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Multilocus genetic and morphological phylogenetic analysis: Unveiling a new genus and species in the Tribe Nannenini of jumping spiders (Araneae, Salticidae)

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Abstract

Jumping spiders (Salticidae) are a diverse group of non-web-building predators and the most species-rich spider family. The Salticidae Tribe Nannenini consists of a small group of Oriental jumping spiders that are very poorly known. The use of explicit phylogenetic analyses to establish its affinities has so far remained limited. The Nannenini genus *Epidelaxia* has a peculiar morphology, making its systematic position uncertain. In this study, we present a comprehensive dataset combining molecular and morphological data for Nannenini, including exemplars from all genera. This dataset comprises DNA sequences of approximately 2400 bp, including nuclear genes (*18S*, *28S* and *H3*) and the mitochondrial gene *CO1*, sequenced for 40 taxa (20 ingroups and 20 outgroups), along with 61 morphological characters. Notably, both DNA sequences and morphological traits were analysed separately and concurrently for the first time. The Nannenini clade is recovered with high support. Further, *Epidelaxia* is monophyletic and sister to *Tubalaxia* gen. n. This is the first hypothesis on the internal phylogenetic structure of *Epidelaxia* and its placement within the Tribe Nannenini. A new genus *Tubalaxia* gen. n. and the following new species are described: *E. bharathi* sp. n., *E. somasundaram* sp. n., *T. castanea* sp. n., *T. aurea* sp. n. The following new combination is proposed: *Tubalaxia minuta* (Prószyński, 1992) **comb. n.** *Epidelaxia albostellata*, *E. albocruciata* and *E. obscura* are redescribed. It is worth noting that the newly described species face endangerment due to their limited distribution and small population sizes.

KEYWORDS

Ceylon, evolution, integrative taxonomy, morphological crypsis, new genera, speciation, synapomorphies, systematics

1 | INTRODUCTION

The jumping spider family Salticidae Blackwall, 1841 includes more than 6639 species in 680 genera (World Spider Catalog, 2023). They are cryptic, small- to large-sized, diurnal hunters that grab pray using their front pair of legs and chelicerae (Bartos, 2013; Bear & Hasson, 1997; Edwards & Jackson, 1993; Foelix, 2011; Li et al., 2003).

urn:lsid:zoobank.org:pub:BEC972EE-9DAB-412A-B033-82792106C4C6

TABLE 1 Material analysed, GenBank accession numbers and ID of vouchered DNA.

Species	Voucher number	Geographic origin	*COI*	*28S*	*18S*	*H3*
Ingroup taxa						
Epidelaxia albocruciata	NIFS_Sal_163	SL, WP, Labugama	**MW417111**	**MW414892**		**MW561196**
Epidelaxia albocruciata	NIFS_Sal_264	SL, Mihintale				**MW561202**
Epidelaxia albocruciata	NIFS_Sal_755	SL, SP, Hiyare				**MW561195**
Epidelaxia albocruciata	NIFS_Sal_966	SL, Singharaja	**MW417114**	**MW414895**	**MW414887**	**MW561200**
*Epidelaxia albocruciata**	NIFS_Sal_1088	SL, Pompakele	**MW558027**	**MW414897**	**MW414889**	**MW561198**
Epidelaxia albocruciata	NIFS_Sal_1286	SL, SP, Hiyare	**MW522569**	**MW414899**		
Epidelaxia albocruciata	NIFS_Sal_1300	SL, SP, Hiniduma		**MW414900**		
Epidelaxia albostellata	NIFS_Sal_445	SL, CP, Hakgala	**MW417112**	**MW414893**	**MW414886**	**MW561201**
*Epidelaxia albostellata**	NIFS_Sal_841	SL, CP, Loolecondera	**MW417113**	**MW414894**		
*Epidelaxia albostellata**	NIFS_Sal_1036	SL, CP, Horton Plains	**MW417115**	**MW414896**	**MW414888**	**MW561199**
*Epidelaxia albostellata**	NIFS_Sal_1095	SL, CP, Piduruthalagala	**MW417117**	**MW414898**	**MW414890**	**MW561197**
Epidelaxia albostellata	NIFS_Sal_1202	SL, CP, Horton Plains	**MW522569**			
*Epidelaxia bharathi**	NIFS_Sal_1144	SL, CP, Pitawala Patana	**MW549008**			
*Epidelaxia somasundaram**	NIFS_Sal_1092	SL, CP, Kataragama Peak	**MW417116**			
Tubalaxia aurea	NIFS_Sal_261	SL, CP, Knuckles		**MW414901**		**MW56119**
*Tubalaxia aurea**	NIFS_Sal_901	SL, CP, Upcot	**MW417118**	**MW414903**	**MW414891**	
*Tubalaxia castanea**	NIFS_Sal_444	SL, CP, Horton Plains		**MW414902**		
*Idastrandia orientalis**		Malaysia: Sabah	EU815608	EU815496	EU815535	
*Langerra longicymbium**		Malaysia		KM003185		
*Nannenus lyriger**		Malaysia		EU815493		
Outgroup taxa						
*Chrysilla volupe**	NIFS_Sal_443	SL, CP, Ballagola	MG910461	MG883389	MG883392	
Chrysilla sp.	NIFS_Sal_239	SL, CP, Kandy				MW573969
*Siler semiglaucus**	NIFS_Sal_731	SL, SP, Galle	KY888770	KY888731	KY888711	MW573967
*Phintella vittata**	NIFS_Sal_816	SL, Mihintale	KY888751	KY888728	KY888698	
*Bristowia gandhii**	NIFS_Sal_357	SL, CP, Badulla	KY888778	KY888738	KY888703	MW573968
*Habrocestum hantanensis**	NIFS_Sal_827	SL, CP, Loolecondera	KY888765	KY888739	KY888716	
*Hasarius adansoni**	NIFS_Sal_268	SL, CP, Kandy	KY888756	KY888749	KY888700	MW573961
Carrhotus silanthi	NIFS_Sal_825	SL, CP, Mihintale	MW655746	MW678611	MW678615	MW573965
Marengo crassipiens	NIFS_Sal_038	SL, CP, Riverston	MT828396	MW699920		
Marengo crassipiens	NIFS_Sal_247	SL, CP, Riverston				MW714332
Ballus segmentatus	NIFS_Sal_851	SL, CP, Hakgala	MT828385			MT828424
Telamonia vlijimi		South Korea	JN817281	JN81706		
Telamonia sp.	NIFS_Sal_1161	SL, NP, Mannar				MW573962
Pancorius sp. B		Malaysia	JX145697	JX145781		
Pancorius sp.	NIFS_Sal_1145	SL, CP, Knuckles				MW573963
Evarcha proszynskii		Canada	KM838343	DQ665765	KM033112	
Evarcha sp.	NIFS_Sal_1048	SL, CP, Loolecondera				MW573964
Plexippus setipes		South Korea	JN817262	AY671967		
Plexippus sp.	NIFS_Sal_162	SL, CP, Udawattakele				MW573970

TABLE 1 (Continued)

Species	Voucher number	Geographic origin	*COI*	*28S*	*18S*	*H3*
Harmochirus sp.	NIFS_Sal_751	SL, SP, Hiyare	JX145693	JX145777		MW573966
Bianor maculatus		Australia	EU815585	EU815469		KM033200

Note: Details of exemplars used in this study including collection localities, GenBank accession and NIFS catalogue numbers. Accession numbers in bold denote sequences generated for this study. * denotes taxa included in the morphological matrix (see Table 3 for details). All species belong to the Family Salticidae. SL: Sri Lanka; CP: Central Province; UP: Uva Province; SP: Southern Province.

TABLE 2 Gene targets, PCR conditions and nucleotide sequences of the primers used in this study; and model selected for Bayesian Inference using the Akaike Information Criterion (AIC).

Gene	Annealing Temperature/time	Primer pair	5′-primer sequence −3′	Reference	AIC
CO1	46°C/ 50 s	CO1-1628 (F) CI-N-2191 (R)	ATAATGTAATTGTTACTGCTCA CCCGGTAAAATTAAAATATAAA	a b	SYM + I
18S	46°C/ 50 s	18S 1F 18S 5R	TACCTGGTTGATCCTGCCAGT CTTGGCAAATGCTTTCGC	c d	SYM + I
28S	60(50)°C/1.5 min	28S O (F) 28S C (R)	GAA ACT GCT CAA AGG TAA ACG G GGT TCG ATT AGT CTT TCG CC	e e	GTR + G + I
H3	60(50)°C/1.5 min	H3a (F) H3a (R)	ATG GTC CGT ACC AAG CAG ACV ATA TCC TTR GGC ATR ATR GTG	f f	SYM + I

Note: a: Simon et al., 1994, b: Dallas et al, c: Giribet & Ribera, 2000, d: Giribet et al., 1996, e: Whiting et al., 1997, f: Colgan et al., 1998.

They live in microhabitats ranging from foliage, flowers, tree bark and leaf litter. Their eye structure, complex vision-based courtship displays, mimicry and predator ecology make them ideal modal organisms for the study of visual physiology, behaviours and other evolutionary phenomena (Benjamin, 2004; Foelix, 2011; Jackson & Pollard, 1996; Kanesharatnam & Benjamin, 2016; Richman & Jackson, 1992).

The Salticidae tribe Nannenini Maddison, 2015 **consists** of a small group of Oriental spiders that are very poorly known. However, they are frequently found in collections of spiders from the region's intact tropical rainforest. They are often overlooked due to their cryptic nature and habitat preference for the leaf litter of the forest floor (Prószyński & Deeleman-Reinhold, 2012; Maddison, 2015, Benjamin, unpublished data). Presently, only *Nannenus* and *Idastrandia* can be unequivocally assigned to the tribe (Maddison, 2015). *Langerra* was recently tentatively placed in Nannenini by Maddison (2015). Further, he suggested that *Epidelaxia*, *Lechia* and *Leuserattus* might be nannenines.

Sri Lanka together with the Western Ghats is one of the 34 biodiversity hotspots with a highly diverse endemic fauna arising most probably from autochthonous diversification (Myers et al., 2000). Sri Lanka is known for several unique lineages of jumping spiders represented by 149 species placed in 66 genera, including 58 endemic species (World Spider Catalog, 2023). During the last two decades, the evolutionary history of the Salticidae in Sri Lankan has been extensively studied (Benjamin, 2004, 2010; Bopearachchi & Benjamin, 2021; Edwards & Benjamin, 2009; Kanesharatnam & Benjamin, 2016, 2018, 2019). In this study, we report on the diversity of a genus endemic to the island.

The genus *Epidelaxia* was erected by Eugène Simon (1902) and encompasses three species: *E. albostellata*, *E. albocruciata* and *E. obscura*. All three species are endemic to Sri Lanka. Members of this genus are characterized by the presence of a prominent, yellow triangular-shaped mark in the prosoma of females and the distinctive morphology of the copulatory organs including, palp and epigyne: short and straight embolus, presence of membranous outgrowth of tegulum and well-developed C or S-shaped membranous atrial rims in females.

Since its initial description, *Epidelaxia* remained taxonomically unrevised and has never been subjected to phylogenetic evaluation. It is placed among the genera listed as Salticinae *incertae sedis* by Maddison (2015). Nannenini are a group of jumping spiders that make up a poorly known but common component of Southeast Asian faunas, especially on leaf litter (Maddison, 2015; Prószyński & Deeleman-Reinhold, 2012). The uncertain phylogenetic placement of *Epidelaxia* is partly due to the Nannenini not having clear morphological synapomorphies defining it, as neither the fixed embolus nor the long macrosetae under tibia I, provides a clear synapomorphy for the group (Maddison, 2015). However, molecular phylogenetic studies combining several genes support the monophyly of Nannenini (Bodner & Maddison, 2012; Maddison, 2015; Maddison et al., 2014).

During fieldwork conducted throughout the island, we collected specimens of all three known species. Specimens from high-elevation montane and sub-montane forests in the central highlands of Sri Lanka matched the description of *E. albostellata*. They have a characteristic black cephalothorax with darkened red-coloured hairs, elongated and darkened abdomen, slightly white-haired thoracic margins, slender palps and a thin, pale saffron-coloured, elongated embolus and an ovate bulbus. Specimens from lowland secondary rainforests of the dry and wet zones of Sri Lanka matched the description of *E. albocruciata*. They have a short and narrow clypeus and dark and oblong-shaped

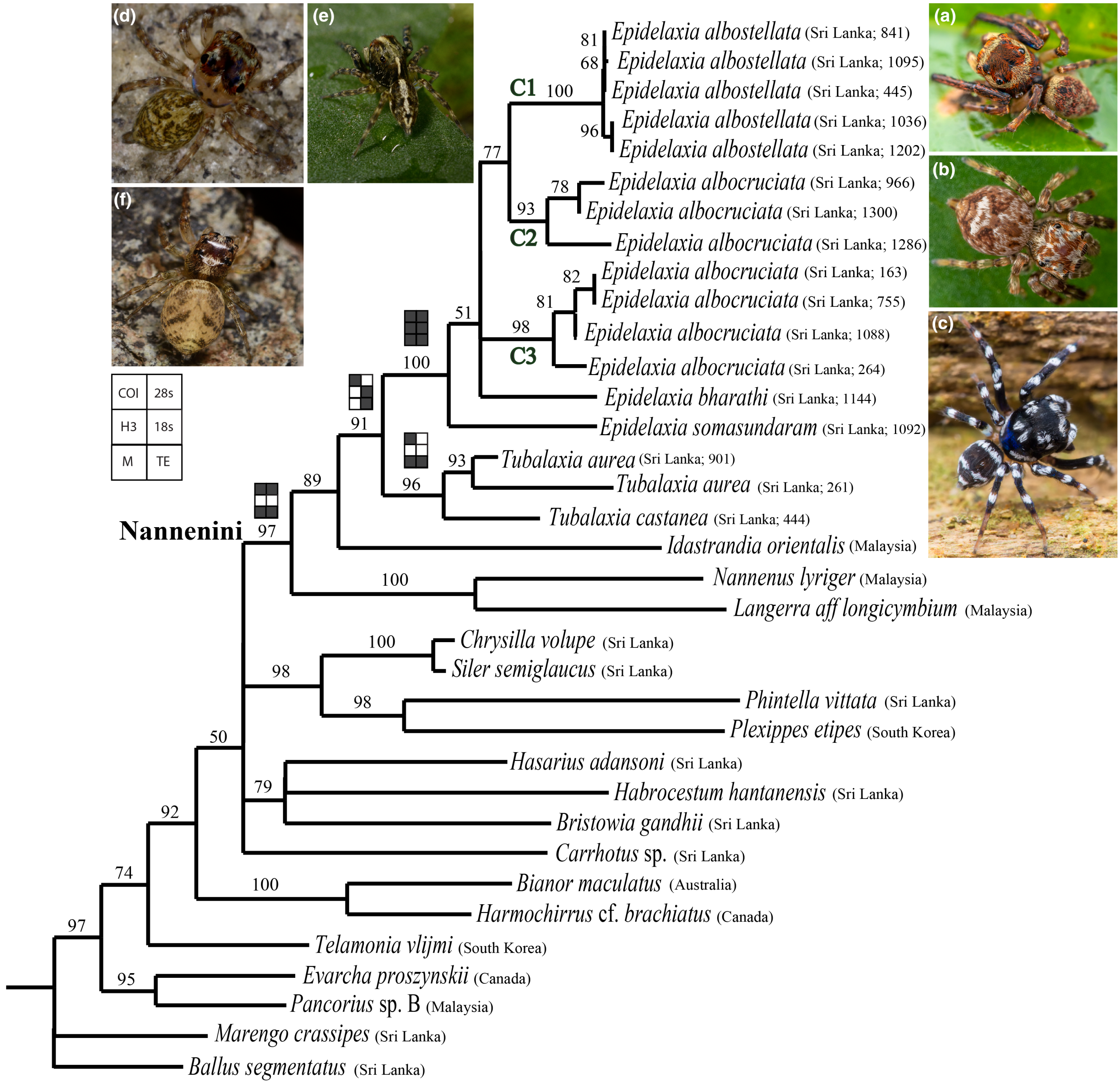

FIGURE 1 The single most likely tree obtained by ML analysis of the combined molecular data in RAxML–VI–HPC. The numbers above the nodes represent bootstrap values (only values 50 and above are given). Nodes that are unsupported have been collapsed. Collection country is given if available. 'Navajo rugs' indicate presence (black) or absence (white) of a given node in the tree specified in the legend. The images of *Idastrandia* from Singapore (a), *Langerra* from Malaysia (b) and *Nannenus* from Singapore (c) are courtesy of Mr. Nicki Bay (a, b) and Mr. K. S. Tan (C). The images of *Epidelaxia albocruciata* (d), *E. albocruciata* (e) and *Tubalaxia aurea* (f) are all from Sri Lanka.

abdomen. Specimens collected from Kandy and Badulla districts matched the description of *E. obscura*. All these specimens have the characteristic short, broad and blackened cephalothorax; thoracic part thin-white lined hairs in the centre, abdomen oblong, dark, blackened, greyish and striated abdomen. Blackened chelicerae and palps; and entirely darkened and blackish colouration on legs I and II.

