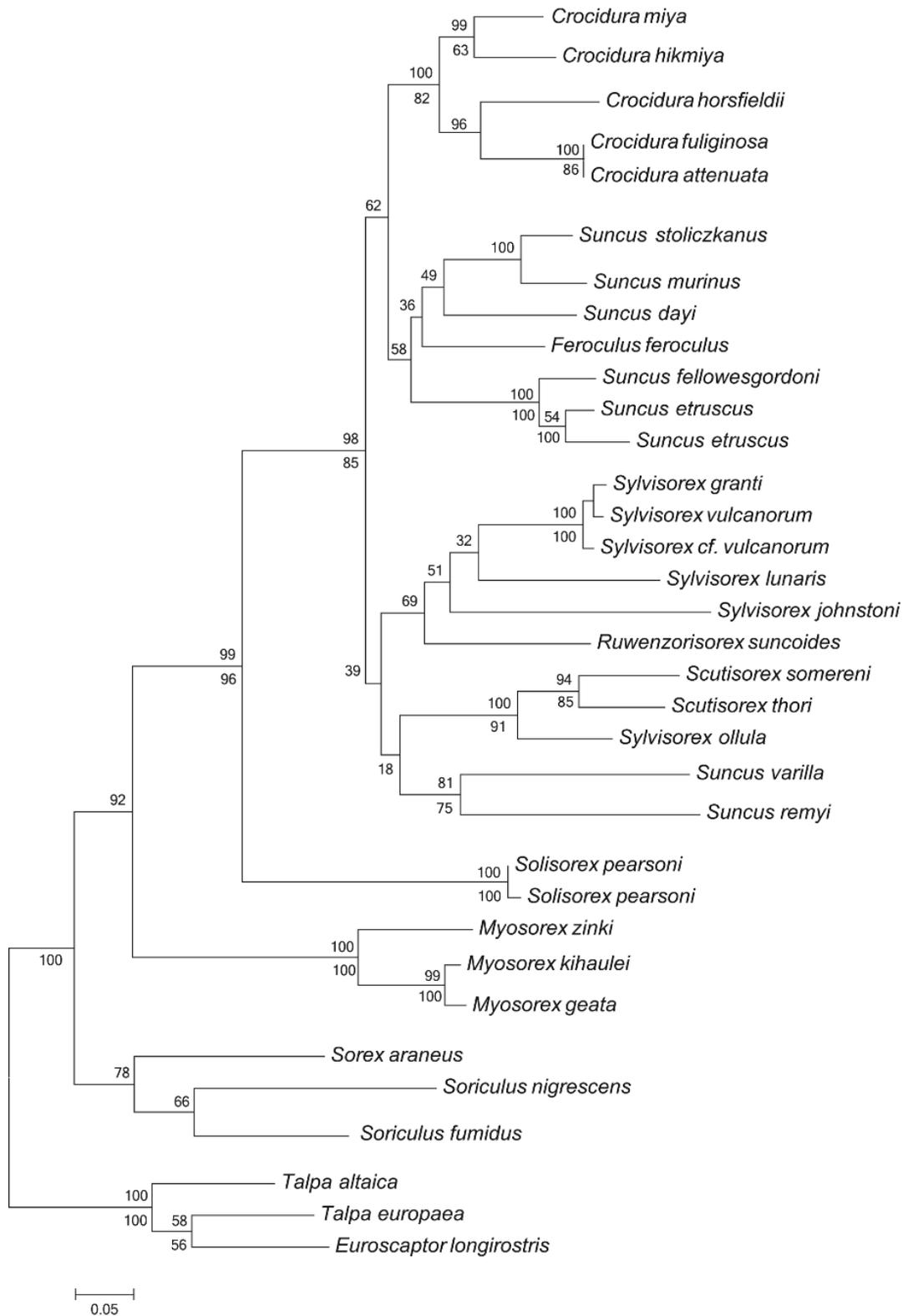
## RESULTS

Phylogenetic relationships inferred under maximum likelihood and maximum parsimony separately resulted in similar overall topologies except for the placement of a few species. In both trees the subfamilies were recovered as clades with high bootstrap support (BS). The clade representing the Myosoricinae (*Myosorex*) had a BS value of 100% in both the ML and the MP trees, and Crocidurinae had a BS of 99% (ML), 96% (MP) (Fig. 1).

*Ruwenzorisorex*, *Scutisorex* and two African *Suncus* species (*S. varilla*, *S. remyi*) fall in the same clade with *Sylvisorex*, though with low BS (39%) in ML tree, but in MP tree this relationship and the most of the relationships of the taxa within are unresolved. *Solisorex pearsoni* was recovered as the sister taxon to all the other crocidurine shrews, which are placed in a single clade with high BS values (98% ML, 85% MP). Placement of Myosoricinae as a sister clade to Crocidurinae is supported in the ML tree with high BS value (92%), but it was unresolved in the MP tree. *Feroculus feroculus* shows close affinities to *Suncus* species from south and southeast Asian region in the clade of Crocidurinae. However, its relationship to other taxa in the clade does not have strong BS support.

