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Twigs that are not twigs: phylogenetic placement of crab spiders of the genus *Tmarus* of Sri Lanka with comments on the higher-level phylogeny of Thomisidae

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Abstract. Sri Lankan species of the genus *Tmarus* are cryptic spiders that live either on greenish moss-covered twigs or brownish dried-out twigs. They have remained taxonomically unrevised. The only known species was misplaced in *Peritraeus* Simon, 1895, which has never been subjected to phylogenetic evaluation. The present study is designed to investigate the phylogenetic placement of Sri Lankan *Tmarus* within Thomisidae as well as to assess the validity of *Peritraeus* and its relationship to *Tmarus* and *Monaeses*, if any. Using a multilocus molecular dataset (16S–ND1, 28S, CO1 and H3) we provide evidence that *Tmarus* and *Monaeses* are paraphyletic and that *Peritraeus* is a junior subjective synonym of *Tmarus*. Four species of *Tmarus*, including three new species, are now recorded from Sri Lanka. The legacy groups *Alcimochthae* and *Tmarae* are confirmed to be polyphyletic. Further, the following new species are described: *Tmarus hiyarensis*, sp. nov., *T. viridomaculatus*, sp. nov. and *T. manojkaushalyai* sp. nov. The following new combination is proposed: *Tmarus hystrix* (Simon, 1895), comb. nov. (this results in a homonym with *Tmarus hystrix* Caporiacco, 1954: we rename the species *Tmarus caporioccoi* Ileperuma Arachchi & Benjamin, replacement name).

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Introduction

Members of the Family Thomisidae Sundevall, 1833 are universally known as crab spiders because of their crab-like, laterigrade leg orientation (e.g. Benjamin 2011; Sirvid *et al*. 2013; Moradmand *et al*. 2014; Silva-Moreira and Machado 2016). They are cryptic dwellers of microhabitats ranging from foliage, flowers, tree bark and leaf litter (e.g. Dippenaar-Schoeman 1985; Metcalfe *et al*. 1997; Benjamin *et al*. 2008; Tang and Li 2009; Gawryszewski *et al*. 2017). Thomisidae is the seventh largest family of spiders and currently includes 2163 species placed in 170 genera (World Spider Catalog 2018).

The National Red List of Sri Lanka (2012) lists 36 nominal species of crab spiders for the island. However, most of what we know of their biodiversity is from their historic initial descriptions. The taxonomy and phylogenetic position of Sri Lankan crab spiders has been the centre of focus in an ongoing island-wide survey of spider diversity (e.g. Benjamin 2000, 2001, 2011, 2016; Benjamin and Jalee 2007; Benjamin *et al*. 2008, 2016; Benjamin and Jaleel 2010). In this study we report on two strikingly similar-looking thomisid genera, *Peritraeus* Simon, 1895 and *Tmarus* Simon, 1875, outlining their taxon boundaries based on target-gene analysis.

The genus *Peritraeus* was erected by Eugene Simon (1895) together with the description of *Peritraeus hystrix*. To date, this is the only known species of the genus. Since its initial description, *Peritraeus* remained taxonomically unrevised and has never been subjected to phylogenetic evaluation. The stated type locality of *P. hystrix* is Kandy, Sri Lanka. The original description contains no illustrations. Further, we were unable to find the type specimen or the corresponding catalogue card in the collections of the Muséum National d'Histoire Naturelle in Paris. However, during recent fieldwork we collected specimens of two species that fit the description of *Peritraeus*. The specimens from Kandy, Dambulla and Kurunegala in Sri Lanka matched the original description of *P. hystrix*. All these specimens have the characteristic, reddish brown V-shaped marking on the prosoma mentioned in Simon's (1895) description. The second species was collected from Galle, Ampara, Gampaha and Anuradhapura Districts in Sri Lanka.

Tmarus Simon, 1875 is a relatively speciose genus (222 species to date) of crab spiders with a worldwide distribution. Altogether, 38 species are known from the Asian region, of which most are from East and South-East Asia. Only six species are recorded from the South Asian region (World Spider Catalog

2018). They are small to medium-sized, moderately elongated spiders characterised by a flat prosoma with a wide, gradually sloping clypeus towards the front, elevated ocular area and an elongated opisthosoma with a prominent caudo-dorsal hump. Their body colours are mainly brown, green, yellow and grey with black/dark brown, intermingled rustic patches. *Tmarus* has been included in recent molecular and morphological analyses of crab spider interrelationships (e.g. Benjamin 2008, 2011; Ramírez 2014; Polotow *et al*. 2015; Wheeler *et al*. 2016; Machado *et al.* 2017). Benjamin *et al*. (2008) recovered *Tmarus* as part of a clade of derived thomisids, that they informally named the Thomisus clade. In Ramírez (2014) *Tmarus* appears as a taxon in a clade also informally named as 'higher thomisids'. Similarly, in Wheeler *et al*. (2017) *Tmarus* is part of the informal clade 'Thomisus group'. However, the monophyly of this cosmopolitan genus has never been explicitly tested.

Monaeses Thorell, 1869 is yet another genus of crab spiders resembling *Tmarus* and *Peritraeus* in morphology and behaviour (e.g. Dippenaar-Schoeman 1984, 1985; Ono 1988; Tang and Li 2009). Species of this genus also usually inhabit plant stems, leafy or dry branches and grasses and are well camouflaged (Dippenaar-Schoeman 1984). Unlike *Peritraeus*, *Monaeses* is well defined and can be distinguished from *Tmarus* by the roughly quadrangle-shaped prosoma which is longer than wide, the elongated abdomen with an abdominal extension that extends beyond the spinnerets, the posterior median eyes relatively closer to the posterior lateral eyes than to each other and the relatively long and slender embolus of the male palp (Dippenaar-Schoeman 1984; Ono 1988). This genus currently consists of 27 species distributed in the Palaearctic, Afro-tropical and Australian regions. It is not recorded from the Nearctic and the Neotropical regions thus far.

In his monograph on spiders, 'Histoire Naturelle des Araignées', Simon (1895) divided Misumeninae (currently Thomisinae) into 18 groups, placing *Peritraeus* and *Tmarus* under two different groups. *Peritraeus* and the genera *Alcimochthes* and *Tarrocanus* were included in Alcimochthae, whereas *Tmarus* and the genera *Smodicinus*, *Pherecydes*, *Philodamia*, *Monaeses*, *Acentroscelus* and *Titidius* were included in Tmarae. Many of these genera are poorly studied, the only exception being *Tmarus*, which has been included in recent molecular phylogenetic and taxonomic studies (e.g. Yang *et al*. 2005; Benjamin *et al*. 2008; Tang and Li 2009; Benjamin 2011; Ramírez 2014; Polotow *et al*. 2015; Astrin *et al*. 2016). Thus, the main objective of this study is to test the monophyly of *Peritraeus* and to assess its relationship to *Tmarus*, if any, using a multilocus molecular phylogeny of them, member of Simon's 'groups' Alcimochthae and Tmarae and a representative sample of other members of the thomisid Tree of Life. Additionally, we describe three new species of *Tmarus* from Sri Lanka.