Our main objectives are to test the monophyly of the tribe Nannenini with a special focus on *Epidelaxia* and to assess its relationships to other Salticidae using a multi-locus molecular (mitochondrial and nuclear) plus morphological dataset. In this endeavour, we described a new genus and four new species. Further, we circumscribe *Epidelaxia* in phylogenetic terms and provide an updated diagnosis.

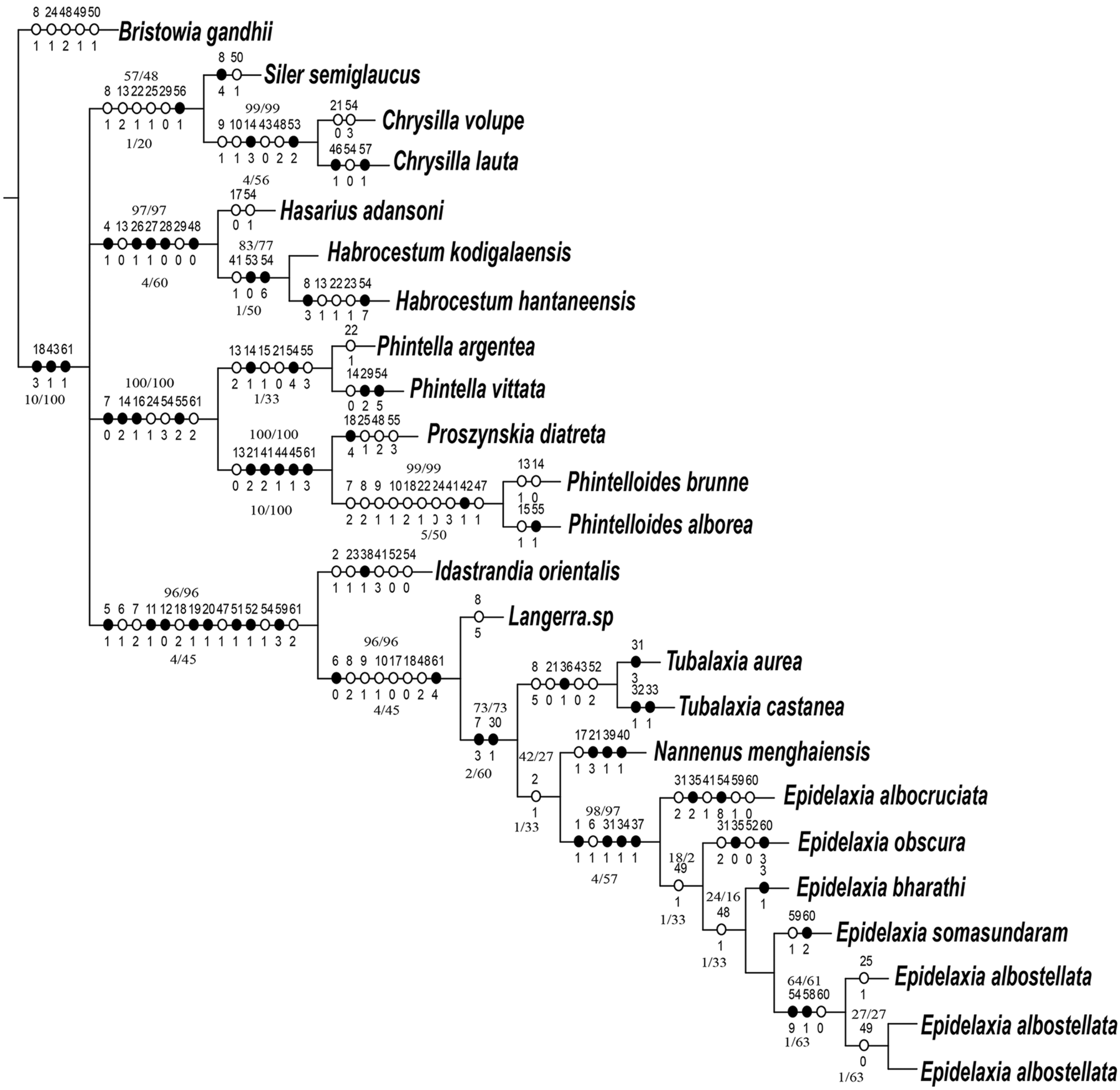

FIGURE 2 Phylogeny of the Nannenines with unambiguous morphological synapomorphies optimized. Black circles indicate uniquely derived apomorphic states, white circles parallel derivations of apomorphic states. Numbers above circles indicate characters, numbers below indicate states. The values above the lines represent sympatric resampling frequency differences, while the values below the line represent Bremer support/relative Bremer support.

TABLE 3 Phylogenetic data matrix scored for taxa.

Taxa	Characters 1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7	8	9	30	1	2	3	4	5	6	7	8	9	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4
Bristowia gandhi	0	0	-	0	0	2	1	1	0	0	1	0	1	4	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	-	0
*Hasarius adansoni**	0	0	-	1	0	2	1	0	0	0	1	0	0	4	0	0	0	-	-	?	1	0	0	0	0	1	1	0	0	0	-	-	-	0	-	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	-
Habrocestum kodigalaensis	0	0	-	1	0	2	1	0	0	0	1	0	0	4	0	0	1	3	0	0	1	0	0	0	0	1	1	0	0	0	-	-	-	0	-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	-	-
Habrocestum hantanensis	0	0	-	1	0	2	1	3	0	0	1	0	1	4	0	0	1	3	0	0	1	1	1	0	0	1	1	0	0	0	-	-	-	0	-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	-	1
Chrysilla volupe	0	0	-	0	0	2	1	1	1	1	1	0	2	3	0	0	1	3	0	0	0	1	0	0	1	0	0	1	0	0	-	-	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	-	-
Chrysilla lauta	0	0	-	0	0	2	1	1	1	1	1	0	2	3	0	0	1	3	0	0	1	1	0	?	?	?	?	?	?	?	?	?	-	?	?	?	?	?	?	?	?	0	0	0	0	1	0	2	0	1	0	0	-	-
Siler semiglaucus	0	0	-	0	0	2	1	4	0	0	1	0	2	4	0	0	1	3	0	0	1	1	0	0	1	0	0	1	0	0	-	-	-	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	-	-
Phintelloides brunne	0	0	-	0	0	2	2	2	1	1	1	0	1	0	0	1	1	2	0	0	2	1	0	0	0	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	1	1	0	1	0	1	1	2	0	0	0	-	-
Phintelloides alborea	0	0	-	0	0	2	2	2	1	1	1	0	0	2	1	1	1	2	0	0	2	1	0	0	0	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	-	-
Proszynskia diatreta	0	0	-	0	0	2	0	0	0	0	1	0	0	2	0	1	1	4	0	0	2	0	0	1	1	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	0	1	1	1	0	0	2	3	0	0	0	-	3
Phintella argentea	0	0	-	0	0	2	0	0	0	0	1	0	2	1	1	1	1	3	0	0	0	1	0	1	0	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	0	1	1	0	0	0	1	3	0	0	0	-	--
Phintella vittata	0	0	-	0	0	2	0	0	0	0	0	0	2	0	1	1	1	3	0	0	0	0	0	1	0	0	0	1	2	0	-	-	-	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1	3	0	0	0	-	4
Epidelaxia albocruciata	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	0	0	1	0	4
Epidelaxia obscura	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	0	0	3	3	4
Epidelaxia bharathi	1	1	1	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	3	1	4
Epidelaxia albostellata	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	1	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	3	0	4
Epidelaxia albostellata	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	3	0	4
Epidelaxia albostellata	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	3	0	4
Epidelaxia somasundaram	1	1	0	0	1	1	3	2	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	2	4
Tubalaxia aurea	2	0	-	0	1	0	3	5	1	1	0	1	-	-	0	0	0	-	-	-	0	0	0	0	0	0	0	1	1	1	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	3	-	4
Tubalaxia castanea	2	0	-	0	1	0	3	5	1	1	0	1	-	-	0	0	0	-	-	-	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	3	-	4
Idastrandia orientalis	2	0	0	0	1	1	2	0	0	0	0	1	-	-	0	0	1	2	1	1	1	0	1	0	0	0	0	1	1	0	-	-	-	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	3	1	2
Nannenus lyriger	1	1	0	0	1	0	3	2	1	1	0	1	-	-	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	1	0	2	1	0	-	0	0	0	1	1	0	0	1	0	0	0	1	2	0	0	0	3	1	-
Langerra sp.	2	0	-	0	1	0	2	5	1	1	0	1	-	-	0	0	0	-	-	-	1	0	0	0	0	0	0	1	1	0	-	-	-	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	4

Note: The first state ‘0’ followed by ‘1’etc.; ‘?’ denotes missing data; ‘?’ denotes missing data, ‘_’is inapplicable.

2 | MATERIALS AND METHODS

2.1 | Taxon selection

The selection of outgroup taxa is based on Maddison (2015). For the separate molecular analysis and simultaneous analysis, we included 16 taxa belonging to 6 tribes (*Bristowia, Hasarius, Habrocestum, Chrysilla, Siler, Phintella, Ballus, Marengo, Schenkelia, Pancorius, Evarcha, Plexippus, Carrhotus, Bianor, Harmochirus, Telamonia*). *Idastrandia orientalis, Langerra* sp., *Nannenus* sp. and all *Epidelaxia* species. were selected as hypothetical ingroup taxa. Based on our analysis of the molecular data and availability of material within Sri Lanka, the following outgroup taxa were selected for the morphological analysis: *Hasarius adansoni* (Audouin, 1826), *Habrocestum kodigalaensis, H.hantanensis* and *Bristowia gandhii* Kanesharatnam & Benjamin, 2016. *Phintella argentea, Phintella vittata, Phintelloides brunne, Phintelloides alborea, Proszynskia diatreta* Kanesharatnam & Benjamin, 2019, *Idastrandia orientalis* Yamasaki et al., 2017, *Langerra oculina* Logunov, 2021, *Nannenus menghaiensis* Cao et al., 2016.

2.2 | Morphology

Phylogenetic relationships among the species of *Epidelaxia* were inferred using a subset of characters from the matrix of Benjamin and Kanesharatnam (2016). The description

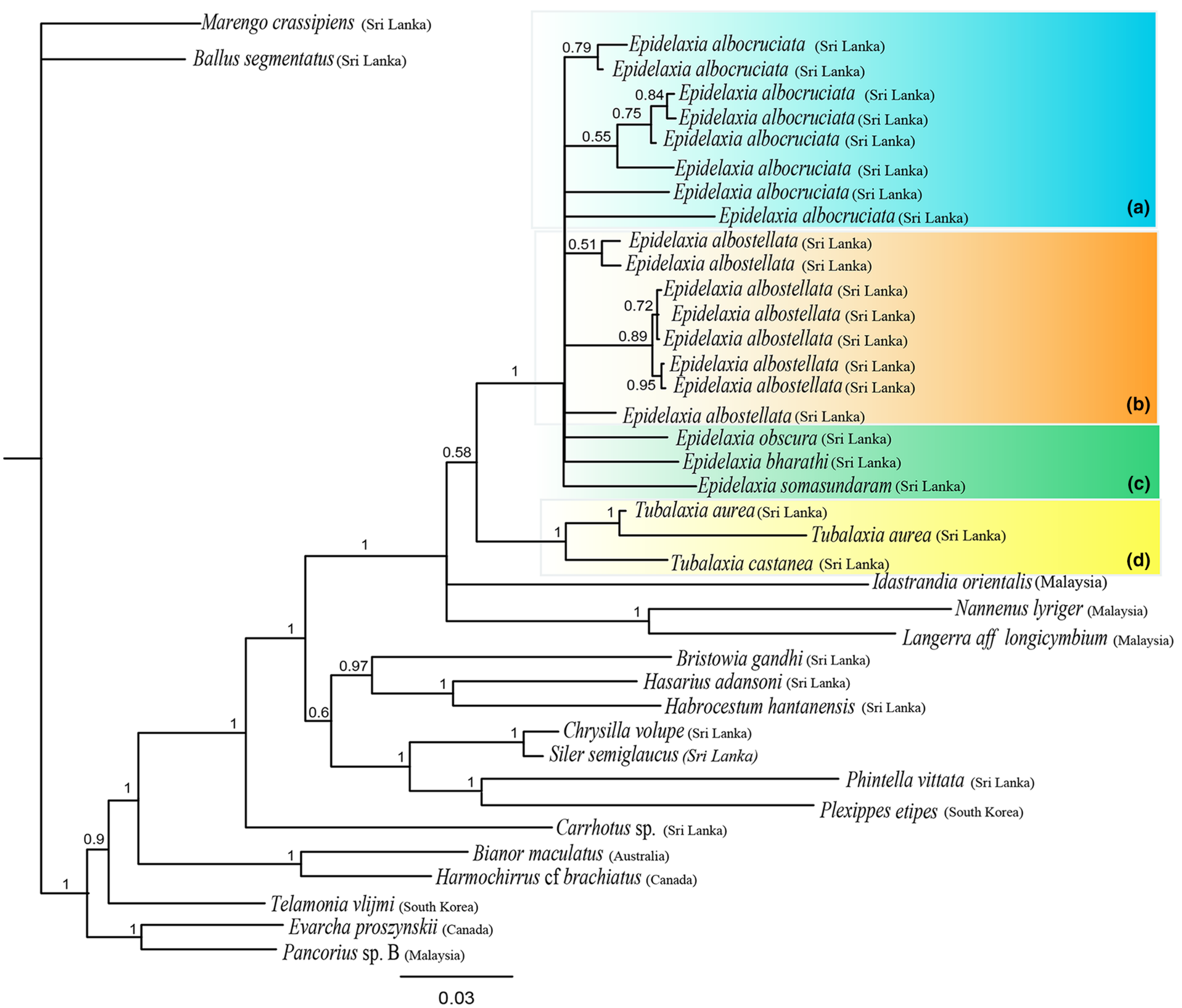

FIGURE 3 Phylogeny of the Nannenines obtained by simultaneous phylogenetic analysis of 61 morphological characters and 2466 aligned DNA nucleotides from two mitochondrial and two nuclear gene loci obtained using Bayesian inference. Numbers adjacent to nodes are posterior probabilities (>0.5).

FIGURE 4 Photographs of live *Epidelaxia albostellata*. Male (a–d) from Corbett's Gap, Knuckles range, Sri Lanka.

FIGURE 5 Photographs of live *Epidelaxia albostellata*. Female (a, b). from Horton Plains NP. Female (c, d) from Hakgala SNR, Sri Lanka.

of new species is based on the format of Benjamin (2004, 2010). Either a Nikon D80 or a D7000 camera with a macro lens was used to take photographs of live spiders. Specimens for the morphological study were preserved in 70% ethanol and studied using an Olympus SZX7 stereomicroscope. Drawings of palps, epigynes and vulvae were made with the aid of a drawing tube attached to Leica DM3000 LED compound microscope. Photographs of palps, epigynes and intact spiders were taken with a Leica MC170 HD camera mounted on a Leica M205C stereomicroscope using Leica Application Suite software (Leica Microsystems Limited, Germany). Images were merged with Helicon Focus image stacking software (version 6, Helicon Soft Ltd). Images were then edited with Adobe Photoshop CC and assembled using Adobe Illustrator CS6. All measurements are in millimetres. Body length was measured as carapace length plus abdomen length (excluding spinnerets). Types and other specimens of species described herein are currently deposited in the National Institute of Fundamental Studies (NIFS) in Kandy, Sri Lanka. Description of characters and their states are given in Supplementary information S2.

2.3 | Gene targets and primers

A multilocus molecular approach was used for this study and the target loci were selected based on prior molecular phylogenetic studies of salticids (e.g., Bodner & Maddison, 2012; Hedin & Maddison, 2001). Partial fragments of the mitochondrial protein-encoding gene Cytochrome *c* oxidase subunit I (*CO1*- 525 bp) and histone *H3* (318 bp), partial fragments of nuclear small and large subunit ribosomal RNA *18S* (878 bp) and *28S* (806 bp) were amplified. Details of each primer pair used, primer sequences, annealing temperatures and related references are given (Table 2).