**Table 1.** Species included in this study, with country of origin, voucher number and/or GenBank accession number.

Species	Country	Voucher number	GenBank accession number	Reference
<i>Crocidura attenuata</i>	Vietnam	MVZ185237	EU122211	Meegaskumbura <i>et al.</i> , 2007
<i>C. fuliginosa</i>	Vietnam	MVZ186404	EU122212	Meegaskumbura <i>et al.</i> , 2007
<i>C. hikmiya</i>	Sri Lanka	WHT 6853	EU122223	Meegaskumbura <i>et al.</i> , 2007
<i>C. horsfieldii</i>	Sri Lanka	WHT 6869	EU122213	Meegaskumbura <i>et al.</i> , 2007
<i>C. miya</i>	Sri Lanka	WHT 6826	EU122216	Meegaskumbura <i>et al.</i> , 2007
<i>Feroculus feroculus</i>	Sri Lanka	WHT 6827	JQ433898	This study
<i>Solisorex pearsoni</i>	Sri Lanka	WHT 6810	JQ433899	This study
		WHT M 184	JQ433900	
<i>Suncus fellowesgordoni</i>	Sri Lanka	WHT 6820	JF914983	Meegaskumbura <i>et al.</i> , 2012a
<i>S. etruscus</i>	Sri Lanka	WHT 6936	FJ716836	Meegaskumbura and Schneider, 2008
<i>S. etruscus</i>	France	–	JF817396	Omar <i>et al.</i> , 2011
<i>S. varilla</i>	Africa	–	DQ630434	Dubey <i>et al.</i> , 2007
<i>S. remyi</i>	Africa	–	DQ630399	Dubey <i>et al.</i> , 2007
<i>S. murinus</i>	Sri Lanka	WHT 6928	EU122224	Meegaskumbura <i>et al.</i> , 2007
<i>S. stoliczkanus</i>	Nepal	–	AB175077	Ohdachi <i>et al.</i> , 2004
<i>S. dayi</i>	India	–	DQ630432	Dubey <i>et al.</i> , 2007
<i>Ruwenzorisorex suncoides</i>	Africa	FMNH 157830	KF110750	Stanley <i>et al.</i> , 2013
<i>Scutisorex somereni</i>	Africa	–	KF110752	Stanley <i>et al.</i> , 2013
<i>Sc. thori</i>	Africa	FMNH 219669	KF110765	Stanley <i>et al.</i> , 2013
<i>Sylvisorex granti</i>	Africa	FMNH 209792	KF876413	Demos <i>et al.</i> , 2014
<i>Sy. lunaris</i>	Africa	FMNH 203754	KF876415	Demos <i>et al.</i> , 2014
<i>Sy. ollula</i>	Africa	–	DQ630398	Dubey <i>et al.</i> , 2007
<i>Sy. cf. vulcanorum</i>	Africa	FMNH 189110	KF876463	Demos <i>et al.</i> , 2014
<i>Sy. vulcanorum</i>	Africa	FMNH 189114	KF876465	Demos <i>et al.</i> , 2014
<i>Sy. johnstoni</i>	Africa	–	DQ630392	Dubey <i>et al.</i> , 2007
<i>Myosorex zinki</i>	Africa	FMNH 174124	JX193702	Kang <i>et al.</i> , 2014
<i>M. geata</i>	Africa	FMNH 158299	JQ433901	This study
<i>M. kahaulei</i>	Africa	FMNH 155611	JQ433902	This study
<i>Soriculus fumudus</i>	Taiwan	GU 981278	AY033086	Fang, 2001
<i>Soriculus nigrescens</i>			GU981300	He <i>et al.</i> , 2010
<i>Sorex araeneus</i>	Switzerland	MVZ 155871	EU122225	Meegaskumbura <i>et al.</i> , 2007
<i>Talpa altaica</i>			AB037602	Tsuchiya <i>et al.</i> , 2000
<i>Talpa europaea</i>	Europe	–	AB037601	Tsuchiya <i>et al.</i> , 2000
<i>Euroscaptor longirostris</i>	Vietnam	MVZ 186406	EU122226	Meegaskumbura <i>et al.</i> , 2007



**Figure 1.** Maximum likelihood tree from MEGA version 6 of cytochrome-*b* sequence data with bootstrap values shown above branches. Bootstrap values obtained from maximum parsimony in PAUP\*v.4.0b10 are given below the branches. Nodes without MP bootstrap values are those that were unresolved in the MP tree.