Materials and methods

Taxon selection

Field work was conducted covering all major climatic-physiographic regions of Sri Lanka for species of *Peritraeus* and *Tmarus*. Spiders were collected by beating vegetation and general hand collecting. The collected specimens were preserved in either 70% or 100% ethanol. Our phylogenetic analysis includes 49 terminal taxa comprising 31 ingroup (19 of 31 were newly sequenced for this study) taxa. Additional sequences of *Tmarus* taxa were obtained from GenBank to represent a geographically widely distributed sample. Accession numbers for all sequences and locality information are given in Table 1.

Included outgroup taxa represent all members of Simon's proposed group Alcimochthae (except for *Domatha*). The selection of outgroup taxa was based on classic systematic groupings of Thomisidae proposed by Simon as well as extensive phylogenetic and cladistic analysis of the family in Benjamin *et al*. (2008) and Benjamin (2011). Outgroup sampling includes 18 taxa belonging to 13 genera (*Monaeses*, *Cetratus*, *Amyciaea*, *Thomisus*, *Runcinia*, *Tarrocanus*, *Oxytate*, *Angaeus*, *Cyriogonus*, *Alcimochthes*, *Xysticus*, *Borboropactus* and *Angaeus*). The last two genera were used to root the phylogenetic tree.

Morphology

Specimens preserved in 70% alcohol were examined using an Olympus SZX7 stereomicroscope. Male palps (left) were dissected and immersed in methyl salicylate, slide mounted, observed and illustrated with the aid of an Olympus BX51 compound microscope with a drawing tube attached. Highly sclerotised or darker areas of palps and epigynum were shaded with an HB pencil. The female epigastric region was dissected and digested in a pancreatin solution (Álvarez-Padilla and Hormiga 2007) for ~3–7 days, slide mounted and illustrated using a microscope with a drawing tube. Digital images of the specimens were taken with a Leica MC170 HD camera mounted on a Leica M205C stereomicroscope using the software package Leica Application Suite, LAS 4.6.2 (Leica Microsystems Limited, Wetzlar, Germany). Acquired image stacks of different depths (15–50 images per stack) were assembled using Helicon Focus 6 (Helicon Soft Ltd) to create a single image with the entire specimen in focus. A Carl Zeiss Gemini FE-SEM housed at Zoological Research Museum Alexander Koenig (ZFMK) was used to study and photograph morphological features; relevant methodology is given in detail in Benjamin (2011). Species descriptions were prepared according to Benjamin (2011). All measurements are given in millimetres. Body length was measured as carapace length plus abdomen length (excluding spinnerets). Types and other specimens were borrowed from the California Academy of Sciences, San Francisco (CAS), the National Institute of Fundamental Studies, Kandy (NIFS), the National Museum of Sri Lanka, Colombo (NMSL), the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Zoological Research Museum Alexander Koenig, Bonn (ZFMK). Types of the new species described herein are deposited in NMSL.

Abbreviations

Abbreviations for morphological items are as follows: ALE, anterior lateral eyes; AME, anterior median eyes; C, conductor; CC, copulatory chamber; CD, copulatory duct; CO, copulatory opening; E, embolus; FD, fertilisation duct; EH, epigynal hood; EO, ejaculatory opening; EpO, epigynal opening;

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

GenBank numbers in bold denote previously published sequences used in this study. Specimen catalog numbers are provided wherever available. All species belong to the family Thomisidae

Species	Family	Locality	16S-ND1	28S	CO1	H3	Catalog number
Ingroup taxa							
Tmarus hystrix	Thomisidae	Sri Lanka, Central Province, Bowatenna	MH717825	–	MH115988	–	IFS_Tho_455
Tmarus hystrix	Thomisidae	Sri Lanka, Central Province, Bowatenna	MH717826	MG873516	MH115989	MG838696	IFS_Tho_456
Tmarus hystrix	Thomisidae	Sri Lanka, North Western Province, Badagamuwa	MH717831	–	MH115990	MG838691	IFS_Tho_548
Tmarus hiyarensis	Thomisidae	Sri Lanka, Southern Province, Hiyare	MH717827	MG873513	–	MG838700	IFS_Tho_525
Tmarus hiyarensis	Thomisidae	Sri Lanka, Southern Province, Hiyare	MH717828	MG873512	–	MG838699	IFS_Tho_526
Tmarus hiyarensis	Thomisidae	Sri Lanka, Eastern Province, Ampara	MH717832	–	MH115985	–	IFS_Tho_387
Tmarus viridomaculatus	Thomisidae	Sri Lanka, Central Province, Hakgala	MH717823	–	–	MG838697	IFS_Tho_113
Tmarus viridomaculatus	Thomisidae	Sri Lanka, Central Province, Upcot	MH717824	–	–	–	IFS_Tho_420
Tmarus viridomaculatus	Thomisidae	Sri Lanka, Central Province, Hakgala	MH717829	MG873510	MH115991	–	IFS_Tho_540
Tmarus viridomaculatus	Thomisidae	Sri Lanka, Central Province, Rattota	–	–	MH115981	MG873524	IFS_Tho_002
Tmarus viridomaculatus	Thomisidae	Sri Lanka, Central Province, Hakgala	MH717830	MG873508	–	MG838694	IFS_Tho_543
Tmarus manojkaushalyai	Thomisidae	Sri Lanka, Central Province, Hakgala	MH717836	MG873509	–	MG838695	IFS_Tho_541
Tmarus manojkaushalyai	Thomisidae	Sri Lanka, Central Province, Hakgala	MH717837	MG873507	MH115993	MG838692	IFS_Tho_547
Tmarus manojkaushalyai	Thomisidae	Sri Lanka, Uwa Province, Namunukula	MH717838	–	MH115984	–	IFS_Tho_353
Tmarus manojkaushalyai	Thomisidae	Sri Lanka, Central Province, Hakgala	–	MG873515	MH115992	MG838693	IFS_Tho_544
Tmarus sp. A	Thomisidae	Madagascar	MH717833	MG873520	MH115982	MG873528	IFS_Tho_157
Tmarus sp. B	Thomisidae	Madagascar	MH717834	MG873521	–	–	IFS_Tho_170
Tmarus sp	Thomisidae	Brazil	–	MG873519	–	MG873526	IFS_Tho_183
Tmarus sp.	Thomisidae	Central America, Honduras	–	MG873522	MH115983	MG873525	IFS_Tho_201
Tmarus piger	Thomisidae	Austria	–	–	**KY269754**	–	
Tmarus angulatus	Thomisidae	Canada	–	–	**DQ127429**	–	
Tmarus piger	Thomisidae	Slovenia	–	–	**KX039418**	–	
Tmarus rimosus	Thomisidae	Korea	–	–	**JN817249**	–	
Tmarus piger	Thomisidae	Korea	–	**JN817033**	**JN817248**	–	
Tmarus sp.	Thomisidae	Madagascar	–	**KM225076**	**KM225127**	**KM225228**	
Tmarus angulatus	Thomisidae	USA	–	–	**EU168179**	**EU157110**	
Tmarus staintoni	Thomisidae	Spain, Extremadura, Cuacos de Yuste	**KY784100**	–	**KY703474**	**KY703545**	
Tmarus punctatissimus	Thomisidae	Spain, Murcia, Alhama de Murcia	**KY784099**	–	**KY703477**	**KY703567**	
Tmarus piochardi	Thomisidae	Greece, Tesalia, Kalambaka	**KY703536**	–	**KY703475**	**KY703536**	
Tmarus stellio	Thomisidae	Greece, Tesalia, Kalambaka	**KY703548**	–	**KY703473**	**KY784096**	
Tmarus holmbergi	Thomisidae	Argentina, Entre Ríos, Parque Nac. El Palmar	–	–	**KY018004**	**KY018501**	
Outgroup taxa							
Xysticus californicus	Thomisidae	USA	MK257681	MG873517	**EU168181**	**EU157131**	IFS_Tho_006
Runcinia albostriata	Thomisidae	Sri Lanka, Central Province, Agrabopath	MK257682	–	**EU168178**	**EU157130**	IFS_Tho_003
Runcinia albostriata	Thomisidae	Sri Lanka, North Central Province, Mihintale	MH717822	MG873505	–	MG838689	IFS_Tho_560
Cyriogonus sp.	Thomisidae	Madagascar, Antananarivo	MK257683	–	**EU168168**	**EU157118**	IFS_Tho_016
Cetratus rubropunctatus	Thomisidae	Australia	–	–	**KM495302**		
Cetratus annulatus	Thomisidae	Australia	–	–	**KM495270**	–	
Australomisidia socialis	Thomisidae	Australia, Western Australia	–	–	**EU168186**	–	
Borboropactus sp.	Thomisidae	Sri Lanka, Central Province, Udawatta kele FR	MH717819	MG873514	–	MG838698	IFS_Tho_008
Amyciaea forticeps	Thomisidae	Thailand, Montha Tarn	–	–	–	**EU157135**	
Angaeus sp.	Thomisidae	Sri Lanka, North Western Province, Ethagala	MH717820	MG873511	–	MH725803	IFS_Tho_538
Oxytate taprobane	Thomisidae	Sri Lanka, Central Province, Rattota	–	MG873523	**EU168161**	**EU157112**	IFS_Tho_001
Alcimochthes limbatus	Thomisidae	Philippines, Luzon Island, laguna Province	–	MG873518	–	MG873529	IFS_Tho_118
Thomisus granulifrons	Thomisidae	Sri Lanka, Western Province, Bellanwila-Attidiya	–	–	**EU168162**	**EU157113**	IFS_Tho_010
Tarrocanus capra	Thomisidae	Sri Lanka, North Western Province, Ethagala	MH717835	–	MH115980	–	IFS_Tho_050
Tarrocanus sp. A	Thomisidae	Sri Lanka, Nothern Province, Mundathivu, Jaffna	–	MH748185	MH115986	–	IFS_Tho_581
Thomisus rigoratus	Thomisidae	Sri Lanka, North Central Province, Mihintale	MH717821	MG873506	–	MG838690	IFS_Tho_558
Monaeses austrinus	Thomisidae	South Africa,Tembe Elephant Park	–	**KY017438**	**KY017989**	**KY018487**	
Monaeses aciculus	Thomisidae	Philippines, Luzon Island, laguna Province	MH717818	MH748184	MH115987	MG873527	IFS_Tho_135