2.4 | DNA extraction, PCR and sequencing

DNA extraction was performed using Qiagen DNeasy Tissue kit (Qiagen Inc., Valencia, CA, USA), following the manufacturer's protocols. Genomic DNA was extracted,

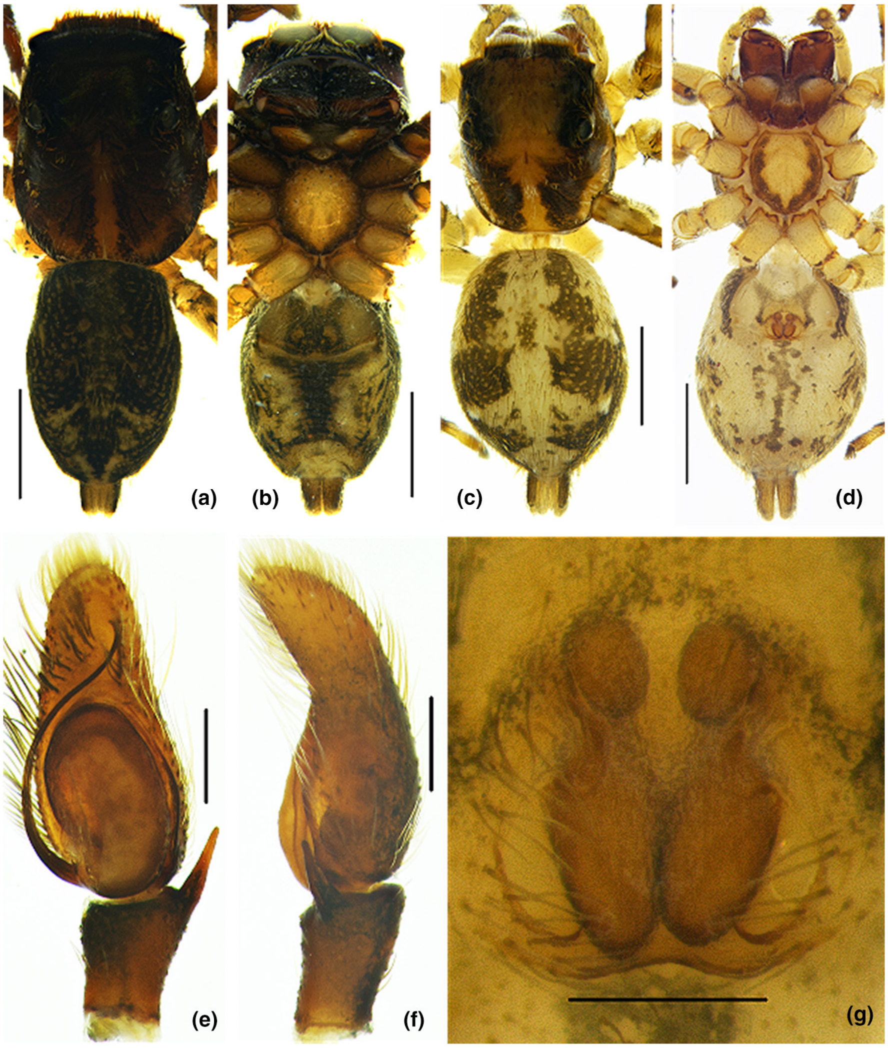

FIGURE 6 *Epidelaxia albostellata* from Piduruthalagala (a–g); (a, b) Male habitus, (IFS_SAL_1096). (a) dorsal view, (b) ventral view. (e, f) Palp, (e) ventral view. (f) retrolateral view. (c, d) Female habitus, (IFS_SAL_1095). (c) dorsal view. (d) ventral view. (g) Epigynum. Scale bars: a–d = 2 mm, e–f = 0.2 mm, g = 0.1 mm.

depending on size, from the first two legs of each specimen and the remainder was stored in 70% ethanol and deposited in the NIFS arachnid collection. Extracted DNA was stored at −21°C until required for Polymerase Chain Reaction (PCR). PCR was carried out using either the Multiplex PCR kit (Qiagen) or the PuReTaq Ready-To-Go™ PCR beads (GE Healthcare, UK). Total reaction mixture consisted of 20 μL, including 2.5 μL undiluted DNA template, 1.6 μL forward and reverse primers, 10 pmμL^{-1}of Q-Solution, 10 μL 'Multiplex PCR Master Mix' containing hot start Taq DNA Polymerase, buffers and 2.3 μL of water (all the components come with the Multiplex kit). In the case of PCR beads, the total reaction mix was 25 μL and included 13 μL of ultrapure RO water. 1 μL of each of the forward and reverse primers (10 pmμL^{-1}) and 10 μL undiluted DNA template. A negative control (minus the template) was included to test for contamination during PCR runs. The primers used for amplification and their sources are given (Table 2).

PCR products were verified on a 1% agarose gel and purified using Gene Clean™ Turbo kit (MP Biomedicals, LLC, USA). All purified PCR products were Sanger sequenced (Sanger et al., 1977) in both directions by Macrogen (Seoul, South Korea).

2.5 | Sequence alignment and editing

Sequences were assembled and edited using Geneious 11.1.5. Sequences were aligned in Geneious with the options: automatically determine sequences 'direction, create alignment of consensus sequences only, gap open penalty 12, gap extension penalty 3, type of global alignment, refinement iterations 2. Edited sequences were

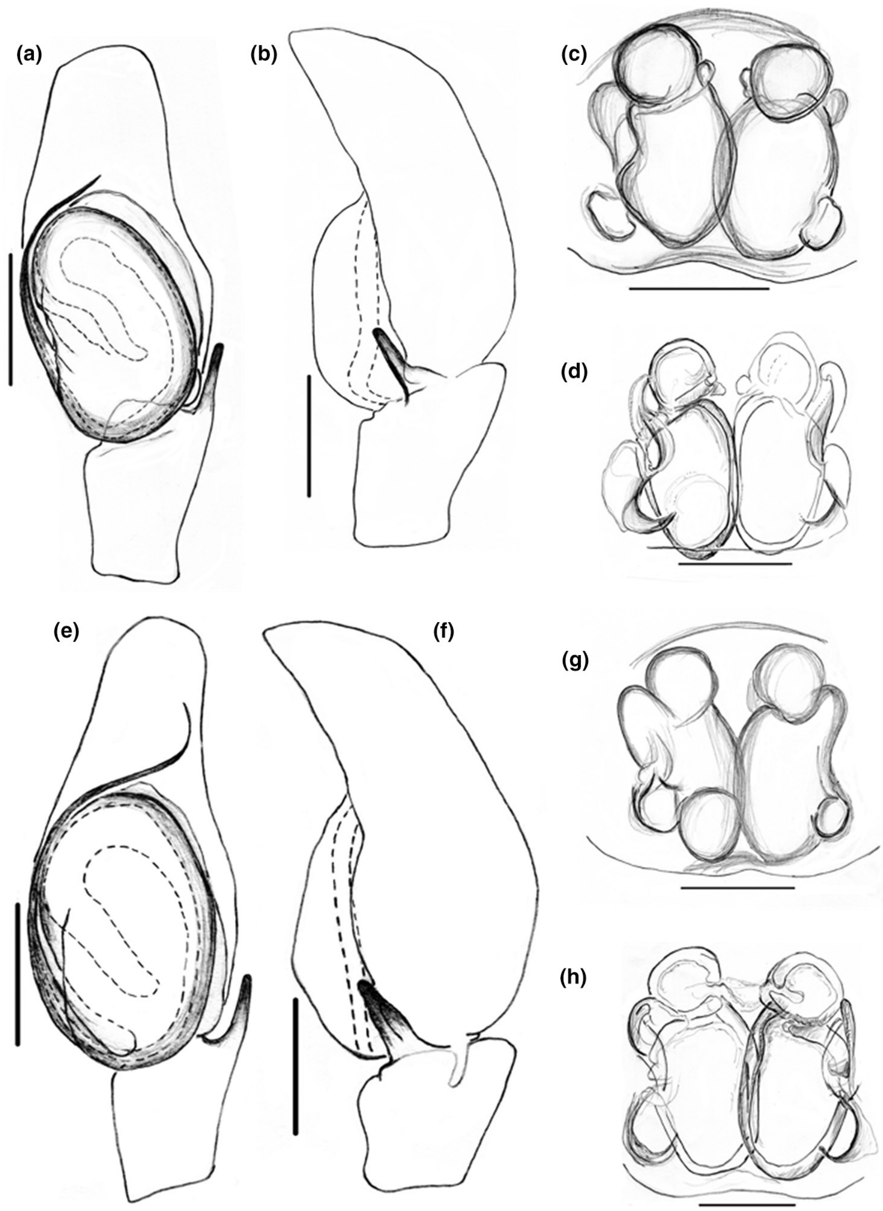

FIGURE 7 *Epidelaxia albostellata* (a–h); (a, b, e, f) Palp. (a, e) ventral view. (b, f) retrolateral view. (c, g) Epigynum, ventral view. (d, h) Vulva, dorsal view. (a–d) Horton plains (IFS_SAL_096, 475), (e–h) Loolecondera (IFS_SAL_841, 842). Scale bars: c, d, g, h = 0.1 mm, a, b, e, f = 0.2 mm.

FIGURE 8 Photographs of live *Epidelaxia albocruciata*. Female (a, b) from Hiyare. male (c, d) from Singharaja Forest Reserve.

FIGURE 9 *Epidelaxia albocruciata* from Pompakele Forest Reserve (a–g); (a, b) Male habitus, (IFS_SAL_1088). (a) dorsal view. (b) ventral view. (e, f) Palp, (e) ventral view. (f) retrolateral view. (c, d) Female habitus, (IFS_SAL_1089). (c) dorsal view. (d) ventral view. (g) Epigynum. Scale bars: a–d = 2 mm, e, f = 0.2 mm, g = 0.1 mm.

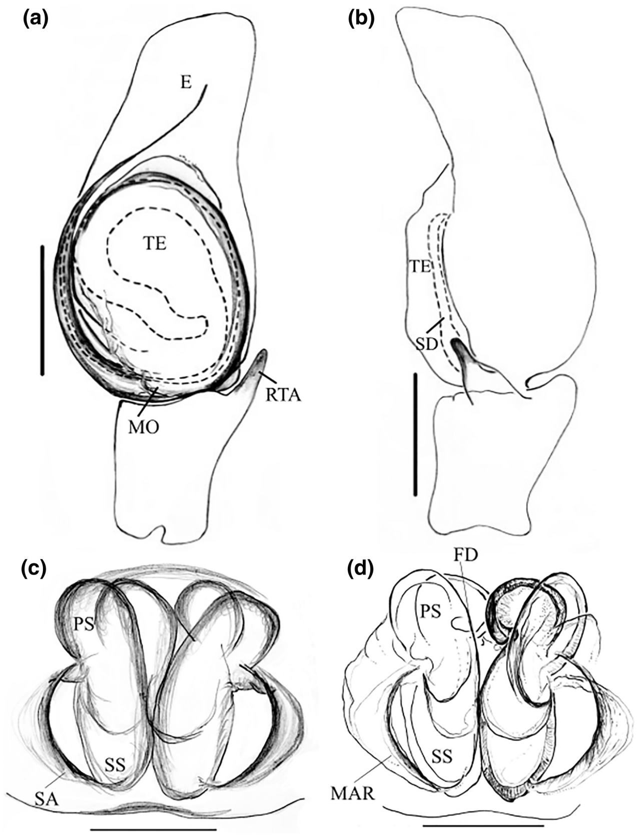

FIGURE 10 *Epidelaxia albocruciata* from Pompakele Forest Reserve (a–d); (a, b) Palp, (IFS_SAL_1088). (a) ventral view. (b) retrolateral view. (c, d) Epigynum, (IFS_SAL_1089). (c) ventral view, (d) dorsal view. E, embolus; FD, fertilization duct; MAR, membranous atrial rim; MO, membranous outgrowth; PS, primary spermathecae; RTA, retrolateral tibial apophysis; SA, sclerotized arch; SD, sperm duct; SS, secondary spermathecae. TE, tegulum; Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

queried by blasting against the NCBI BLAST database (http://blast.ncbi.nlm.nih.gov) to check for possible contamination. The sequences obtained from NCBI were imported and aligned with our sequences in Geneious. The alignment of the non-coding *28S* was further refined manually in Mesquite by trimming. Finally, the fragments were assembled into five separate multiple sequence alignments (*CO1*-single gene, *H3*-single gene *28S*-single gene, *18S*-single gene and concatenated *CO1* + *18S* + *28S* + *H3*). The combined gene matrix was converted to tnt format using the program Sequence Matrix. All new sequences were submitted to GenBank; accession numbers are given (Table 1). The lengths of the targeted fragments after excluding primers were as follows: *18S*716 bp, *28S* 806 bp, *CO1* 524 bp and *H3* 317 bp. The assembled matrix of the concatenated mitochondrial and nuclear markers includes 40 taxa (20 ingroups, 20 outgroups). The total length of the final matrix was 2466 bp. The final matrix has been uploaded to figshare: 10.6084/m9.figshare.25516138.

2.6 | Phylogenetic analyses

The morphological character matrix and the concatenated dataset of aligned nuclear and mitochondrial DNA sequences were analysed simultaneously using Bayesian Inference (BI). Additionally, to provide an independent comparison, the morphological and combined molecular datasets were analysed separately using parsimony with equal and implied weighting. Further, molecular data of the individual gene fragments were also analysed separately using BI and ML.

Twenty-four nucleotide substitution models were tested for each locus using JModeltest ver.2.1.6 (Darriba et al., 2012; Guindon & Gascuel, 2003) on the CIPRES gateway (Miller et al., 2011). Models were selected using the Akaike Information Criterion (AIC) and a gamma distribution was assumed for the morphological dataset (Lewis 2001; Table 2). Using these models, BI was conducted in MrBayes v.3.2.7 (Ronquist & Huelsenbeck, 2003) with unlinked parameters for all partitions and the following settings: mcmc; nchains = 4; print frequency = 1000; sample frequency = 1000; diagnosing frequency = 1000; burnin = 0.25; savebrlens = yes. The analysis was terminated after 25 million generations when the standard deviation of the split frequencies was below 0.01.

The ML analysis was conducted using RAxML (Boc et al., 2012; Stamatakis, 2006). The best-fit model for likelihood analysis was searched by running the 'find best DNA/protein model (ML)' option in MEGA X and models with the lowest values of Bayesian Information Criteria and Akaike Information Criteria were selected. A rapid bootstrap analysis with 1000 replicates was used to search for the ML tree. The parameters used were as follows: substitution model (GTRGCAT), algorithm executed (Hill climbing -default), seed (12345), outgroup (Marengo_sp) and the number of alternative runs on distinct starting trees (1000). The trees were viewed using the same program.

Parsimony analysis of the morphological data matrix (61 potentially informative characters) and the four-gene combined molecular data matrix was carried out using 'traditional search' mode in TNT 1.1 (Goloboff et al., 2003, 2008). Under equal and implied weights, traditional searches were performed with the following settings: 1000 random addition sequence replicates and tree bisection reconnection (tbr) swapping algorithm saving 10 trees per replication. The concavity constant (K) was set to values of 3–10, max trees were set to 100,000. Group support values and Bremer and Relative Bremer indices (Bremer, 1988, 1994) were calculated using the 'aquickie.run' script in TNT. Ambiguous character optimizations were resolved to favour early gains of features with subsequent reversals (Farris optimization or

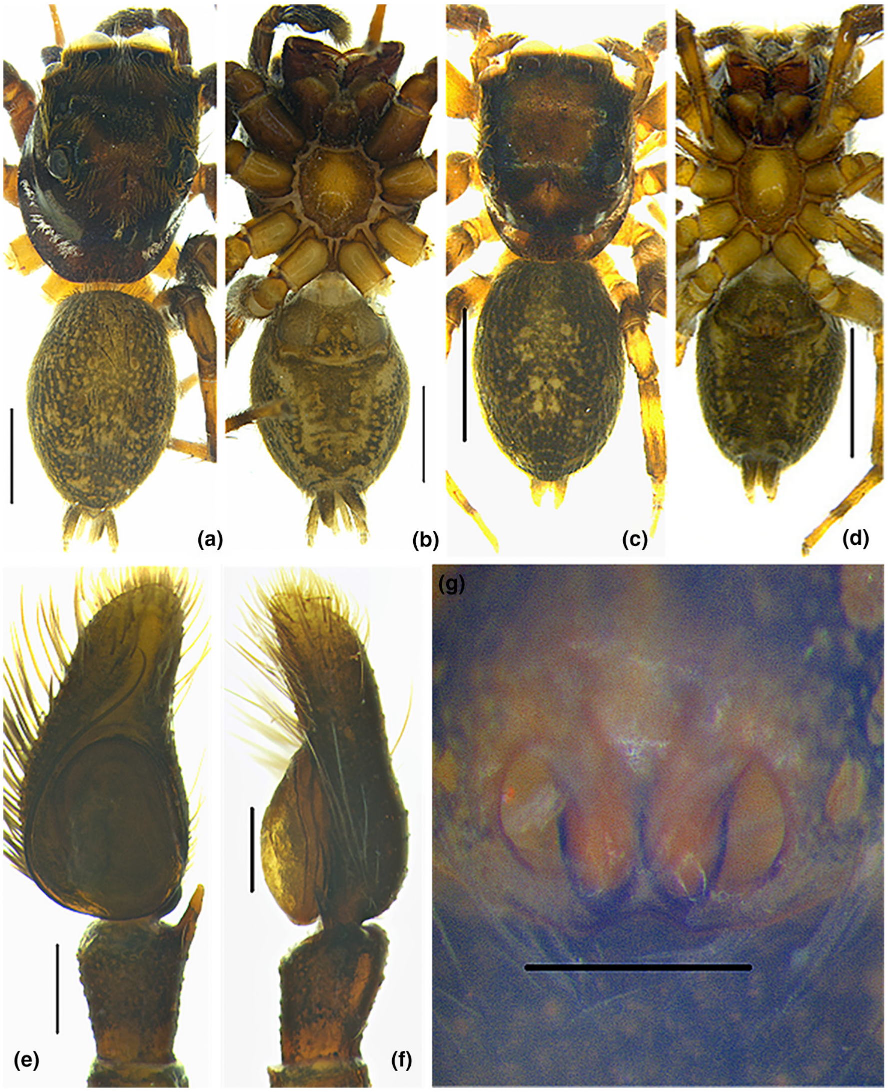

FIGURE 11 *Epidelaxia obscura* from Knuckles Forest Reserve (a–g); (a, b) Male habitus, (IFS_SAL_722). (a) dorsal view. (b) ventral view. (e, f) Palp, (e) ventral view. (f) retro lateral view. (c, d) Female habitus, (c) dorsal view. (d) ventral view. (g) Epigynum, (IFS_SAL_721). Scale bars: a–d = 2 mm, e, f = 0.2 mm, g = 0.1 mm.