## DISCUSSION

Though resolution of evolutionary relationships among taxa using DNA-sequence data has become an increasingly powerful method, only two studies so far have included a majority of crocidurine lineages in a molecular phylogeny. Querouil *et al.* (2001) included all African crocidurine genera except *Surdisorex*, while Dubey *et al.* (2007) included species from the Soricinae and representatives of three crocidurine genera (*Suncus*, *Crocidura* and *Sylvisorex*). The present study includes two monotypic genera, *Solisorex* and *Feroculus*.

The placement of the Myosoricinae has been ambiguous in the literature (Repenning, 1967; Hutterer, 1993; Querouil *et al.*, 2001; Dubey *et al.*, 2007). In this analysis, the Soricinae, Myosoricinae and Crocidurinae were all reciprocally monophyletic with high BS, with the Myosoricinae forming the sister group to Crocidurinae in the ML tree but not in MP tree. Querouil *et al.* (2001) found that the Myosoricinae formed the sister group of Soricinae, albeit with low bootstrap support (58%). The placement of Myosoricinae as the sister group to Crocidurinae was also observed by Dubey *et al.* (2007), who used 3314 bp of mitochondrial (cytochrome-*b* and 16S rRNA) and nuclear genes (BRCA1 and ApoB) sequences to construct the phylogeny. However, they did not recognize Myosoricinae as a separate subfamily, arguing that the branch lengths among the crocidurine shrews and myosoricine shrews are similar to those seen among some of the tribes in Soricinae. Regardless of the Linnaean taxonomic rank assigned, the currently recognized subfamilies, including the Myosoricinae, are clearly monophyletic. Similar to our ML tree, the placement of *Ruwenzorisorex*, *Scutisorex* and African *Suncus* species (*S. remyi*, *S. megalura*) with *Sylvisorex* in a single clade was reported by Stanley *et al.* (2013), based on partial sequences from the von Willebrand factor Exon 28 gene. However, *Scutisorex* is placed as a sister taxon to other crocidurine shrews (*Ruwenzorisorex*, *Suncus*, *Sylvisorex* and *Crocidura*) in a partial cytochrome-*b* gene tree (Stanley *et al.*, 2013). In both studies, however, the relationships among these taxa is not well resolved nor strongly supported.

The inclusion of the Sri Lankan endemic genera in the phylogeny revealed that *Solisorex* is indeed an ancient lineage: it forms the sister taxon to all the other crocidurine shrews. This relationship is well supported in both MP and ML trees. The position of *S. pearsoni* suggests an African origin for *Solisorex* and a dispersal event from Africa to Sri Lanka. It also suggests that there may have been

numerous extinctions of shrews after the period in which *Solisorex* and other African genera evolved, as there are no species or genera that show phylogenetic or morphological affinities to these genera in the Indian subcontinent or regions between Sri Lanka and Africa. Morphological characters of *Solisorex* also support the placement of *Solisorex* between myosoricine shrews and crocidurine shrews (Nowak, 1999). Morphologically, *Solisorex* and myosoricine shrews (*e.g.*, *Myosorex*, *Congosorex* and *Surdisorex*) share several characters: lack of long scattered hairs on the tail, larger manus claws, and three unicuspid teeth on the upper jaw instead of four as in the others. Other Crocidurinae genera share at least one of the above characters with Myosoricinae and *Solisorex*. For example, *Sylvisorex*, *Ruwenzorisorex* and *Scutisorex* lack long scattered hairs on the tail but have small claws and four unicuspid teeth; *Feroculus* have large manus claws but lack the other two characters; *Suncus* species do not share any of these characters with Myosoricinae and *Solisorex*, except *S. dayi*, which lacks long scattered hairs on the tail. *Crocidura/Paracrocidura* species share the same number of unicuspid teeth with Myosoricinae and *Solisorex*, and long tail hairs are present in some species but not others.

*Feroculus feroculus* shows closer phylogenetic affinities to *Suncus* species than to any of the other genera studied. Morphologically, *Feroculus* and *Suncus* share the same number of upper jaw teeth (18), with 4 unicuspid teeth and tails with long scattered hairs (except for *S. dayi*, which lacks these) on the tail. There are, however, distinct morphological characters that support the recognition of *Feroculus* as a distinct genus: large manus claws (as in *Solisorex*) and fully furred ears, whereas *Suncus* has small manus claws and semi-naked ears. *Feroculus* is also semi-aquatic, whereas *Suncus* is a land dweller (Phillips, 1980).

In summary, our analysis finds that *Solisorex* is an ancient lineage forming the sister taxon to all the other crocidurine shrews suggesting an African origin for the genus while *Feroculus* shows close affinities to south and southeast Asian *Suncus* species. This is the first attempt to investigate the phylogenetic position of these two monotypic genera. The lack of resolution in the phylogeny clearly points to the need for both greater taxonomic representation as well as increased data from the nuclear genome.

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