Table 2. Gene targets, PCR conditions and primer data used in this study

Gene target	Annealing temperature/time	Primer pair	5′-Primer Sequence-3′	Reference
CO1	46°C / 50s	LCO-1490(F)	GGT CAA CAA ATC ATA AAG ATA	Hedin and Maddison (2001)
		C1-N-2568(R)	GCT ACA ACA TAA TAA GTA TCA T	Sirvid *et al*. (2013)
	46°C / 50s	C1-N-1718(F)	GGA GGA TTT GGA AAT TGA TTA	
		C1-N-2568(R)	GTT CC GCT ACA ACA TAA TAA GTA TCA T	
28S	60(50)°C /1.5 min	28S O(F)	GAA ACT GTC CAA AGG TAA ACG G	Hedin and Maddison (2001)
		28S C(R)	GGT TCG ATT AGT CTT TCG CC	Spagna and Gillipse (2008) Sirvid *et al*. (2013)
H3	60(50)°C /1.5 min	H3aF	ATG GCT CGT ACC AAG CAG ACV	Colgan *et al.* (1998)
		H3aR	GC ATA TCC TTR GGC ATR ATR GTG AC	Benjamin *et al.* (2008) Sirvid *et al*. (2013)
16S-ND1	60(50)°C /1.5 min	ND1-Thom(F)	GAG CTA CTC TTC GAA TTG ATC C	Garb and Gillespie (2006)
		LR-N-12945(R)	CGA CCT CGA TGT TGA ATT AA	

Table 3. Length of gene partition alignment prior, and subsequent, to treatment with Gblocks 0.91b

Partitions	Original length of alignment (bp)	Fraction retained by Gblocks (%)	Final length of alignment (bp)
16S–ND1	611	70	430
28S rRNA	748	70	526

ER, epigynal ridge; ITA, intermediate tibial apophysis; MOA, median ocular area; PLE, posterior lateral eyes; PME, posterior median eyes; RTA, retrolateral tibial apophysis; S, spermathecae; TA, tegular apophysis; TR, tegular ridge; VTA, ventral tibial apophysis. Additional abbreviations are: FR, forest reserve; NP, national park; SNR, strict nature reserve.

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 thomisids (e.g. Benjamin *et al*. 2008; Garb and Gillespie 2009; Sirvid *et al*. 2013). Partial fragments of nuclear genes, histone H3 (H3), 28S rDNA (28S), and mitochondrial protein-coding genes, cytochrome *c* oxidase subunit 1 (COI) and a spanning section from 16S to NADH dehydrogenase subunit 1 (16S–ND1) were amplified. H3, 16S–ND1 and CO1 gene regions are more suitable to resolve more recent evolutionary events, whereas 28S is more effective in resolving deeper nodes in phylogenetic trees (Edgecombe and Giribet 2006). H3 and 28S have been previously used successfully in thomisid phylogenetics (Benjamin 2008; Sirvid *et al*. 2013). Details of each primer pair used, primer sequences, annealing temperatures, expected fragment sizes and related references are given in Table 2.

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 typically extracted, depending on size, from the first two legs from each specimen and the remainder stored in 70% ethanol and deposited in NIFS arachnid collection. Extracted DNA was stored at –21°C until required for Polymerase Chain Reaction (PCR). PCR were carried out using either the Multiplex PCR' kit (Qiagen) or the PuReTaq Ready-To-Go™ PCR beads (GE Healthcare, UK). Total reaction mixes consisted of 20 μL, including 2.5 μL undiluted DNA template, 1.6 μL forward and reverse primers, 10 pm μL^{-1} of Q-Solution, 10 μL 'Multipex PCR Master Mix' containing hot start Taq DNA polymerase, buffers and 2.3 μL of water (all the latter components come with the Multiplex kit). In the case of PCR beads, the total reaction mix was 25 μL and included 19.3 μL of ultrapure RO water, 1.6 μL each of the forward and reverse primers (10 pm μL^{-1}) and 2.5 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 in Table 2.

PCR products were verified on a 1% agarose gel and purified using Gene Clean™ Turbo Kit (MP Biomedicals, LLC, USA). The weak bands were purified using the Illustra® ExoProStar® (GE Healthcare, UK) PCR clean-up system, according to manufacturer's protocol. All purified PCR products were Sanger sequenced (Sanger *et al*. 1977) in both directions by MACROGEN (Seoul, South Korea).