ACCTRAN). All multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch, 1971) as no transformation series could be inferred. Winclada version 1.00.08 (Nixon, 2002) was used for mapping of characters and characters stated onto a preferred parsimonious tree and strict consensus tree.

3 | RESULTS

The assembled matrix of the concatenated mitochondrial and nuclear markers included 94 sequences of 41taxa; 39 of these sequences were newly generated for this study. The morphology of 74 adult specimens was studied. Fifty-four potentially informative characters (40 binary and 15 multistate) were identified and scored for 24 taxa. Thirty-six characters describe morphology of the copulatory organs and 41 describe somatic morphology. The results of the phylogenetic analyses are summarized in Figures 1–3, which combine all evidence in Bayesian and ML analyses.

3.1 | Simultaneous analyses

The ML cladogram resulting from simultaneous analyses of all molecular data is shown in Figure 1. The Nannenini clade is recovered with high support. *Epidelaxia* is monophyletic and sister to *Tubalaxia*. Within *Epidelaxia*, both *E. albostellata* and *E. albocruciata* together are sister species to *E. bharathi* and *E. somasundaram*. However, *E. albocruciata* is paraphyletic. All internal nodes received high support. The BI cladogram resulting from simultaneous analyses of all evidence is shown in Figure 3. This total evidence cladogram also recovers Nannenini with high support. Further, *Epidelaxia* is monophyletic and sister to *Tubalaxia*. However, relationships within *Epidelaxia* are same as in the ML cladogram resulting from simultaneous analyses of all molecular data

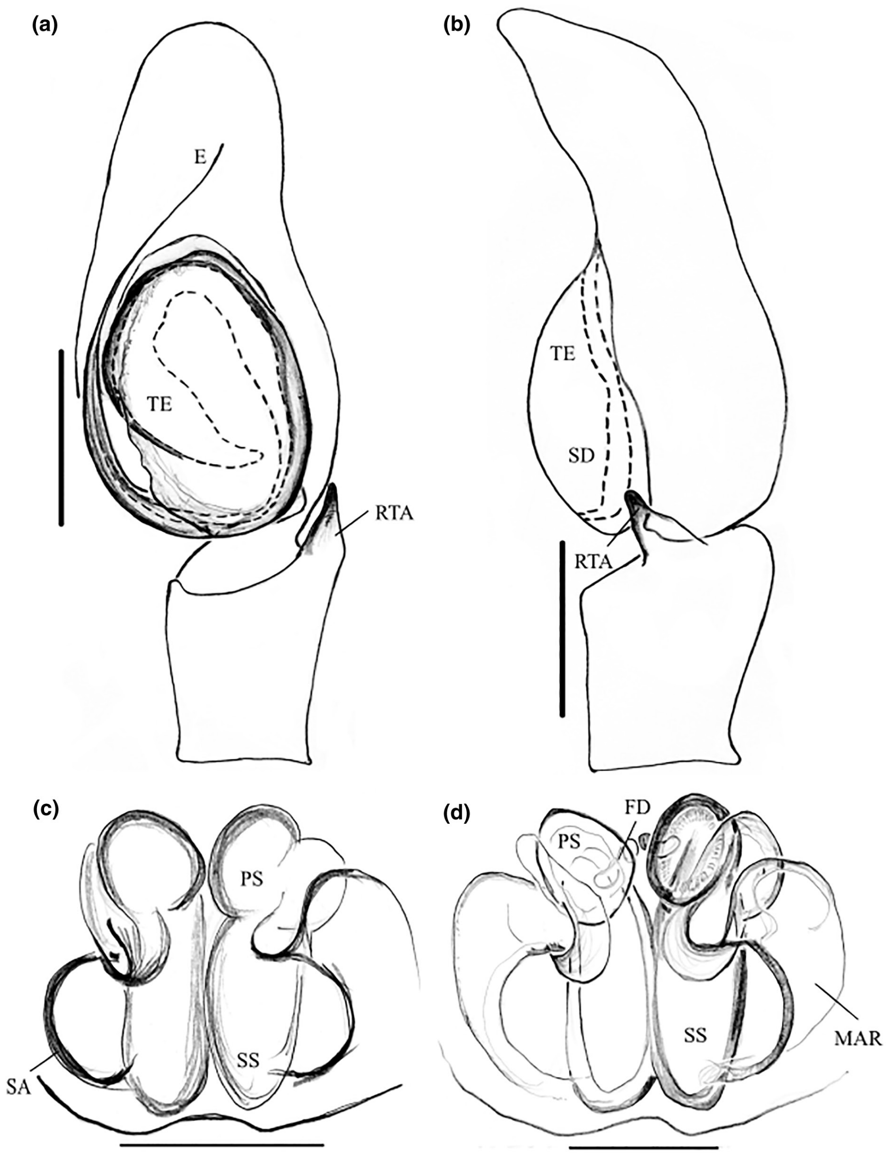

FIGURE 12 *Epidelaxia obscura* from Knuckles Forest Reserve (a–d); (a, b) Palp, (IFS_SAL_722). (a) ventral view. (b) retrolateral view. (c, d) Epigynum, (IFS_SAL_721). (c) ventral view. (d) dorsal view. Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

(Figure 1). Further, the branch separating *Epidelaxia* and *Tubalaxia* only received moderate support (0.58, Figure 3).

3.2 | Separate analyses of molecular data

The cladograms resulting from the analyses of individual molecular datasets (*CO1*, *28S*, *18S* and *H3*) are given in Figures S1–S4. The clustering patterns are similar to those of the combined analysis. In all separate analyses, *Epidelaxia* and *Tubalaxia* are monophyletic.

3.3 | Analyses of morphological data

Initial phylogenetic reconstructions based on parsimony of our morphological matrix under equal weights resulted in two most parsimonious trees (best score of 111). The same data matrix reanalyzed under implied weights resulted in a single most parsimonious tree (best score of 6.825) with fully resolved branches (L = 198, CI = 51, RI = 74). This cladogram is shown in Figure 2. The distribution of characters and their character states is given in Table 3.

The Nannenini clade is recovered with high support. As in all previous analyses, *Epidelaxia* is monophyletic and sister to *Tubalaxia*. The monophyly of Nannenni is supported by the following putative synapomorphies: oval-shaped bulbus (1-1), origin of the embolus in ventral view (5-1); retrolateral position of embolic base in left palp (6-0), the presence of a cymbial modification (11-1), large PLT (19-1), prolateral PLT (20-0), triangular-shaped mark on the prosoma of females (52-3) and the presence of 7 promarginal and 8 cusped retromarginal cheliceral teeth (54-2).

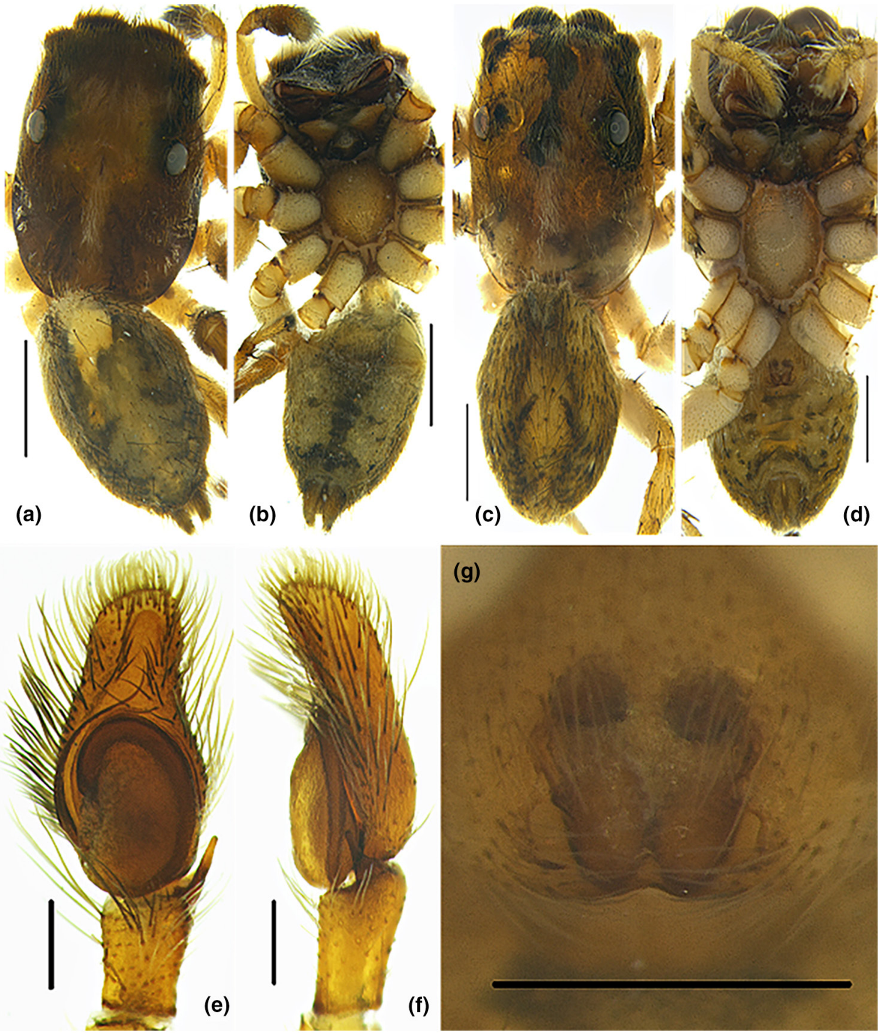

FIGURE 13 *Epidelaxia bharathi* sp. n. from Knuckles Forest Reserve (a–g); (a, b) Male habitus. (IFS_SAL_1144), (a) dorsal view, (b) ventral view. (e, f) Palp, (e) ventral view. (f) retrolateral view. (c, d) Female habitus. (IFS_SAL_1168). (c) dorsal view. (d) ventral view. (g) Epigynum. Scale bars: a–d = 2 mm, e, f = 0.2 mm, g = 0.1 mm.

The monophyly of *Epidelaxia* is supported by the following putative unambiguous synapomorphy: presence of membranous atrial rims (34-1). Further, the proximal position of the embolic base (6-1) and the oval-shaped secondary spermathecae (31-1) are potential synapomorphies.

The monophyly of *Tubalaxia* is supported by the putative unambiguous synapomorphy: presence of round-shaped secondary spermathecae (31-0). Further, the position of the embolic base at the prolateral part of bulbus (6-2); the RTA bent backwards dorsally (21-0); andbrown spots forming W-shaped band patterns on the dorsal abdomen in males (48-1) are potential synapomorphies.

A new genus *Tubalaxia* gen. n. and the following new species are formally described in supplementary information S1: *E. bharathi* sp. n., *E. somasundaram* sp. n., *T. castanea*sp. n., *T. aurea*sp. n. (Figures 13–21). The following new combination is proposed: *Tubalaxia minuta* (Prószyński, 1992) comb. n. *Epidelaxia albostellata* Simon, 1902, *Epidelaxia albocruciata* Simon, 1902 and *Epidelaxia obscura* Simon, 1902 are redescribed (Figures 4–12).

3.4 | Taxonomic acts (See supplementary Information, S1 for details)

***Epidelaxia bharathi*, sp. n.**

(Figures 13a–g and 14a–d).

urn:lsid:zoobank.org:act:629AFF25-D63E-4515-AFA6-9D9624A5F7C2.

Type material. Holotype. 1♂ (IFS_SAL_1144): Sri Lanka, Central Province, Matale District, Pitawala Pathana, Knuckles range, 07°32′50″N; 80°45′18″ E, 856 m, beating, 21 November 2017, leg. S.P. Benjamin et al. ***Paratype***. 1♀ (IFS_SAL_1168) same locality and collection data as holotype, 26 April 2018, leg. N. Athukorala et al.

Diagnosis. This species can be distinguished from other congeners by prominent oval-shaped bulbus, short embolus and the presence of two folded membranous outgrowths of the tegulum.

***Epidelaxia somasundaram*, sp. n.**

(Figures 15a–g and 16a–d).

urn:lsid:zoobank.org:act:F50FAA8A-EF23-40B0-8E55-2AEDD84AD4AF.

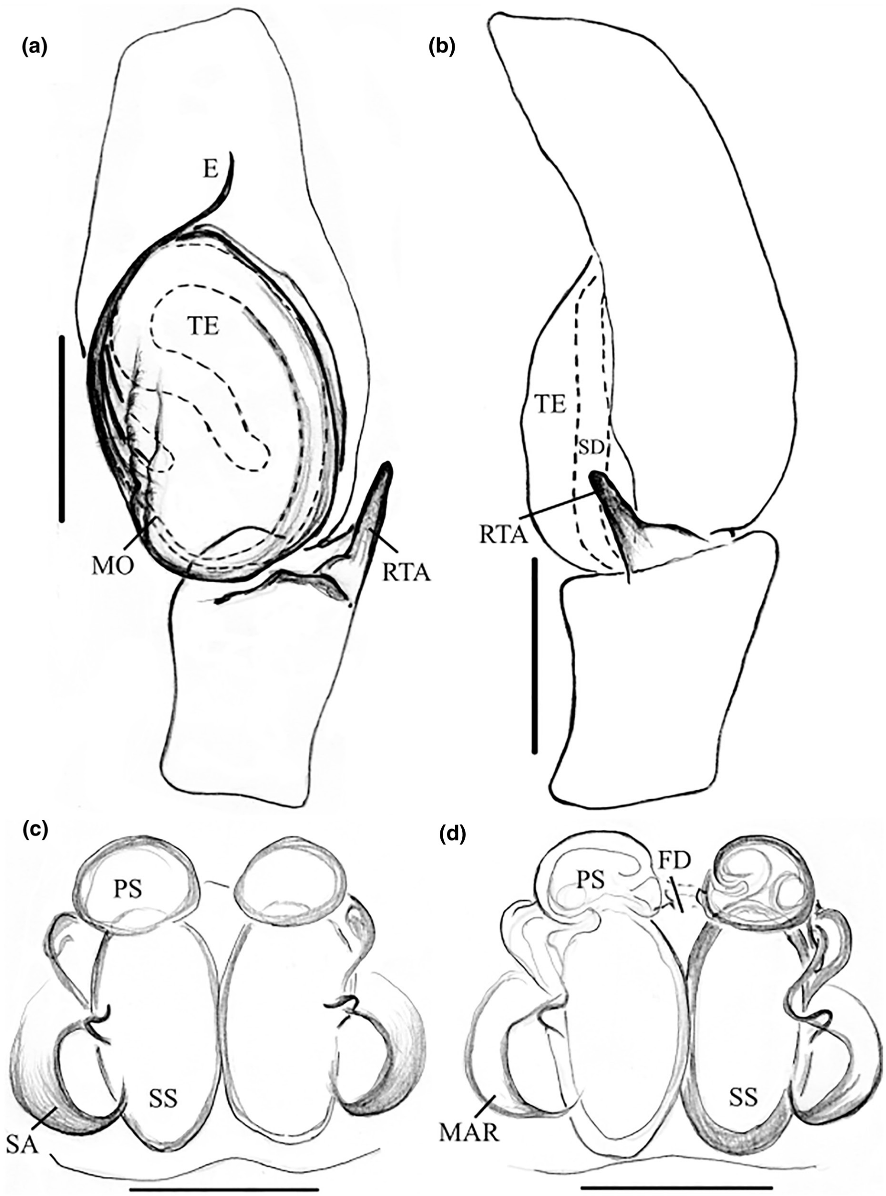

FIGURE 14 *Epidelaxia bharathi* sp. n. Knuckles Forest reserve (a–d); (a, b) Palp, (IFS_SAL_1144). (a) ventral view, (b) retrolateral view. (c, d) Epigynum, (IFS_SAL_1168). C. ventral view, (d) dorsal view. Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

Type material. Holotype. 1♂ (IFS_SAL_1093), Sri Lanka, Uva Province, Monaragala District, Kataragama Peak, 06°23′20″ N; 81°19′52″ E, hand collection, 22–23 November 2017, leg. S.P Benjamin et al. ***Paratype***. 1♀ (IFS_SAL_1092): same locality and collection data as holotype.

Diagnosis. This species can be distinguished from other congeners by the elevated carapace in both sexes.