Phylogenetic analysis

Sequences were edited and assembled using the Geneious 6.1.5 software package. Sequence alignment was also done with the same software using default parameters and then assembled, aligned and edited manually using Mesquite 2.72 (Maddison and Maddison 2009). The protein-coding COI and H3 sequences were easily aligned. These alignments were refined using protein sequence translations before downstream treatment. Mesquite edited 16S–ND1 and 28S sequences were subsequently treated with Gblocks 0.91b (Castresana 2000; Talavera and Castresana 2007) to cull positions of ambiguous homology. Gblocks parameters were defined as follows: minimum number of sequences for a conserved position (50%), maximum number of contiguous non-conserved positions (10), minimum length of a block (5) and allowed gap positions (none). The final

alignments of the four gene fragments were then concatenated using Mesquite. Details of the fragments are provided in Table 3.

Parsimony- and model-based (maximum likelihood, ML) approaches were used to infer the phylogenetic relationships of the targeted taxa. The best-fit model for likelihood analysis was searched by running the 'find best DNA/protein model (ML)' option in MEGA 6.06 and models with the lowest values of Bayesian Information Criteria and Akaike Information Criteria were selected. After selecting the model, the phylogenetic tree was obtained through the online servers for RAxML (Stamatakis 2006; Boc *et al.* 2012). The parameters used are as follows: substitution model (GTRGAMMAI), algorithm executed (Hill climbing – default), and the number of alternative runs on distinct starting trees (100). Parsimony analysis was carried out using the '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 swapping algorithm saving 10 trees per replication in TNT. The concavity constant (K) was set to values between 3 and 10, maxtrees was set to 100 000. Group support values and Bremer and Relative Bremer indices (Bremer 1994) were calculated using the 'aquickie.run' script in TNT.

Results and discussion

The lengths of the targeted fragments after excluding primers were as follows: 16S–ND1 422 bp, 28S 545 bp, CO1 562 bp and H3 262 bp. The assembled matrix of the concatenated mitochondrial and nuclear markers includes 49 taxa (31 ingroups, 18 outgroups). The total length of the final matrix was 1791 bp. The best-fit model for the combined data matrix generated using MEGA was GTR+G +I and, accordingly, GTRGAMMAI was selected as the compatible model in the RAxML.

The phylogenetic tree resulting from ML analysis of the combined data matrix is presented in Fig. 1. A well supported clade that includes exemplars of *Tmarus*, *Monaeses* and *Peritraeus* is recovered. Within this clade *Peritraeus hystrix* is sister to *T. hiyarensis* and both together are sister to *Tmarus* sp. B (from Madagascar). Two other new *Tmarus* species, *T. viridomaculatus* and *T. manojkaushalyai*, is sister to this clade. The parsimony analysis of the same combined data matrix recovers 12 trees. The strict consensus of these 12 trees is given in Fig. 2. The topology of this preferred tree is very similar to that of the recovered ML tree. The placement of *Peritraeus* and *Tmarus* species from Sri Lanka is as in the ML tree; *Peritraeus* is recovered as a branch within *Tmarus* spp. from Sri Lanka.

The phylogenetic relationships inferred here are preliminary in the absence of a greater taxon sample of the two large genera *Tmarus* and *Monaeses*. However, several key outcomes are worthy of discussion. First, an interesting, though unexpected, result is the placement of *Monaeses* within *Tmarus* in both the ML and parsimony analyses (Figs 1, 2). This is in contradiction to current thinking in higher-level thomisid systematics and their perceived morphological distinctiveness. This result also renders both genera paraphyletic. It is very possible that *Monaeses* could be a specialised clade within *Tmarus*. Second, as seen in both ML and parsimony analyses, *Peritraeus* (synonymised as *Tmarus hystrix* as depicted in Figs 1 and 2) appears within the *Tmarus* clade (Figs 1, 2) as sister to *T. hiyarensis* and also to the two sister species, *T. viridomaculatus* + *T. manojkaushalyai*. Further, *Tmarus* species of Sri Lanka form two clusters: the two greenish species that inhabit central highland cloud forests of Sri Lanka, *T. viridomaculatus* sp. nov. + *T. manojkaushalyai* sp. nov. and the two lowland forest species *T. hystrix* + *T. hiyarensis*. These two clusters appear as sister to each other in both trees. This study recovers four species of *Tmarus* from Sri Lanka, including three new species.

None of our searches recover Simon's (1895) groups *Alcimochthae* or *Tmarae*. Of the four genera (*Alcimochthes*, *Peritraeus*, *Tarrocanus* and *Domatha*) in Alcimochthae, we were unable to include only *Domatha* Simon, 1895 in this analysis due lack of molecular grade material. *Tmarus* is not recovered as sister to either *Alcimochthes* and/or *Tarrocanus*. This is not very surprising and closely mirrors the results of other phylogenetic studies of other spider families (e.g. Benjamin 2004, 2008).

A major conclusion of the molecular study of Benjamin *et al.* (2008) was that none of the conventional subfamilies of Thomisidae were monophyletic. This study provides further evidence. It is now increasingly apparent that thomisid higher-level taxa have been mostly defined on the basis of plesiomorphic character states.

Taxonomy

Family **Thomisidae** Sundevall, 1833

Genus ***Tmarus*** Simon, 1875

Tmarus Simon, 1875: 259. Type species *Aranea pigra* Walckenaer, 1802: 229.

Peritraeus Simon, 1895: 980. Type species by monotypy *Peritraeus hystrix* Simon, 1895: 980. New synonymy.

Diagnosis

Species of *Tmarus* can be separated from other Thomisidae by a dorsoposterior tubercle or hump, which is more prominent in females (Fig. 3*B*, *D*, *H*), an elevated ocular area with well developed lateral eyes (ALE > PLE), a pyriform opisthosoma and relatively wide clypeus gradually sloping towards the front. Despite the highly variable genital morphology within the genus, males can be identified by a tegulum with or without apophyses, and a stout or elongated embolus. Females can be distinguished by the epigynum having a broad epigynal hood (Figs 10*C*, *D*, 11*G*, *H*) or a vertical epigynal ridge (Fig. 11*C*) and small spermathecae.

Remarks

Sri Lankan species of *Tmarus* are cryptic spiders that live either on greenish moss-covered twigs or brownish dried-out twigs. Why Simon (1895) decided to erect a new genus for a single species (*Peritraeus hystrix*) with a general appearance and habitus (share broad, gradually sloping prominent clypeus, wide, convex prosoma, characteristic caudo-dorsal hump of opisthosoma, mottled, multichromatic body) that suggest the possibility of placement in *Tmarus* is unclear.

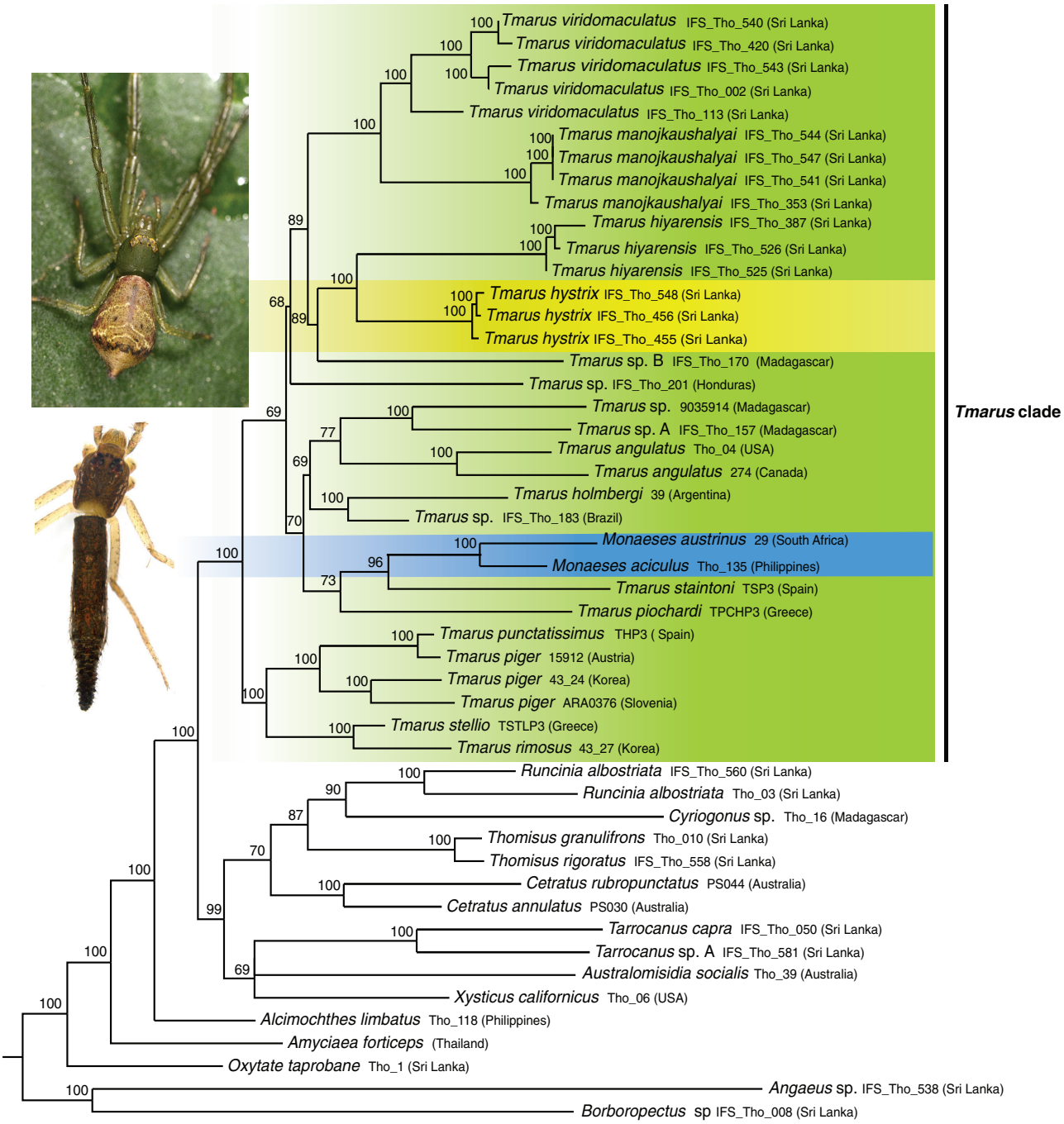

Fig. 1. Phylogenetic placement of crab spiders of the genus *Tmarus* Simon, 1875 of Sri Lanka. The single most likely tree resulting from the analysis of the combined dataset of 1771 bp in RaxML is shown. Nodes that are unsupported have been collapsed. Collection locality is given within parentheses. Bootstrap support values >40 are indicated above branches. Green, yellow and blue colour boxes highlight the *Tmarus* clade, *Peritraeus hystrix* and the *Monaeses* clade respectively. *Tmarus manojkaushalyai* is shown at upper left and *Monaeses* cf. *aciculus* (Tho_135) is shown at lower left.

The few characters that Simon mentioned that differentiate '*Peritraeus*' from *Alcimochthus*, *Tarrocanus* and *Domatha* are the gradually sloping cephapothorax (towards its posterior margin), prominent lateral eye tubercles and a body covered with long and spiniform setae (Simon, 1895). He also mentioned that Alcimochthae and Tmarae share similarities in eye pattern, shape of cephalothorax and opisthosoma, size and habitat with some generic-level differences. This implies that he considered the possibility that *Tmarus* and *Peritraeus* might be closely related.

Circumscription of *Tmarus* based on genital morphology, especially of males, differ in publications. Some authors have described male palpi of *Tmarus* as consisting of a simple tegulum without any aphopyses (Ono 1977, 1988; Yang *et al*. 2005; Kim