***Tubalaxia* gen. n.**

urn:lsid:zoobank.org:act:ACD91693-9393-4431-9088-5F7ED4305A86.

Type species. *Tubalaxia aurea* sp. n.

Diagnosis. This genus can be readily distinguished from other genera of the tribe Nannenini by the brown spot forming W-shaped bands in the abdominal dorsum in males and females (Figures 17a,b) and the distinctive copulatory organs: embolus longer than cymbium, embolic base originating from the apical-retrolateral part of the palp in males and the presence of copulatory ducts that go behind the spermathecae (in ventral view) prior to entering it.

Composition. *Tubalaxia aurea* sp. n., *Tubalaxia castanea* sp. n. and *Tubalaxia minuta* (Prószyński, 1992) **comb. n**.

***Tubalaxia aurea* sp. n.**

(Figures 17a–d, 18a–g and 19a–d).

urn:lsid:zoobank.org:act:7A61EB08-10EA-48E6-89BD-7A43F13137F3.

Type material. Holotype. 1♂ (IFS_SAL_901), Sri Lanka, Central Province, Nuwara Eliya District, Upcot,

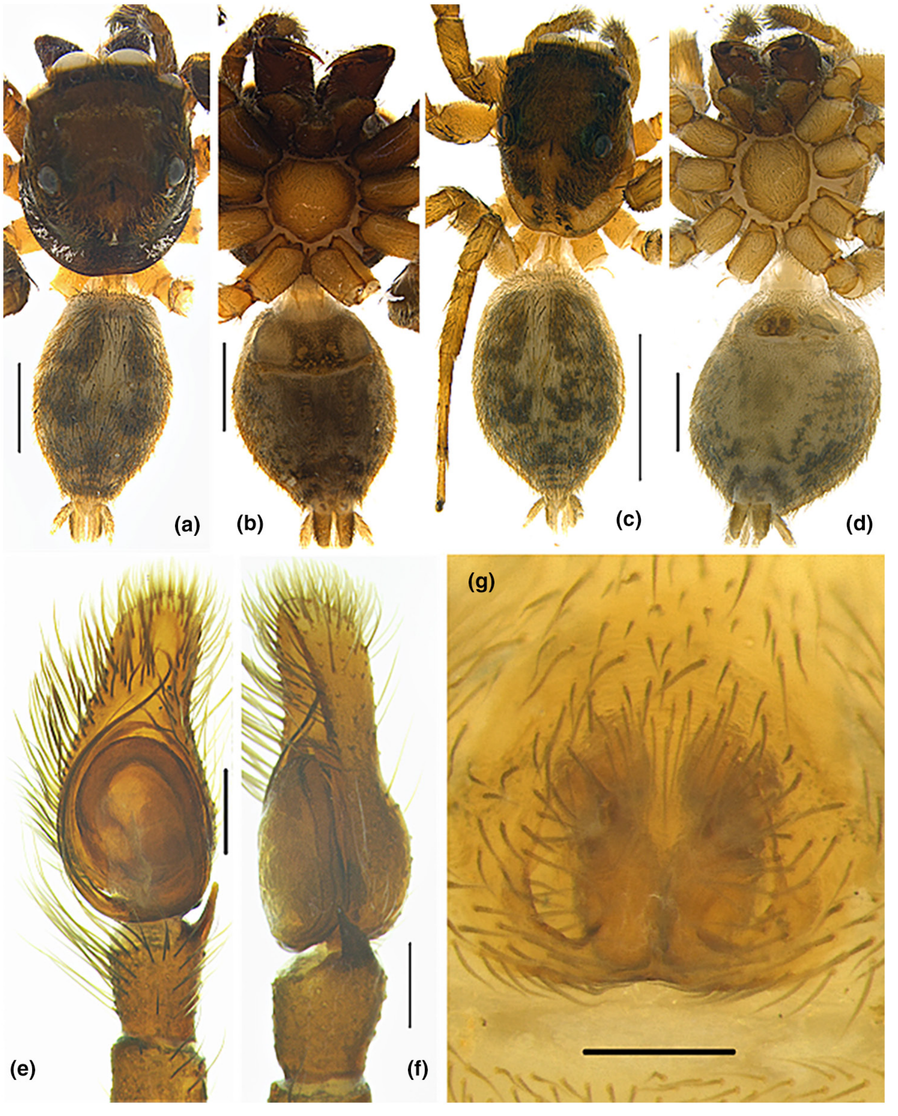

FIGURE 15 *Epidelaxia somasundaram* sp. n. from Kataragama (a–g); (a, b) Male habitus, (IFS_SAL_1093). (a) dorsal view, (b) ventral view. (e, f) Palp, ventral view, (f) retrolateral view. (c, d) Female habitus, (IFS_SAL_1092). (c) dorsal view, (d) ventral view. (g) Epigynum. Scale bars: a–d = 2 mm, e–f = 0.2 mm, g = 0.1 mm.

06°47′35.9″ N; 80°36′20.5″ E, 1199 m, beating, 03 October 2016, leg. N. Athukorala et al.

Diagnosis. This species can be distinguished from other congeners by the curved RTA in males and the presence of bean-shaped secondary spermathecae.

***Tubalaxia castanea* sp. n.**

(Figures 20a–g and 21a–d).

urn:lsid:zoobank.org:act:D4001C4F-BC1A-43F4-AF29-3C3A89317DD7.

Type material. Holotype. 1♂ (IFS_SAL_099), Sri Lanka, Central Province, Badulla District, Ohiya, 06°50′32″ N; 80°53′05″ E, 1280 m, Beating, 30 August 2011, leg. S.P. Benjamin et al. ***Paratype***. 1♀ (IFS_SAL_098): same locality and collection data as holotype.

Diagnosis. This species can be distinguished from other congeners by the straight, slanted RTA and the presence of secondary spermathecae that are the same in size as primary spermathecae.

4 | DISCUSSION

This study presents the first molecular and morphological phylogeny of Nannenini that includes representatives of all its genera. The phylogenetic relationships presented here are congruent with previous molecular hypotheses for Salticinae (Maddison, 2015). The phylogenetic relationships presented here also confidently place *Epidelaxia* within Nannenini in the subfamily Salticinae. The placement of *Epidelaxia* in Nannenini was previously proposed (Maddison, 2015), however, never phylogenetically tested. Unfortunately, due to the lack of molecular-grade tissue, *E. obscura* was not included in the molecular matrices used in the phylogenetic analyses. The individual gene regions, analysed separately, provide independent support for the placement of *Epidelaxia* within Nannenini in the subfamily Salticinae. Figures S1–S4 show the resulting trees.

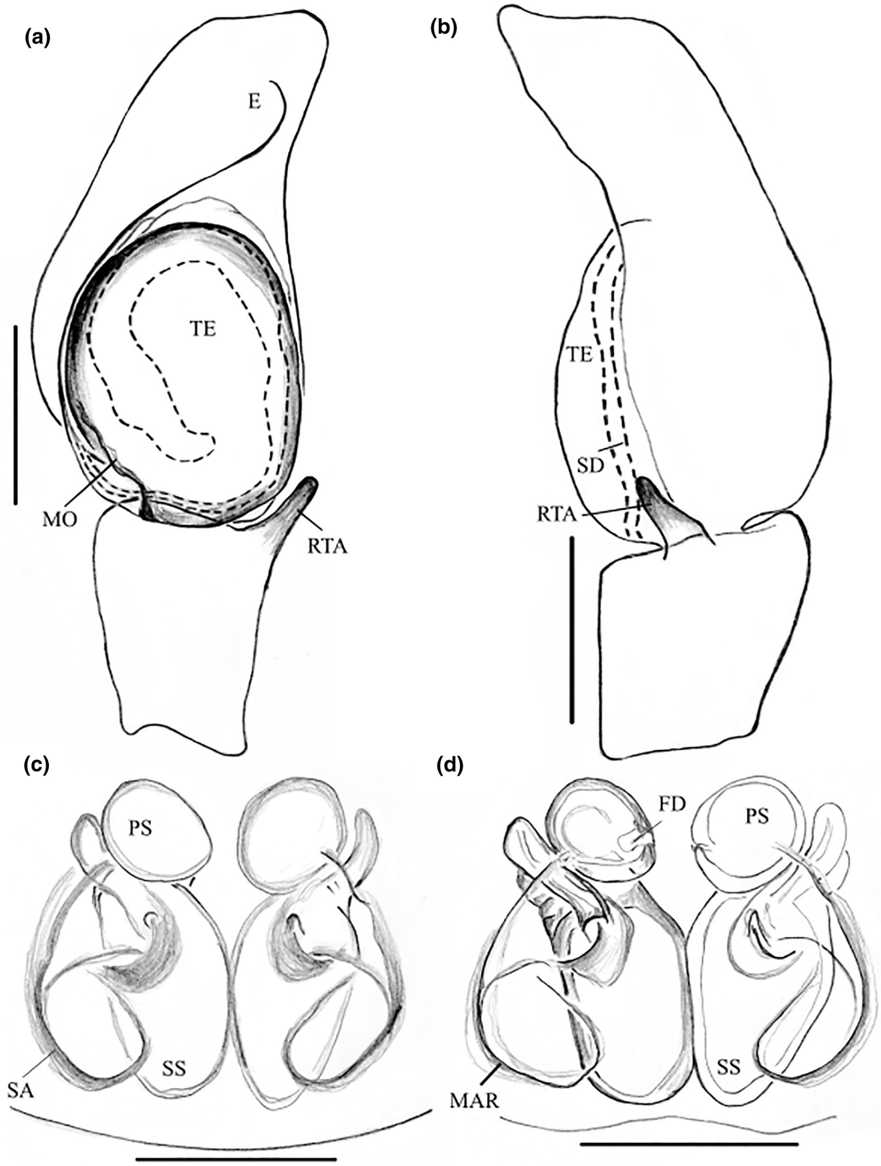

FIGURE 16 *Epidelaxia somasundaram* from Kataragama (a–d); (a, b) (IFS_SAL_1093). Palp, (a) ventral view, (b) retrolateral view. (c, d) Epigynum, (IFS_SAL_1092). (c) ventral view, (d) dorsal view. Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

The *Epidelaxia* species of Sri Lanka form three clades in the ML tree (labelled C1 to C3 in Figure 1). Clade C1, consist of specimens of *E. albostellata* which inhabits the high-elevation central highland cloud forests of Sri Lanka (1400 m to 2400 m; IFS_SAL_841, 445, 1036, 1095, 1202). Clade C2, consists of specimens of *E. albocruciata*, which inhabits the lowland rainforest of Sri Lanka (150 m to 250 m; IFS_SAL_966, 1286, 1300). These two clades are sister to each other and together sister to Clade C3. Clade C3, except for one sample also consists of specimens that inhabit tiny remnants of the lowland rainforest of Sri Lanka. These two clusters together are sister to *E. bharathi* sp. n. and *E. somasundaram* sp. n. This clustering pattern is recovered in all analyses of the individual molecular datasets (Figures S1–S4).

The phylogenetic relationships inferred here are preliminary in the absence of *E. obscura* in the ML analysis; the extent of relatedness of *E. obscura* with other species is yet unknown due to the unavailability of molecular data for *E. obscura*. However, the paraphyletic nature of the groups identified as *E. albocruciata* calls for further study. All specimens identified as *E. albocruciata* are consistent with Simon's original description as well as our diagnosis. However, there might be cryptic species within the *E. obscura* species complex. Thus, species delimitation based on DNA barcoding might be pursued to understand the true biodiversity of *Epidelaxia* in Sri Lanka.

An interesting outcome of this study is the discovery of a new lineage of Nannenini; *Tubalaxia* gen.n. The genus *Tubalaxia* is confirmed as a member of the tribe Nannenini and is closely related to *Epidelaxia*. All molecular trees recover *T. aurea* sp. n. and *T. castanea* sp. n. as sister species with high support (Figures 1 and 3). This is also validated in the morphological tree where *T. aurea* and *T. castanea* are also recovered as sister species (Figure 2). This study describes five species of *Epidelaxia*

FIGURE 17 Photographs of live *Tubalaxia aurea* sp. n. female (a, b) from Hakgala SNR and male (c, d) from Upcot.

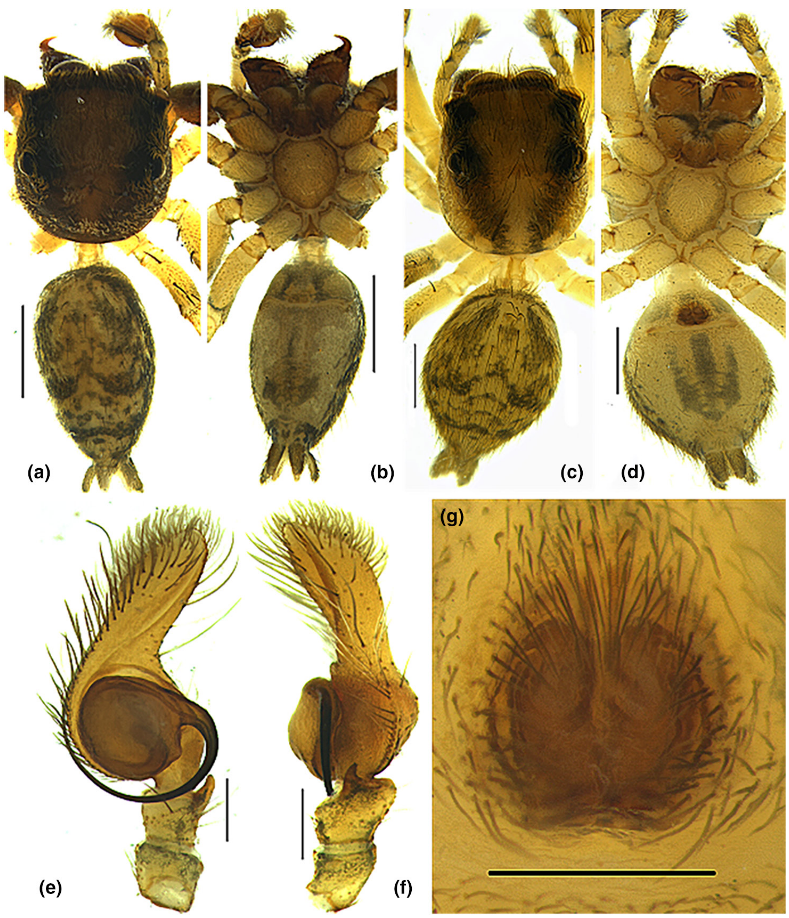

FIGURE 18 *Tubalaxia aurea* sp. n. (a–g); (a, b) Male habitus, from Upcot (IFS_SAL_901). (a) Dorsal view. (b) Ventral view. (e, f) Palp, ventral view. (f) Retrolateral view. (c, d) Female habitus, (c) Dorsal view. (d) Ventral view. (g) Epigynum, Knuckles Forest Reserve (IFS_SAL_1278). Scale bars: a–d = 2 mm, e, f = 0.2 mm, g = 0.1 mm.