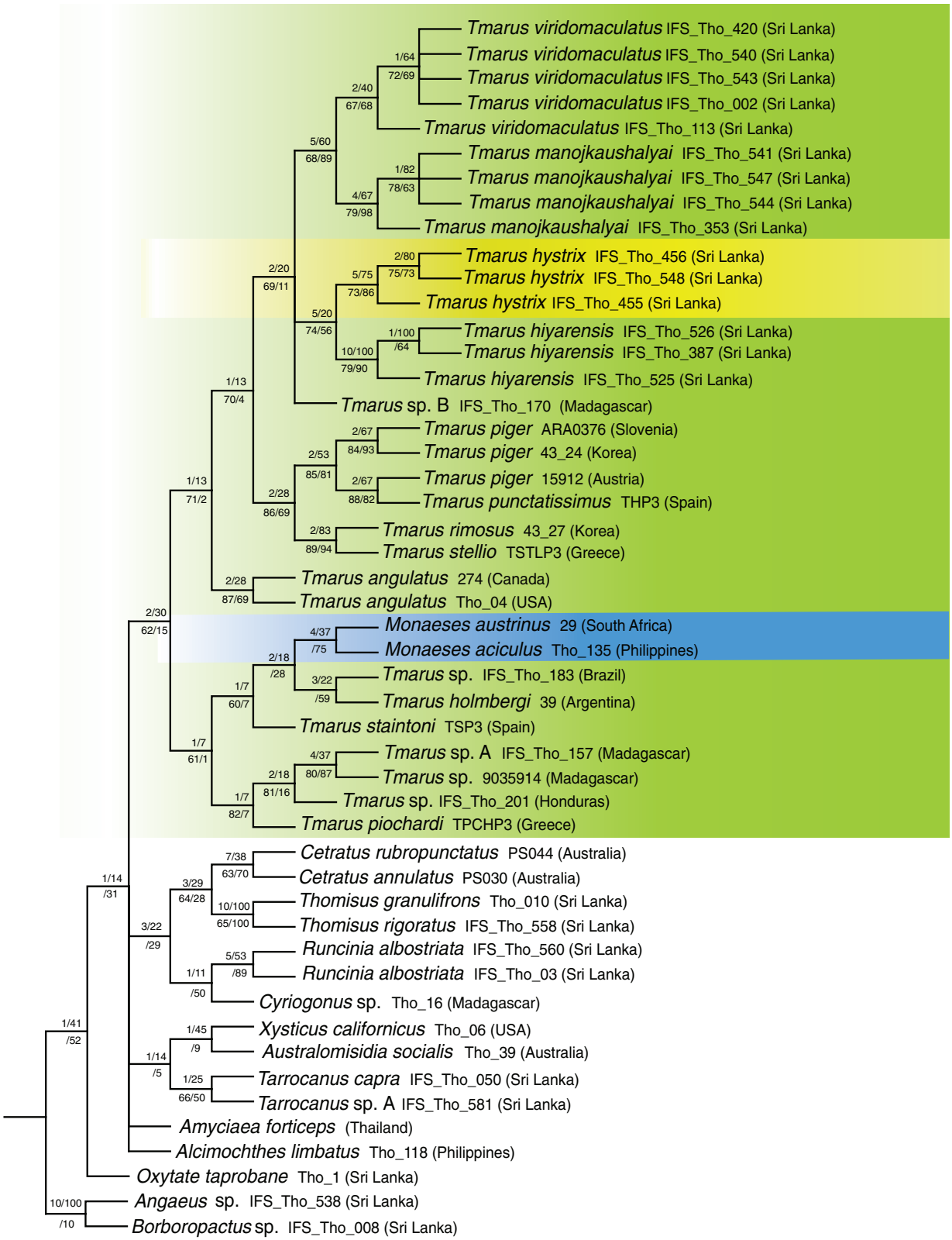

Fig. 2. Phylogenetic placement of crab spiders of the genus *Tmarus* Simon, 1875 of Sri Lanka. Strict consensus of the three most parsimonious trees obtained in TNT for the combined dataset of 1771 bp (L = 1919, Ci = 47, Ri = 50) is shown. The values above the lines represent Bremer support/relative Bremer support, while the values below the line represent symmetric resampling frequencies/symmetric resampling frequency differences. Green, yellow and blue colour boxes highlight the *Tmarus* clade, *Peritraeus hystrix* and the *Monaeses* clade respectively.

Fig. 3. *Tmarus* species of Sri Lanka in life. (*A*) *Tmarus viridomaculatus* sp. nov., male, Central Province, Nuwara Eliya District, Hakgala SNR; (*B*) as previous, female, same locality; (*C*) *T. manojkaushalyai*, sp. nov., male, same locality; (*D*) as previous, female, same locality; (*E*) *T. hiyarensis*, sp. nov., male, Southern Province, Galle District, Hiyare FR; (*F*) as previous, same locality (*G*) *T. hystrix*, comb. nov., male, Central Province, Matale District, Bowatenna FR; (*H*) *T. hystrix*, comb. nov., female, same locality. All photos by Suresh P. Benjamin.

and Lee 2012; Sen *et al*. 2015; Zamani 2015) and some have stated that the tegulum is armed with several tegular apophyses (Chickering 1965*a*, 1965*b*; Dippenaar-Schoeman 1984). Ono (1988) distinguished *Tmarus* from *Monaeses* by the longer embolus in the latter. However, palpi seem to be highly variable in *Tmarus*, ranging from simple to several apophyses (e.g. *T. hiyarensis*) and from long to short emboli. This discrepancy could be due to authors only considering the diversity (of genital morphology) of species of their preferred study area (e.g. Ono 1988). However, a recent taxonomic study of *Tmarus* of Xishuangbanna, in China, by Tang and Li (2009) demonstrates that even species in a single locality might have diverse genitalia.

Distribution

Distributed worldwide; however, most species are from the temperate and tropical areas.

Tmarus manojkaushalyai, sp. nov

(Figs 3*C*, *D*, 5*C*, *D*, 6*C*, *D*, 7*C*, *D*, 10*E*–*H*)

Materials examined

Holotype. 1♂, **Sri Lanka**: Central Province: Nuwara Eliya District: Hakgala SNR, 06°55′44″N, 80°48′55″E, 1786 m, beating, 30.vi.2016, leg. N. Athukorala *et al*. (IFS_Tho_545).

Paratype. ♀, same data as holotype (IFS_Tho_546).

Non-type material. **Sri Lanka**: 1♀, Kandy District: Loolkandura estate (IFS_Tho_662); 1♀, Badulla District: Namunukula (IFS_Tho_353); Nuwara Eliya District: 3♂ 9♀, same data as holotype (IFS_Tho_541, IFS_Tho_542, IFS_Tho_566, IFS_Tho_544, IFS_Tho_547, IFS_Tho_551, IFS_Tho_553, IFS_Tho_567, IFS_Tho_568, IFS_Tho_569, IFS_Tho_570); 1♀, Horton Plains NP (IFS_Tho_326); 1♀, Upcot (IFS_Tho_172); 1♀, same data (IFS_Tho_421); 1♀, same data (IFS_Tho_622).

Diagnosis

Males of *T. manojkaushalyai* can be separated from those of *T. viridomaculatus* and *T. byssinus* Tang & Li, 2009 by having relatively longer VTA, and a more robust RTA with its short and `pointed apex (which is more prominent and tooth-like in *T. byssinus*) (Figs 7*C*, *D*, 10*E*, *F*). Females can be distinguished from all other congeners by the pouch-like copulatory chambers and the U-shaped spermathecae. Further, *T. manojkaushalyai* is similar to known congeners with respect to its plain green body colour whereas the body colour is greyish green in *T. byssinus*. Also, the RTA of *T. manojkaushalyai* is peg-like with a tooth-shaped projection at the apex of the dorsal margin whereas it is broader with a slender and pointed apex in *T. komi* Ono, 1996. Relative to other *Tmarus* species, the body is sparsely covered with setae.

Description

Male (holotype)

Total length: 2.9; prosoma length 1.1, width 1.3; opisthosoma length 1.6, width 0.9. Overall body colour is light green. Prosoma light green, without markings, sparsely covered with setae (Fig. 3*C*). Opisthosoma is greenish yellow with pale reddish brown patches on sides and near spinnerets dorsally. Eye tubercles yellowish green. AME 0.06; ALE 0.12; PME 0.08; PLE 0.1; AME–AME 0.2; AME–ALE 0.12; PME–PME 0.2; PME–PLE 0.24. MOA length 0.3, front width 0.36, back width 0.34. Leg measurements: I: 10 (3.0, 0.9, 2.6, 1.1, 2.4); II: 9.7 (2.9, 0.8, 2.5, 1.1, 2.4); III: 6.8 (2.4, 0.8, 1.8, 0.6, 1.2); IV: 6.9 (2.6, 0.8, 1.8, 0.5, 1.2). Legs pale green, covered with numerous short setae and sparsely distributed long setae (Fig. 3*C*, *D*). Palp: tegulum plain without any apophyses, VTA with a long stem and a hook-like blunt apex. RTA peg-like with a tooth-shaped projection at the dorsal margin of apex (Fig. 11*E*, *F*).

Female (paratype)

Total length 4.6: prosoma length 1.2, width 1.6; opisthosoma length 2.8, width 2.0. Somatic morphology as in male except for more reddish brown patches on opisthosoma (Fig. 3*D*). Eye measurements: AME 0.08; ALE 0.16; PME 0.01; PLE 0.14; AME–AME 0.18; AME–ALE 0.14; PME–PME 0.3; PME–PLE 0.32. MOA length 0.36, front width 0.34, back width 0.48. Leg measurements: I: 8.6 (2.9, 1.0, 2.4, 0.8, 1.5); II: 10 (2.8, 1.1, 2.4, 1.9, 1.8); III: 4.2 (1.4, 0.6, 1.2, 0.4, 0.6); IV: 3.9 (1.6, 0.5, 0.8, 0.4, 0.6). Epigynum and vulva with a narrow triangular-shaped hood, copulatory opening is slit-like, placed diagonally across the copulatory chamber, copulatory ducts relatively short, spermathecae tube-like and elongated (Fig. 11*G*, *H*).

Intraspecific variations

Range of measurements in males ($n = 4$) and females ($n = 6$, in parentheses) in non-type series: total length: 2.8–2.9 (4.5–4.6); prosoma length 1.1–1.2 (1.2–1.3), width 1.2–1.3 (1.4–1.6); opisthosoma length 1.6–1.8 (2.8–3.0), width 0.9–1.1 (1.8–2.0).

Distribution and habitat

This species occurs in high-elevation montane and submontane forests of Sri Lanka (Fig. 4), with a limited distribution. It is found in similar habitats as *T. viridomaculatus*, sp. nov.

Etymology

The specific epithet is in honour of the first author's husband, Manoj Kaushalya Rathnayake.

Tmarus hiyarensis, sp. nov

(Figs 3*E*, *F*, 5*E*, *F*, 6*E*, *F*, 7*E*, *F*, 9*A*–*E*, 11*A*–*D*)

Material examined

Holotype. 1♂, **Sri Lanka**, Southern Province: Galle District: Hiyare, Kombala-Kottawa FR, 06°03'53'N, 80°18'05'E, 252 m, beating, 24–26.v.2016, leg. N. Athukorala *et al*. (IFS_Tho_525).

Paratype. 1♀, same data as holotype (IFS_Tho_526).

Other material examined. **Sri Lanka**: 2♀, Central Province: Matale District, Dambulla, IFS Arboretum (IFS_Tho_626, IFS_Tho_629); Eastern Province: 1♂, Ampara District, Namal Oya FR (IFS_Tho_387); 1♂ 1♀, North Central Province, Anuradhapura District, Kahatagasdigiliya, Allepothana, Kok-ebe FR (IFS_Tho_627, IFS_Tho_628); 1♂, North Western Province, Kurunegala District, Ethagala (IFS_Tho_424); 1♂, Western Province: Gampaha District, Pilikuttuwa Forest (IFS_Tho_565).

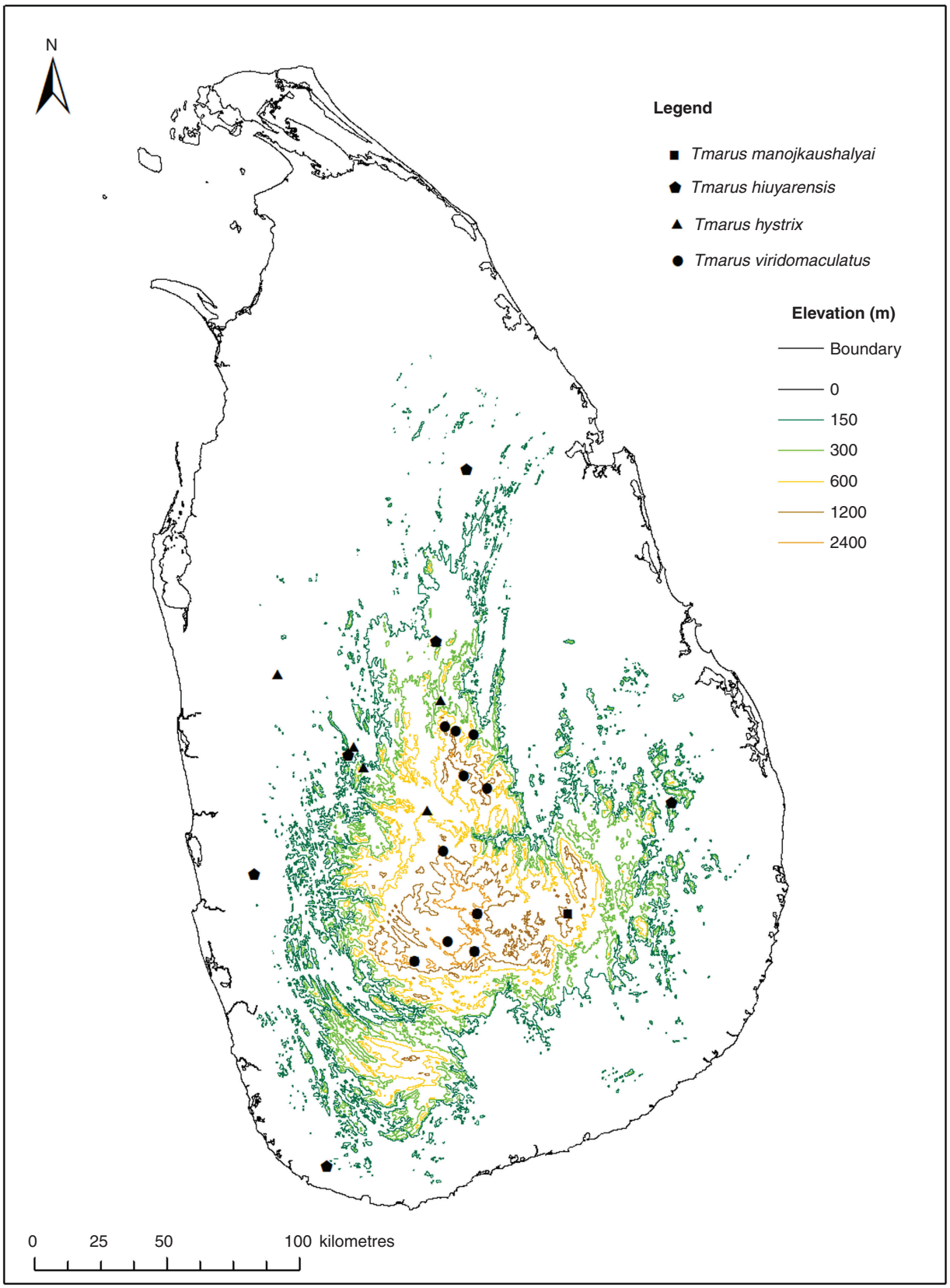

Fig. 4. Distribution of *Tmarus viridomaculatus*, sp. nov., *T. manojkaushalyai*, sp.nov, *T. hiyarensis*, sp. nov. and *T. hystrix*, comb. nov. of Sri Lanka.

Fig. 5. Habitus (dorsal view) of *Tmarus* species of Sri Lanka. (*A*) *T. viridomaculatus*, sp. nov., male, Central Province, Nuwara Eliya District, Hakgala SNR; (*B*) as previous, female, same locality; (*C*) *T. manojkaushalyai*, sp. nov., male, same locality; (*D*) as previous, female, same locality; (*E*) *T. hiyarensis*, sp. nov., male, Southern Province, Galle District, Hiyare FR; (*F*) as previous, same locality; (*G*) *T. hystrix*, comb. nov., male, Central Province, Matale District, Bowatenna FR; (*H*) as previous, female, same locality. Scale bars: *A*, *C–E*, G, *H*, 1 mm; *B*, *F*, 2 mm.