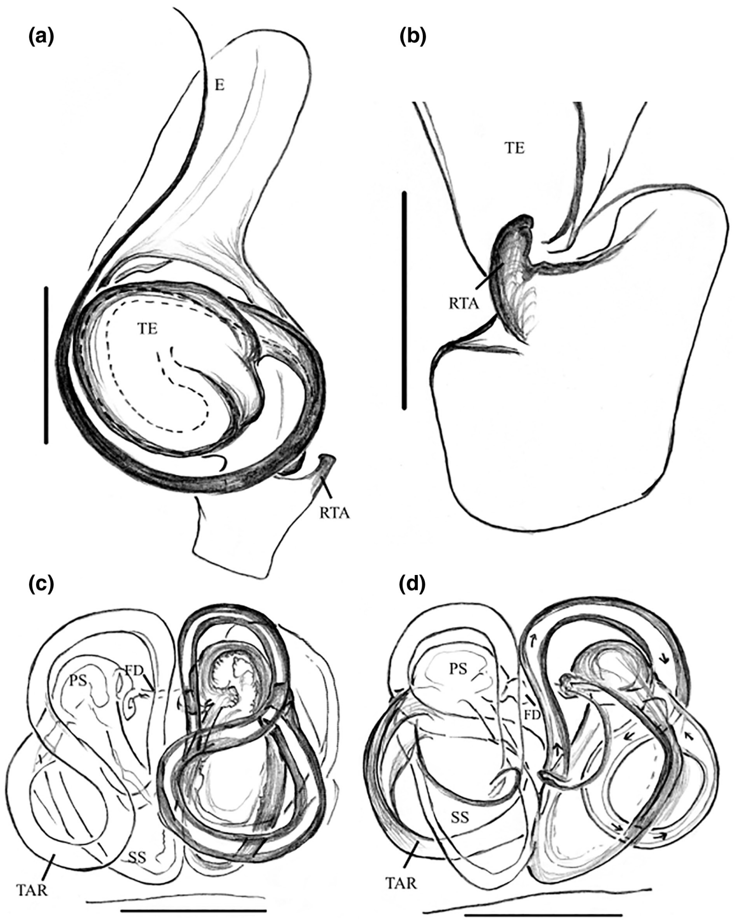

FIGURE 19 *Tubalaxia aurea* sp. n. (a–d); (a, b) Palp, from Upcot (IFS_SAL_901). (a) ventral view. (b) Retrolateral view. (c, d) Epigynum, Knuckles Forest Reserve (IFS_SAL_1278). (c) Ventral view. (d) Dorsal view. Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

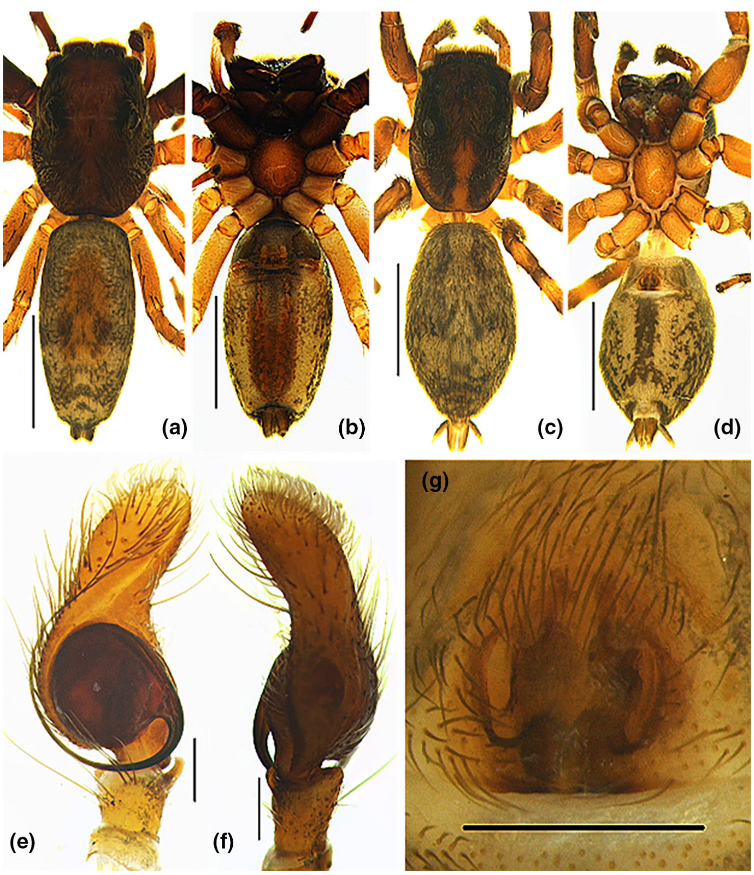

FIGURE 20 *Tubalaxia castanea* sp. n. from Ohiya (a–g); (a, b) Male habitus, (IFS_SAL_099). (a) Dorsal view. (b) Ventral view. (e, f) Palp, ventral view. (f) Retro lateral view. (c, d) Female habitus, (IFS_SAL_098). (c) Dorsal view. (d) Ventral view. (g) Epigynum. Scale bars: a–d = 2 mm, e, f = 0.2 mm, g = 0.1 mm.

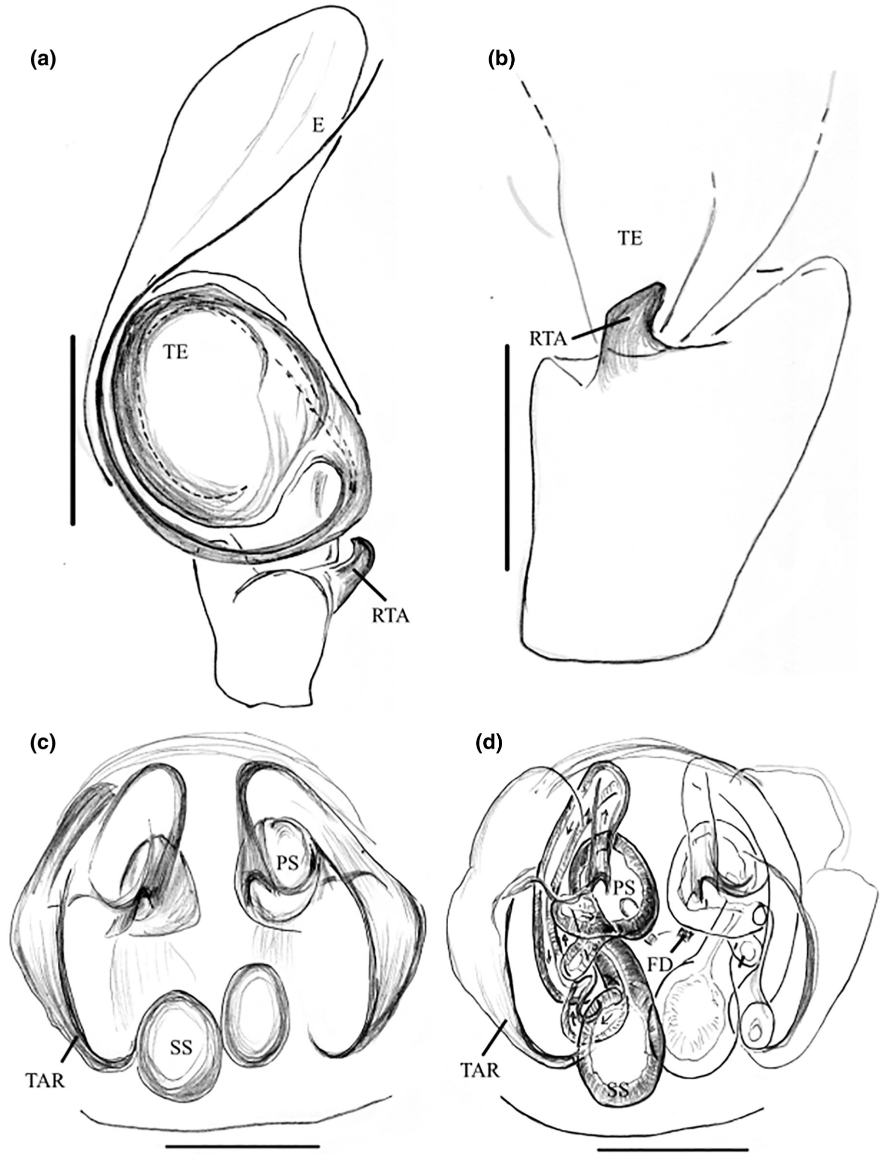

FIGURE 21 *Tubalaxia castanea* sp. n. from Ohiya (a–d); (a, b) Palp, (IFS_SAL_099). (a) Ventral view, (b) Retrolateral view. (c, d) Epigynum, (IFS_SAL_098). (c) Ventral view, (d) Dorsal view. Scale bars: a, b = 0.2 mm, c, d = 0.1 mm.

(two new) and two species of *Tubalaxia* gen. n. (both new; Figure 22).

The placement of *Epidelaxia* and *Tubalaxia* is shown in the ML tree. All resulting single-gene ML phylogenies were examined to assess their differences from the preferred tree. *Epidelaxia* is recovered as a separate lineage in the ML tree inferred from the four genes with high support (Figure 2). *Tubalaxia* gen. n. is recovered as a separate lineage in all of our analyses with high support (Figure 2). The genera, *Idastrandia*, *Langerra* and *Nannenus* each received high bootstrap values. Relationships among the Nannenines obtained by the ML analysis were congruent with those obtained by the morphological analysis except for the position of *Langerra*, and are mostly well supported.

The placement of *Nannenus* and *Idastrandia* in Nannenini is unambiguous (Maddison, 2015). *L. oculina*, the type and only species of the genus, is a small spider (around 4 mm) like many Nannenini. It has a stout, tall prosoma and an oval abdomen. It is characterized by the structure of the epigyne: the entrance to the copulatory openings is from the side of the epigastric furrow, copulatory ducts go towards the pedicel and turn back towards the posterior into the spermathecae (Żabka, 1985: figures 251–254). The palps are very similar to that of *Tubalaxia* (Figure 21).

Lechia and *Leuserattus* are excluded from Nannenini. After the transfer of *Tubalaxia minuta* (Prószyński, 1992) **comb. n.**, *Lechia* currently contains only its type species. *Lechia squamata* Żabka, 1985. It possesses characters such as the large dorsal scutum of the male, tegulum with sclerites, tibia with two apophyses, absence of MAR, copulatory ducts that go away from the pedicel and enter spermathecae, short copulatory ducts and spermathecae that lack accessory glands (Logunov & Jäger, 2015: figures 52–61, Zhang & Maddison, 2015:

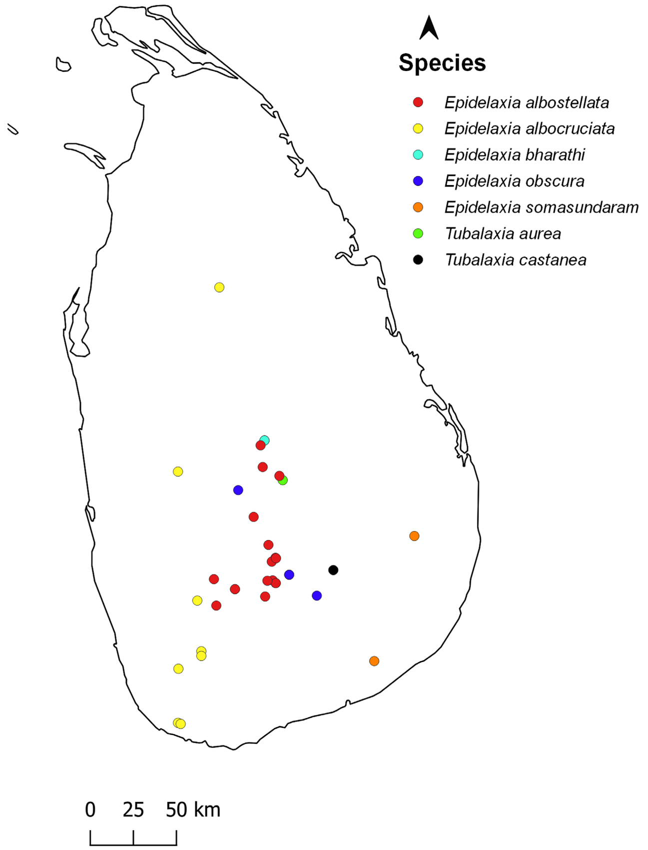

FIGURE 22 Approximate distribution map of the genus *Epidelaxia* genus *Tubalaxia* in Sri Lanka.

figures 504–523). *Leuserattus* has an embolus that sits flat on the tegulum, unlike any known Nannenini and also has a very unique epigynum (Deeleman-Reinhold & Miller, 2021: figures 1–12).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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SUPPLEMENTARY MATERIAL

S1

Multilocus genetic and morphological phylogenetic analysis: unveiling a new genus and species in the Tribe Nannenini of jumping spiders (Araneae, Salticidae)

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Appendix S1

TAXONOMY
Family SALTICIDAE Blackwall, 1841
Subfamily *Salticinae* Blackwall, 1841
Tribe *Nannenini* Maddison, 2015

Type genus. **Nannenus Simon, 1902**

Diagnosis. All Nannenini are small to medium sized (around 4 mm) compact bodied jumping spiders with a stout, tall prosoma and an oval abdomen. The following combination of characters distinguished Nannenini from other jumping spiders: oval bulbus (1-1) except for *Idastrandia* and *Tubalaxia*, embolus base invisible in ventral view (5-1), except for *Idastrandia*, long filiform embolus more than half the length of the cymbium, presence of various cymbial modifications (11-1), absence of ATL (12-0) except for *Idastrandia*, lateral copulatory openings with ducts leading anteriorly and switching back, relative abdominal length longer than 2x of width (47-2), and, prominent, laterally stretched out, triangular-shaped mark on the prosoma of females (52-3) and 7 promarginal, 8 cusped retromarginal cheliceral teeath (54-2) except for *Idastrandia*.

Composition. *Epidelaxia* Simon, 1902, *Idastrandia* Strand, 1929, *Langerra* Żabka, 1985 *Nannenus* Simon, 1902, *Tubalaxia* gen. n. *Idastrandia* and *Langerra* are monotypic. *Lechia* and *Leuserattus* are excluded from Nannenini (see discussion below).

Distribution. The Oriental region: China, India, Malay Archipelago, Singapore, Sri Lanka, Vietnam.

Epidelaxia Simon, 1902

Type species. *Epidelaxia albostellata* Simon, 1902.
Monophyly and phylogenetic placement. Monophyly of *Epidelaxia* is recovered in all molecular trees and the morphological tree (Figures 1, 2, 3). The monophyly of *Epidelaxia* is supported by the following putative unambiguous synapomorphies: the presence of membranous atrial rims (34-1), and the presence of a sclerotized arch (37-1). Further, the proximal position of the embolic base (6-1), and the oval-shaped secondary spermathecae (31-1) are potential synapomorphies.

Diagnosis. This genus can be readily distinguished from other genera of the tribe Nannenini by the combination of the following characters: oval tegulum without a proximal or an apical lobe (PLT and ALT), presence of primary and secondary spermatheca (PS and SS) that are prominent and yellow, triangular-shaped mark on the prosoma of females, abdominal dorsal markings in males and females, and the distinctive copulatory organs morphology: short and straight embolus, presence of membranic outgrowth of tegulum, presence of well-developed C- or S-shaped membranous atrial rims in females.

Description. Medium-sized spiders, male with white tuft of hairs on the clypeus; prosoma with blackish/ reddish brown hairs around AME; yellow triangular-shaped mark behind the eye field; leg I slightly robust in males; abdomen with blackish or brownish-grey longitudinal median band bordered by pale yellow bands; filiform long embolus; embolic base originating from the proximal part of bulbus, folded membranous outgrowth of tegulum, short and robust RTA. Female with black patches on the eye field and surrounding PME, behind PLE and posterior slope of prosoma;

abdomen with white dots forming a crosswise or star like pattern; oval-shaped spermatheca: spermathecal chamber at the posterior part of spermathecae; presence of membranous C-shaped, S-shaped, widened C-shaped atrial rim, presence of sclerotized arch. See species descriptions below.

Composition. Genus *Epidelaxia* currently includes five species: *E. albocruciata*, *E. albostellata*, *E. bharathi* sp. n., *E. obscura* and *E. somasundaram* sp. n.

Distribution**.** Currently known only from Sri Lanka. Probably present in India.

Epidelaxia albostellata **Simon, 1902**

(Figures 4A–D, 5A–D, 6A–G, 7A–H)

Epidelaxia albostellata Simon, 1902: 367.

Epidelaxia albostellata Simon, 1903: 797, figure. 917.

Epidelaxia albostellata Prószyński, 1987: 22.

Type material**.** *E. albostellata*. 1♂, 2♀ syntypes from Colombo! Matara! Galle! (Sri Lanka). No more locality data given; MNHN 20474 examined.

Other material examined**.** 1♂ (IFS_SAL_841): Sri Lanka, Central Province, Kandy District, Deltota, Loolecondera estate, 07°08'45''N;80°41'53''E, 1480 m, beating, 22 June 2016, leg. S.P. Benjamin et al**.** 1♀ (IFS_SAL_842): same locality and collection data as above. 1♂ (IFS_SAL_1052) same locality and collection data as above 15 November 2017, leg. K. Nilani. 1♀ (IFS_SAL_453): same locality and collection data as above, hand collection, 13 July 2010, S.P. Benjamin and S. Batuwita et al. 1♀ (IFS_SAL_285): Panvila, Dikhinna village, 07°24'27.3''N;80°44'44.4''E, 939 m, 17 December 2013, leg. N. Athukorala et al**.** 1♂ (IFS_SAL_519): Matale District, Riverstone, Knuckles range, 07°32'36''N;80°45'13''E, 1000 m, hand collection, 02 December 2009, leg. S.P. Benjamin and S. Batuwita. 1♀ (IFS_SAL_346): same locality and collection data as above, 02 February 2010, leg. S.P. Benjamin, S. Batuwita, P.M.H. Sandamali. 1♀ (IFS_SAL_346): same locality and collection data as above, 02 February 2010, leg. S. Batuwita and P.M.H Sandamali et al. 1♀ (IFS_SAL_524): same locality and collection data as above. 2♂ (IFS_SAL_426-427): Nuwara Eliya District, Agrabopath FR, 1660 m-1800 m, 18–21 February 2007, leg. S.P. Benjamin and Ziyard Jaleel. 5♂ (IFS_SAL_445-449): Hakgala SNR, 06°54'40"N;80°47' 36"E, 1913 m, beating, 22 January 2015, leg. S.P. Benjamin et al. 2♀ (IFS_SAL_450-451): same locality and collection data as above. 1♀ (IFS_SAL_855): same locality and collection data, 30 June 2016, leg. N. Athukorala et al .1♀ (IFS_SAL_091): Peak wilderness sanctuary, hand collection, 22 February 2007, leg. S.P. Benjamin and Z. Jaleel. 5♀ (IFS_SAL_130-134): Horton Plains NP, 06°46'N; 80°36'E, 2000 m, hand collection, 20–21 February 2007, leg. S.P. Benjamin and Ziyard Jaleel. 2♂ (IFS_SAL_096-097) same locality and collection data as above. 1♂ (IFS_SAL_474): Horton Plains NP, 06°68'05"N;80°50'19"E, 1951 m, beating, 27 March 2012, leg. S.P. Benjamin et al**.** 2♀ (IFS_SAL_475-476): same locality and collection data as above (IFS_SAL_474). (IFS_SAL_129): same locality and collection data as above. (IFS_SAL_130-134). 1♂ (IFS_SAL_1036): Horton Plains NP, 06°47'54"N; 80°48'51"E, 2142 m, beating, 22 July 2017, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_1202): Horton Plains NP, Dayagama trail, 06°48'46"N;80^{0}47'53"E, 2086 m, hand collection, 03 July 2019, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_486): Upcot, 06°46'N; 80°36'E, beating, 14 February 2012, S.P. Benjamin and N. Athukorala. 1♂ (IFS_SAL_1096): Piduruthalagala, between 3–4km post, 06^{0}59'36"N; 80º46’15"E, 2400 m, 14 February 2018, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_1095), same locality data as above. 2♀ (IFS_SAL_193-194): Agrabopath FR, 1660–1800 m, hand collection, 18–21 June 2007, leg. S.P. Benjamin and Z. Jaleel. 1♀ (IFS_SAL_504): Sri Lanka, Sabaragamuwa Province, Rathnapura District, Belihul Oya Village, 06°42'36.8"N;80°45'38.8"E, litter, 02 January 2012, leg. S.P. Benjamin et al. 2♀ (IFS_SAL_382-383): Sri Lanka, North Western Province, Kurunegala District, Nikavaravatiya, hand collection, 1–3 February 2007, leg. Z. Jaleel.

Diagnosis. Males of *E. albostellata* can be distinguished from other congeners by the presence of longitudinal light yellow colour belt on the prosoma and opisthosoma and an oval shaped bulbus with short and robust RTA. Further, both sexes have an abdominal dorsal pattern with white hairs forming a “star-like” pattern.

Description. Male: Total length 3.3: Colour in ethanol: blackish brown, yellow patches. Carapace: prosoma length 1.38; width.1.07. Prosoma black, covered with dark black blotches around AME, PLE, lightly broader than opisthosoma. Sternum yellowish brown, pentagonal shaped, edges bordered, dark brown Clypeus black, white hairs. Chelicerae brownish, black. Eye measurements:

AME 0.28; ALE 0.18; PME 0.1; PLE 0.14; PME-PME 0.82; PLE-PLE 0.84; ALE-PME 0.32; ALE-PLE 0.42 Abdomen: opisthosoma length 1.35, width 0.87. Leg I more robust than rest, legs I and II blackish, white hairs around proximal region of patella, tibia and metatarsus, legs III and IV brownish yellow. Leg measurements: I: 2.3 (0.5, 0.6, 0.2, 0.54, 0.46); II: 1.94 (0.46, 0.3, 0.36, 0.4, 0.42); III: 3.36 (1.18, 0.9, 0.24, 0.64, 0.4); IV: 2.86 (1, 0.3, 0.4, 0.72, 0.44).

Palp covered with pale yellow scales, RTA robust and broader at the base, tip narrower and bent towards venter. Cymbium yellowish brown, short and distal part tapered. Oval shaped bulbus. Membranic outgrowth of the tegulum with one membranic edge. Sperm duct clearly visible at distal portion of tegulum. Embolic origin at 6'o clock position. Embolus slender, long, more than half of cymbium and embolic base starting at the posterior part of the bulbus (Figures 6E, 7A–B).

Female: As in male except for the following Total length 4.9: Carapace: prosoma length 1.8, width 1.05. Ethanol preserved specimens, prosoma yellowish brown. ALE, PME, PLE covered with black blotches. Chelicerae, labium light brown, edges dark brown. Prosoma with laterally stretched out yellowish colour triangular-shaped mark. Posterior prosoma moderately truncated. Eye measurements: AME 0.48; ALE 0.3; PME 0.06; PLE 0.2; PME-PME 1.22; PLE-PLE 1.18; ALE-PME 0.22; ALE-PLE 0.54. Abdomen: Opisthosoma length 2.31, width 1.83. Leg measurements: I: 3.24(0.9, 0.44, 0.98, 0.52, 0.4); II: 3.1(0.8, 0.44, 0.86, 0.58, 0.42); III: 3.36 (1.18, 0.9, 0.24, 0.64, 0.4); IV: 2.86 (1, 0.3, 0.4, 0.72, 0.44).

Epigyne: Anterior epigynal border present, poorly sclerotized. CO directly leading into narrowed region of the large chamber of secondary spermatheca. Copulatory ducts progressed in S-shape, forming small C-shaped atrial rims. Spermatheca double chambered, primary S round, anterior portion joined with oval-shaped posterior secondary chamber. Secondary S relatively larger, primary S. FD lanceolate, originating from antero-mid wall of primary chamber (Figures 6G, 7B. A–D).

Distribution and habitat. This species is widely distributed in the high-elevation montane and submontane forests of the central highlands of Sri Lanka. Specimens were collected by beating vegetation up to a height of 0.5 to 2 m.

Intraspecific variation. Several variations were observed among the specimens collected from different localities: shape of the tegulum and cymbium (oval to round), length of the embolus (relatively short to long) (Figures 7A, B). Further, the shape of the RTA seems to be variable among the observed specimens (Figures 7C, D). In females, the shape of the spermathecae and shape of the atrial rims were variable (Figures 7E-H). The palpal variations are mainly observed in male specimens collected from Loolecondera (Figures 7B, D) and Horton Plains (Figures 7A, C) (IFS_SAL_1096, IFS_SAL_1052 respectively). In addition, a few specimens were observed to be darker than the rest.

***Epidelaxia albocruciata* Simon, 1902**

(Figures 8A–D, 9A–G, 10A–D)

Epidelaxia albocruciata Simon, 1902: 367.

Type material. *Epidelaxia albocruciata* Simon, 1902: ♂♀ syntypes from Colombo!, Galle!, Matara! Sri Lanka. No more locality data given, MNHN 20444 examined.

Other material examined. 1♂ (IFS_SAL_1089): Sri Lanka, Sabaragamuwa Province, Rathnapura District, Pompakele FR, 06°42'24"N;80°24'08"E, beating, 21 November 2017, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_1088), same data as above. 2♂ (IFS_SAL_347-348): Eastern Singharaja, Morning side section, 06°35'80"N;80°48'90"E, hand collection, 23 February 2007, leg. 2♂ (IFS_SAL_966-967): Singharaja FR, Kudawa, Secondary Forest, hand collection, 06°26'26"N;80°25'25"E, 367 m, 11–13 October 2016, S.P. Benjamin and Ziyard Jaleel. 1♀ (IFS_SAL_1203): Singharaja FR, Kudawa, Secondary Forest, hand collection, 06°26'26"N;80°25'25"E, 367 m, 06 March 2019, leg. S.P. Benjamin et al. leg. S.P. Benjamin et al. 1♀ (IFS_SAL_090): Gilimale FR, Hand collection, 11 November 2007, leg. S.P. Benjamin and Z. Jaleel. 1♂ (IFS_SAL_163) Sri Lanka, Western Province, Colombo District, Labugama, beating, 06°51'43.1"N;80°10'08.8"E, 145–180 m, 21 April 2015, leg. S.P. Benjamin et al. 3♂ (IFS_SAL_621-623): Sri Lanka, North Central Province, Anuradhapura District, Mihintale sanctuary, 08°21'02"N; 80°31'01"E, 123 m, 13 May 2013, leg. I. Sandunika et al. 1♂ (IFS_SAL_264): same locality and collection data as above. 1♀ (IFS_SAL_224): Sri Lanka, North Western Province, Kurunegala District, Ethagala, hand collection, 04 October 2009, leg. Z. Jaleel. 1♂ (IFS_SAL_1279): same locality and collection data as above. 1♂ (IFS_SAL_755): Sri Lanka, Southern Province, Galle District, Hiyare, Kombala-Kottawa FR, 06°03'53"N;80°18'05"E, 252 m, 24–26 May 2016, leg. N. Athukorala et al**.** 1♀ (IFS_SAL_757): same locality and collection data as above. 1♀ (IFS_SAL_1286): same locality and collection data as above, 17 February 2020, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_1300): Haycock, beating, 06°20'55''N; 80°18'12''E, 145–180 m, 19 February 2020, leg. S.P. Benjamin et al.

Diagnosis. This species can be distinguishable from other congeners by the abdominal crosswise brown striated stripes (Figures 8A–D). Males of *E. albostellata*, *E. obscura, E. bharathi* and *E. somasundaram* differ by the presence of round-shaped bulbus (Figures 9E, 10A).

Description. Almost all characters are similar to males of *E. albostellata* except for the following. Total length 4.4; Carapace: prosoma length 1.71, width 1.5. Yellowish brown prosoma with black patches behind ALE and PLE in preserved specimens. Chelicerae brownish black, white hairs at base. Eye measurements: AME 0.5; ALE 0.28; PME 0.1; PLE 0.24; PME-PME 1.14; PLE-PLE 1.06; ALE-PME 0.32; ALE-PLE 0.6. Abdomen: Opisthosoma length 1.98, width 1.53. Medium-sized opisthosoma, tapering posteriorly. Dorsum, herringbone pattern, white dots forming a stripe. Ventrum and spinnerets yellowish-brown. Leg measurements: I: 10.06 (0.52, 0.22, 0.5, 0.74, 0.42); II: 1.62 (0.3, 0.2, 0.4, 0.72, 0.52); III: 2.74 (0.48, 0.3, 0.54, 0.84); IV: 2.78 (0.5, 0.22, 0.82, 0.92, 0.32).

Palp: similar to *E. albostellata* except for the following. RTA robust and broader at base, narrower and bent forward ventrally at the tip. Cymbium reddish-brown, long, distal part elongated. Round-shaped bulbus. Embolus filiform, long, more than half of the cymbium and embolic base starting at the posterior part of the bulbus (Figures 9E, F, 10A, B).

Female. As in male except for the following. Total length 4.5: prosoma length 1.89, width 1.65. Prosoma with prominent yellow colour triangular-shaped mark. Posterior prosoma steep and slightly truncated. Chelicerae, labium yellowish-brown, edges brown. Eye measurements: AME 0.32; ALE 0.22; PME 0.06; PLE 0.18; PME-PME 0.84; PLE-PLE 0.78; ALE-PME 0.16; ALE-PLE 0.42. Abdomen: Opisthosoma length 1.95, width 1.5. Leg I dark yellowish brown, brown patches. Legs II, III, and IV yellowish-brown, brown patches. Leg measurements: I: 2.2 (0.64, 0.48, 0.28, 0.48, 0.32); II: 2.34 (0.6, 0.5, 0.3, 0.66, 0.28); III: 2.24 (0.64, 0.24, 0.4, 0.66, 0.3); IV: 1.72 (0.5, 0.14, 0.34, 0.48, 0.26).

Epigyne: similar to *E. albostellata* except for the following. Copulatory ducts progressed in curve by forming large C-shaped membranous atrial rims. Secondary S relatively much larger in size than primary S. FD lanceolate, originating from antero-lateral wall of primary chamber (Figures 9G, 10C, D).

Distribution and habitat. This species occurs in the lowland rainforests of the dry and wet zones of Sri Lanka. Specimens were collected by beating vegetation up to a height of 1 to 2 m.

Epidelaxia obscura **Simon, 1902**

(Figures 11A–G, 12A–D)

Epidelaxia obscura Simon, 1902: 368.

Type material. *Epidelaxia obscura* Simon, 1902: ♂ Holotype from Kandy!, Sri Lanka. No more locality data given; MNHN 20540 examined.

Other material examined. 1♂ (IFS_SAL_722): Sri Lanka, Central Province, Kandy District, Knuckles range, site I, 07°17'11''N;80°37'93''E, beating, 19 February 2015, leg. N. Athukorala et al. 1♀ (IFS_SAL_721), same locality and collection data as above. 1♂ (IFS_SAL_143): Sri Lanka, Uva Province, Badulla District, Ohiya, 06°50'32''N;80°53' 05''E, 1280 m, beating, 16 October 2011, leg. S.P. Benjamin et al. 1♂ (IFS_SAL_499): Diyaluma falls, 06°43'57''N; 81°01'58''E, 660 m, hand collection, 04 August 2011, leg. S.P. Benjamin and S. Batuwita**.**

Diagnosis. This species can be easily distinguished from other congeners by darkened and yellow-spotted abdominal pattern in males as well as females. Further, *E. obscura* differs from *E. albostellata* by the presence of a widened copulatory duct, C-shaped distinctive membranous atrial rims, oval-shaped and well-developed spermatheca in females. Males differ from the *E. albostellata, E. albocruciata, E. bharathi* and *E. somasundaram* by the dark blackened, oblong-shaped bulbus and straight RTA in males (Figures 11E, F, 12A, B).

Description. Male. Total length 4.85; Colour in Ethanol: blackish brown and yellow. Carapace: Prosoma length 2.01, width 1.38. Prosoma black covered with dark black blotches around the AME and PLE, slightly broader than abdomen. Blackish clypeus with sparsely distributed white hairs. Chelicerae brownish-black, covered with white hairs at its base. Sternum yellowish-brown and pentagonal-shaped, edges bordered with dark brown. Eye measurements: AME 0.62; ALE 0.36; PME 0.08; PLE 0.3; PME-PME 1.36; PLE-PLE 1.22; ALE-PME 0.28; ALE-PLE 0.7. Abdomen: opisthosoma length 1.8, width 1.35. Thickened first pair of legs. Leg I more robust than others, legs I and II blackish with white hairs around proximal region of patella, tibia and metatarsus, legs III and IV blackish-yellow. Leg measurements: I: 5.34 (1.58, 0.7, 1.28, 1.24, 0.54); II: 3.92 (0.84, 0.5, 1.18, 0.86, 0.54); III: 3.6(1, 0.9, 0.96, 0.74); IV: 4.08 (1.16, 0.68, 0.92, 0.8, 0.52).

Palp with dark brown scales. RTA robust and broader at the base, narrower and bent forward ventrally at the tip. Cymbium blackish, distal part of cymbium elongated. Oval-shaped bulbus. Membranic outgrowth of tegulum is present with one membranic edge. One part of sperm duct is clearly visible at the distal portion of tegulum. Embolus origin starting at 7'o clock position. Embolus filiform, long, more than half of cymbium, base at posterior part of bulbus, originating from under membranous outgrowth of tegulum (Figures 11C, D, 12A, B).

Female. As in male except for the following. Total length 3.85: Carapace: Prosoma length 1.77, width 1.65. Prosoma with stretched out yellowish-brown colour triangular-shaped mark. Posterior prosoma moderately steep and slightly truncated. Eye measurements: AME 0.5; ALE 0.28; PME 0.12; PLE 0.24; PME-PME 1.24; PLE-PLE 1.1; ALE-PME 0.22; ALE-PLE 0.52. Abdomen: Opisthosoma length 1.8, width 1.35. Leg measurements: I: 3.38 (1.1, 0.5, 0.64, 0.62, 0.52); II: 2.88 (1.08, 0.3, 0.4, 0.6, 0.5); III: 3.14 (0.84, 0.42, 0.44, 0.9, 0.54); IV: 3.3 (0.7, 0.5, 0.9, 0.68, 0.52).

Epigyne: similar to *E. albostellata* except for the following. Copulatory ducts are widened and progressed in curved shape by forming large C-shaped membranous atrial rims. Spermatheca double chambered with primary round-shaped anterior portion joined with elongated oval-shaped posterior secondary chamber. FD triangular-shaped, originating from antero lateral wall of primary chamber (Figures 11G, 12C, D).

Distribution and habitat. This species occurs in the montane and submontane forests in the central highlands of Sri Lanka. Specimens were collected by beating vegetation up to a height of 1 to 2 m.

***Epidelaxia bharathi*, sp. n.**

(Figures 13A–G, 14A–D)

urn:lsid:zoobank.org:act:629AFF25-D63E-4515-AFA6-9D9624A5F7C2

Type material. Holotype*.** 1♂ (IFS_SAL_1144): Sri Lanka, Central Province, Matale District, Pitawala Pathana, Knuckles range, 07°32'50''N;80°45'18''E, 856 m, beating, 21 November 2017, leg. S.P. Benjamin et al. ***Paratype. 1♀ (IFS_SAL_1168) same locality and collection data as holotype, 26 April 2018, leg. N. Athukorala et al.

Diagnosis. This species can be distinguished from other congeners by prominent oval -shaped bulbus, short embolus and the presence of two folded membranous outgrowths of the tegulum. Presence of a well- developed S-shaped membranous and transverse copulatory duct also separates this species from *E. albocruciata* and *E. obscura.*

Etymology: The specific epithet is in honour of the first author's mother, Mrs. Bharathithevi Satkunanathan.

***Description*.** Male. (holotype). Total length 5.75; Colour in Ethanol: brown and yellow. Carapace: Prosoma length 2.25, width 1.74. Prosoma brown covered with dark black blotches around the PME and PLE, slightly broader than abdomen. Chelicerae brownish, covered with white hairs at its base. Sternum yellowish brown and pentagonal-shaped, edges bordered with dark brown. Eye measurements: AME 0.6; ALE 0.24; PME 0.1; PLE 0.32; PME-PME 1.36; PLE-PLE 1.42; ALE-PME 0.4; ALE-PLE 0.8. Abdomen: Opisthosoma length 2.82, width 1.98. Slightly thickened first pair of legs. Leg measurements: I: 4.6 (0.82, 0.8, 1.48, 0.86, 0.64); II: 3.22 (0.7, 0.4, 0.8, 1.02, 0.3); III: 3.38 (0.84, 0.8, 0.82, 0.5, 0.42); IV: 3.04 (0.7, 0.3, 0.5, 1.02, 0.52).

Palp covered with pale brown scales, except for light brown cymbium. RTA is straight, thin and long. Cymbium long and distal part of the cymbium tapered or blunted. Oval-shaped bulbus. Membranic outgrowth of tegulum with two membranic edges. Half of sperm duct is clearly visible at distal portion of tegulum. Embolic origin starting 8'o clock position. Embolus slender, long more than half of cymbium and embolic base starting at the middle of the bulbus originating from under the membranic outgrowth of the tegulum (Figures 13E, F, 14A, B).

Female. (paratype). As in male except for the following. Total length 5.35. Carapace: prosoma length 2.55, width 2.1. Prosoma with stretched out yellowish brown triangular-shaped mark. Posterior prosoma highly truncated. Chelicerae, labium dark brown, edges dark brown. Oval - shaped sternum, yellowish brown, edges light brown. Eye measurements: AME 0.62; ALE 0.4; PME 0.38; PLE 0.12; PME-PME 1.52; PLE-PLE 1.64; ALE-PME 0.68; ALE-PLE 0.22. Abdomen: Opisthosoma length 2.25, width 1.62. Leg I dark yellow and thicker. Legs II, III, and IV yellow. Leg measurements: I: 3.74 (0. 84, 0.76, 1.3, 0.44, 0.4); II: 3.22 (0.8, 0.52, 1, 0.4, 0.5); III: 4.2 (1, 0.7, 1.1, 0.8, 0.6); IV: 4.2 (1.4, 0.46, 0.8, 0.9, 0.64).

Epigyne: similar to *E. albostellata* except for the following. Copulatory ducts, well-developed, S-shaped, membranous atrial rims. Spermatheca double chambered, primary round-shaped, anterior portion joined with cylindrical posterior secondary chamber. FD triangular-shaped, originating from antero-mid wall of primary chamber (Figures 13G, 14C, D).

Distribution and habitat. This species occurs only in the type locality. Specimens were collected by beating foliage up to a height of two meters from a remnant patch of montane-wet evergreen forest in the central highlands.

***Epidelaxia somasundaram*, sp. n.**
(Figures 15A–G, 16A–D)
urn:lsid:zoobank.org:act:F50FAA8A-EF23-40B0-8E55-2AEDD84AD4AF

Type material. Holotype. 1♂ (IFS_SAL_1093), Sri Lanka, Uva Province, Monaragala District, Kataragama Peak, 06°23'20"N;81°19'52"E, hand collection, 22–23 November 2017, leg. S.P Benjamin et al. ***Paratype.*** 1♀ (IFS_SAL_1092): same locality and collection data as holotype.

Diagnosis. This species can be distinguished from other congeners by the elevated carapace in both sexes. The species is similar to *E. albocruciata* in morphology. However, it is separated by the presence of a prominent dark brown triangular mark on the prosoma of the male and females.

Etymology: The specific epithet is in honour of the first author’s father, Mr. Somasundaram Satkunanathan.

Description. Male. (holotype). Total length 4.7. Colour in ethanol: reddish brown and yellow. Carapace: Prosoma length 1.8, width 1.89. Prosoma brown covered with red hairs around the eyes, slightly broader than abdomen. Chelicerae blackish brown. Dark brown clypeus with white hairs in thoracic region. Sternum light brown and pentagonal shaped, edges bordered with dark brown. Eye measurements: AME 0.56; ALE 0.32; PME 0.1; PLE 0.26; PME-PME 1.42; PLE-PLE 1.24; ALE-PME 0.26; ALE-PLE 0.9. Abdomen: Opisthosoma length 2.16, width 1.44. Leg I more robust than others, legs I and II dark brown with white hairs around proximal region of patella, tibia and metatarsus, legs III and IV light brown. Leg measurements: I: 4.74 (1.38, 0.52, 1.02, 1.2, 0.62); II: 4.5 (0.8, 0.56, 1.5, 1.2, 0.44); III: 4.2 (0.7, 0.6, 1.24, 1.1, 0.56); IV: 4.44 (1, 0.8, 1.3, 0.84, 0.5).

Palp covered with pale yellow scales, except for reddish brown cymbium. RTA robust and broader at the base, narrower and bent forward ventrally at tip. Cymbium longer and distal part of cymbium elongated. Oval-shaped bulbus. Membranic outgrowth of tegulum with double membranic ledge. Sperm duct visible at the distal portion of tegulum. Embolic origin starting at 6’o clock position. Embolus filiform, long more than half of the cymbium and embolic base starting at the posterior part of the bulbus, originating from under the membranic outgrowth of the tegulum (Figures 15E, F, 16A, B).

Female. (paratype). As in male except for the following. Total length 5.6: prosoma length 2.1, width 1.65. Chelicerae, labium light brown, edges dark brown. Posterior prosoma slightly truncated. Eye measurements: AME 0.64; ALE 0.38; PME 0.1; PLE 0.26; PME-PME 1.2; PLE-PLE 01.06; ALE-PME 0.32; ALE-PLE 0.7. Abdomen: Opisthosoma length 2.58, width 1.3. Leg measurements: I: 3.88 (0.84, 1, 1.02, 0.62, 0.4); II: 3.8 (0.9, 0.86, 0.92, 0.72, 0.4); III: 4.16 (0.92, 0.64, 0.92, 1.04, 0.64); IV: 4.56 (0.84, 0.76, 1.16, 1.24, 0.56).

Epigyne: similar to *E. albostellata* except for the following. Copulatory ducts progressed in S-shape by forming small C-shaped atrial rims. Spermatheca double chambered with primary round-shaped anterior portion joined with bean-shaped posterior secondary chamber. FD lanceolate, originating from antero-mid wall of primary chamber. (Figures 15G, 16C, D).

Distribution and habitat. Specimens were collected by beating dry bushes and shrubs with a height less than two meters. This species occurs in the Kataragama Peak dry zone forest in Monaragala district.

***Tubalaxia* gen. n.**

urn:lsid:zoobank.org:act:ACD91693-9393-4431-9088-5F7ED4305A86

Type species. *Tubalaxia aurea* sp. n.

Etymology. Combination of 'tubal', (meaning 'tubular shape'), which refers to the distinctive presence of tubular S-shaped atrial rims on epigynes of females and "laxia" meaning "loosened'' derived from *Epidelaxia*. This name also refers to the sister relationship between *Tubalaxia* gen. n. and *Epidelaxia*.

Monophyly and phylogenetic placement. Monophyly of *Tubalaxia* gen. n. is recovered in all three phylogenetic analyses (Figures 1, 2, 3) and is supported by the following unambiguous putative synapomorphy: the antero-lateral origin of FD from the wall of spermathecae (36-1).

Diagnosis. This genus can be readily distinguished from other genera of the tribe Nannenini by the brown spot forming W-shaped bands in the abdominal dorsum in males and females (Figures 17A, B) and the distinctive copulatory organs: embolus longer than cymbium, embolic base originating from the apical-retrolateral part of the palp in males and the presence of copulatory ducts that go behind the spermathecae (in ventral view) prior to entering it.

Description. Medium-sized spiders, male with yellow tuft of hairs on the clypeus; prosoma with blackish hairs around AME; yellow triangular-shaped mark behind the eye field; abdomen with brown spots forming a W-shaped band pattern in males and females, leg I darkened and robust in males; more or less straight and long embolus, embolus longer than cymbium; embolic base originating from proximal part of bulbus, short and bent RTA. Female with black patches on the eye field and surrounding PME, behind ALE and posterior slope of prosoma; beans-shaped spermatheca: spermathecal chamber at posterior part of the spermathecae; presence of tubular S-shaped atrial rim. See species descriptions below.

Composition. *Tubalaxia aurea* sp. n., *Tubalaxia castanea* sp. n. and *Tubalaxia minuta* (Prószyński, 1992) **comb. n.**

***Tubalaxia aurea* sp. n.**

(Figures 17A–D, 18A–G, 19A–D)

urn:lsid:zoobank.org:act:7A61EB08-10EA-48E6-89BD-7A43F13137F3

Type material. Holotype. 1♂ (IFS_SAL_901), Sri Lanka, Central Province, Nuwara Eliya District, Upcot, 06°47'35.9"N;80°36'20.5"E, 1199 m, beating, 03 October 2016, leg. N. Athukorala et al.

Other material examined. 1♂ (IFS_SAL_261): Sri Lanka, Central Province, Kandy District, Knuckles, Along Dothalugala Nature Trail, 07^{o}33'19"N;80^{o}84'27"E, 1104 m, beating, 28 November 2013, leg. N. Athukorala et al. 1♂ (IFS_SAL_1152): Knuckles, Along Dothalugala Nature Trail, 07^{o}20'19"N;80^{o}51'3"E, 1202 m, beating, 03 May 2017, leg. S.P. Benjamin et al. 1♂ (IFS_SAL_1310): Knuckles, Along Dothalugala Nature Trail, 07^{o}20' 19"N;80^{o}51'3'E, 1202 m, beating, 08 June 2020, leg. N. Athukorala et al. 1♀ (IFS_SAL_1278): Matale District, Pitawala Pathana, Knuckles range, 07°32'50"N;80°45' 18"E, 856 m, beating, 26 April 2018, leg. N. Athukorala et al. 2♀ (IFS_SAL_719-720), Sri Lanka, Central Province, Nuwara Eliya District, Hakgala SNR, 06^{o}55'52'N;80^{o}48'46'E, 1942 m, beating, 20 January 2015, leg. N. Athukorala et al. 1♂ (IFS_SAL_718): same locality and collection data as IFS_SAL_719-720. 1♀ (IFS_SAL_856): Hakgala SNR, 06°55'44"N;80° 48'55"E, 2044 m, beating, 30 June 2016, leg. N. Athukorala et al. 2♂4♀ (IFS_SAL_1504-1509): Unique view road, 06°57'40"N;80° 45'31"E, 1998 m, beating, 25 February 2019, leg. N. Athukorala et al. 1♀ (IFS_SAL_482): Uva Province, Badulla District, Namunukulla peak, Along Passara road, 06°55'57.7"N;81°06' 44.3"E, 2000 m, beating, 27 February 2015, leg. S.P. Benjamin et al.

Diagnosis. This species can be distinguished from other congeners by the curved RTA in males and the presence of bean-shaped secondary spermathecae.

Etymology. The specific epithet is derived from the Latin word ‘aurea’ meaning ‘golden’ referring to its golden yellowish body colour.

Description. Male (holotype). Total length 4.3. Colour in Ethanol: brown and yellow. Carapace: Prosoma length 1.68, width 1.47. Prosoma brown covered with dark black blotches around the PME and PLE. Brownish clypeus covered with sparsely distributed white hairs. Chelicerae dark brown. Sternum yellowish brown and pentagonal shaped. Eye measurements: AME 0.44; ALE 0.24; PME 0.2; PLE 0.1; PME-PME 1.2; PLE-PLE 1.4; ALE-PME 0.56; ALE-PLE 0.2. Abdomen: Opisthosoma length 1.98, width 1.08. Thickened and darkened first pair of legs. Leg I robust and darker than others, legs II, III and IV yellow. Leg measurements: I: 3.64 (0.64, 0.72, 0.98, 0.8, 0.5); II: 3.52 (1, 0.54, 0.7, 0.68, 0.6); III: 3.12 (0.66, 0.6, 0.64, 0.72, 0.5); IV: 3.46 (0.76, 0.52, 0.82, 0.84, 0.52).

Palp covered with pale yellow scales, except for yellowish cymbium. RTA short and bent backwards dorsally at tip. Cymbium longer and distal part of cymbium elongated. Round shaped bulbus. Sperm duct visible at distal portion of the membranic outgrowth of the tegulum. Embolic origin starting at 2’o clock position. Embolus filiform, medium less than half of cymbium and embolic base starting at the anterior part of the bulbus (Figures 18E, F, 19A, B).

Distribution and habitat. This species occurs in the montane and submontane forests in the central highlands of Sri Lanka. Specimens were collected by beating vegetation up to a height of 0.5 to 2 m.

***Tubalaxia castanea* sp. n.**

(Figures 20A–G, 21A–D)

urn:lsid:zoobank.org:act:D4001C4F-BC1A-43F4-AF29-3C3A89317DD7

Type material. Holotype. 1♂ (IFS_SAL_099), Sri Lanka, Central Province, Badulla District, Ohiya, 06^{0}50'32"N;80^{0}53'05"E, 1280 m, Beating, 30 August 2011, leg. S.P. Benjamin et al. ***Paratype.*** 1♀ (IFS_SAL_098): same locality and collection data as holotype.

Other material examined. 4♀ (IFS_SAL_275-278), Sri Lanka, Uva Province, Badulla District, Ohiya, 06°50'32'N; 80°53'05'E, 1280 m, beating, 26 May 2012, leg. S.P. Benjamin et al. 1 ♂ (IFS_SAL_424): Ohiya, 06° 50' 32"N, 80° 53' 05"E, 1280 m, beating, 26 May 2012, leg. S.P. Benjamin et al. 3♂ (IFS_SAL_315-317): Namunukulla peak, Along Passara road, 06°55'57.7"N;81°06'44.3"E, 2000 m, beating, 23 January 2014, leg. S.P. Benjamin et al. 1♀ (IFS_SAL_318): same locality and collection data as (IFS_SAL_315-317). 1♂ (IFS_SAL_444), Sri Lanka, Central Province, Nuwara Eliya District, Horton plains NP, 06°68'05"N;80°50'19"E, 1951 m, beating, 27 March 2012, leg. S.P. Benjamin et al.

Diagnosis. This species can be distinguished from other congeners by the straight, slanted RTA in males and presence of secondary spermathecae that are the same in size as primary spermathecae and the presence of a curved duct between the primary and secondary spermathecae in females.

Etymology. The specific epithet is derived from the Latin word '*castanea*' meaning 'chestnut' referring to its chestnut brownish body colour.

Description. Almost all characters are similar to the male of *Tubalaxia aurea* except for the following. Total length 6.25. Carapace: Prosoma length 2.16, width 2.1. Eye measurements: AME 0.56; ALE 0.32; PME 0.24; PLE 0.1; PME-PME 1.5; PLE-PLE 1.46; ALE-PME 0.7; ALE-PLE 0.26. Abdomen: Opisthosoma length 2.88, width 1.65. Leg measurements: I: 5.14 (1.9, 0.5, 1, 1.3, 0.44); II: 1.6 (1, 0.6, 0.5, 0.98, 0.4); III: 5.96 (1.7, 0.8, 1.7, 0.8, 1.7); IV: 4.14 (1.6, 0.4, 0.24, 1.3, 0.6).

Palp. similar to *E. albostellata* except for the following. RTA short and bent backwards dorsally at the tip. Round shaped bulbus (Figures 20E, F, 21A, B).

***Female.* (**paratype). Total length 6. Carapace: Prosoma length 2.04, width 1.74. Ethanol preserved specimens, prosoma yellowish brown. ALE, PME, PLE covered with black blotches. Prosoma with stretched out yellowish brown colour triangular-shaped mark. Posterior prosoma moderately truncated. Chelicerae, labium light brown, edges dark brown. Pentagon-shaped sternum, light yellow, edges light brown. Abdomen: Opisthosoma length 2.82, width 1.98. Eye measurements: AME 0.56; ALE 0.3; PME 0.1; PLE 0.32; PME-PME 1.4; PLE-PLE 1.5; ALE-PME 0.2; ALE-PLE 0.7. Leg I dark yellow and thicker. Legs II, III, and IV yellow. Leg measurements: I: 4.74 (0.

8, 1.44, 1.4, 0.6, 0.5); II:3.86 (1, 0.7, 1.22, 0.6, 0.34); III: 3.9 (1, 0.8, 1.2, 0.58, 0.32); IV: 3.76 (0.6, 0.7, 1.1, 0.9, 0.46).

Epigyne: Anterior epigynal border present and poorly sclerotized. CO directly leading into narrowed region of large chamber of spermatheca. Copulatory ducts progressed into well-developed S-shaped tubular atrial rims. Transverse and white membranous window absent. Spermatheca double-chambered with primary round-shaped anterior portion joined with bean-shaped posterior secondary chamber. Secondary S relatively larger in size than primary S. FD triangular-shaped, originating from antero-mid wall of primary chamber (Figures 20G, 21C, D).

Distribution and habitat. This species was found in high elevation montane and submontane forests in the central highlands of Sri Lanka. Specimens were collected by beating vegetation up to a height of 0.5 to 2m.

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