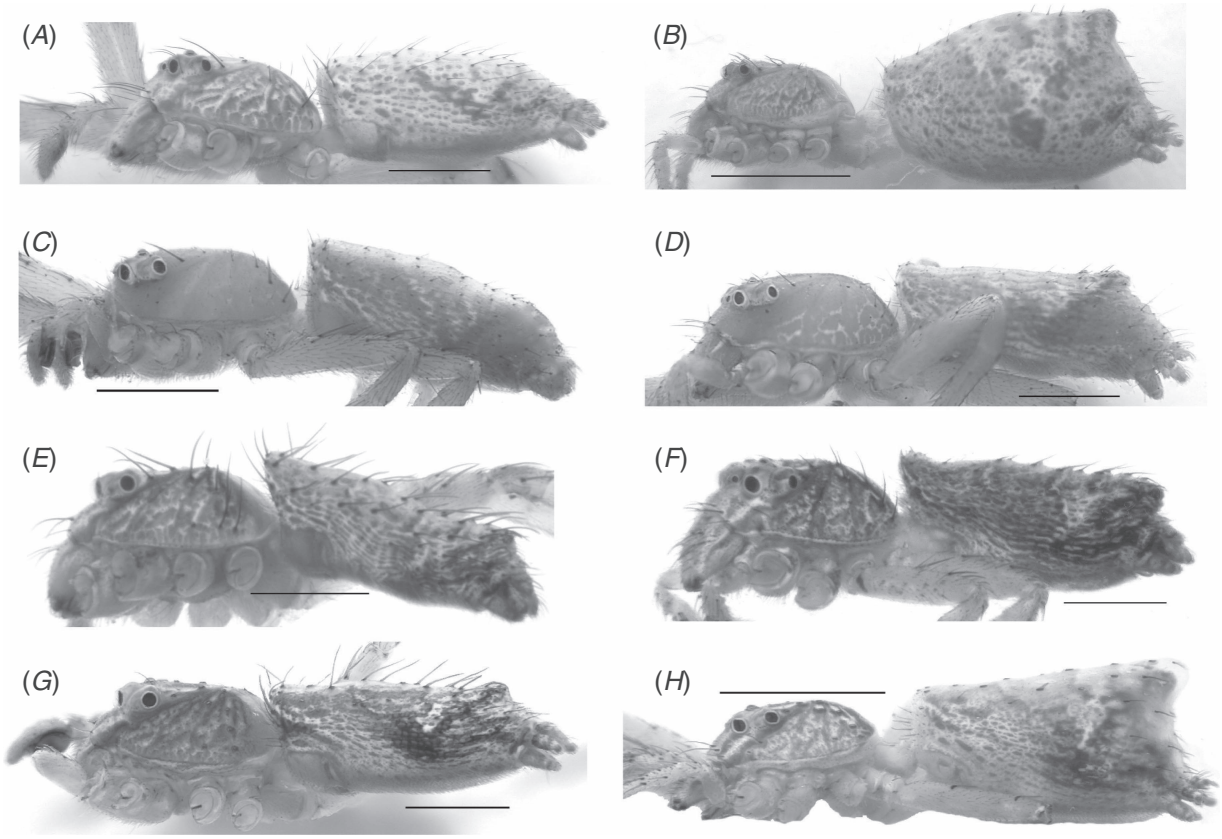

Fig. 6. Habitus (lateral view) of *Tmarus* species in Sri Lanka. (*A*) *Tmarus viridomaculatus*, sp. nov., male, Central Province, Nuwara Eliya District, Hakgala SNR; (*B*) as previous, female, same locality; (*C*) *T. manojkaushalyai*, sp. nov., male, same locality; (*D*) as previous, female, same locality; (*E*) *T. hiyarensis*, sp. nov., male, Southern Province, Galle District, Hiyare FR; (*F*) as previous, same locality; (*G*) *T. hystrix*, comb. nov., male, Central Province, Matale District, Bowatenna FR; (*H*) as previous, female, same locality. Scale bars: *A*, *C–E*, *G*, *H*, 1 mm; *B*, F, 2 mm.

Diagnosis

Males of *T. hiyarensis* can be separated from those of *T. hystrix* by presences of two tegular apophyses (one median tegular apophysis in *T. hystrix*), and by the elliptic and leaf-like ITA (TA 1 and TA 2: Figs 9*A*, *B*, *D*, 11*A*). Tegular apophyses pointed and well developed in *T. menglae* and the tegular apophyses are continuous whereas the two tegular apophyses are blunt and less-developed in *T. hiyarensis*. Females are distinguished from those of *T. hystrix* by having a longitudinal epygynal ridge, and from those of *T. spicatus* by having kidney-shaped spermathecae (Fig. 11*C*, *D*).

Description

Male (holotype)

Total length 3.1; prosoma length 1.5, width 1.4; opisthosoma length 1.7, width 1.1. Prosoma as long as wide, greyish-green speckled with white, dull yellow patches, intermittent lines around and just behind the PME, white half-circular patch posteriorly. Dorsum of opisthosoma greenish brown, mottled with yellow and white patches, covered with setae, 2–3 transverse rippled white lines on opisthosoma posteriorly (Fig. 3*E*, *F*). Eye tubercles grayish-green. Eye measurements: AME 0.05; ALE 0.16; PME 0.07; PLE 0.18; AME–AME 0.22; AME–ALE 0.18; PME–PME 0.29; PME–PLE 0.34. MOA length 0.38 with front width 0.32 and back width 0.45. Legs are whitish-grey with black spots and covered with setae. Leg measurements: I: 7.9 (2.3, 0.8, 2.1, 2.0, 0.7); II: 7.9 (2.3, 0.8, 2.2, 1.7, 0.9); III: 4.8 (1.6, 0.6, 1.3, 0.8, 0.5); IV: 4.6 (1.7, 0.6, 1.1, 0.7, 0.5). Palp: RTA a broad-based, long stem, spear-shaped, well sclerotised apex with blunt point at inner retrolateral margin at proximal end. VTA hooked-shaped, broad based. ITA is elliptical, leaf-like, placed approximately perpendicular to VTA. Tegulum disk-shaped with two median apophyses (TA 1 and TA 2), TA 2 > TA 1. Embolus long, filiform (Figs 7*E*, *F*, 9*A*, *B*, *D*, 11*A*, *B*)

Female (paratype)

Total length 3.9; prosoma length 1.6, width 1.6; Opisthosoma length 2.3, width 1.1. Somatic morphology same as that of male (Figs 5*F*, 6*F*). Eye measurements: AME 0.05; ALE 0.14; PME 0.09; PLE 0.15; AME–AME 0.25; AME–ALE 0.18; PME–PME 0.32; PME–PLE 0.34. MOA length 0.36 with front width 0.36 and back width 0.48. Leg measurements: I: 6.6 (2.0, 0.8, 1.7, 1.4, 0.7); II: 6.5 (2.0, 0.8, 1.7, 1.4, 0.6); III: 4.1 (1.2, 0.5, 1.2, 0.7, 0.5); IV: 3.8 (1.5, 0.4, 0.8, 0.6, 0.5). Epigynum

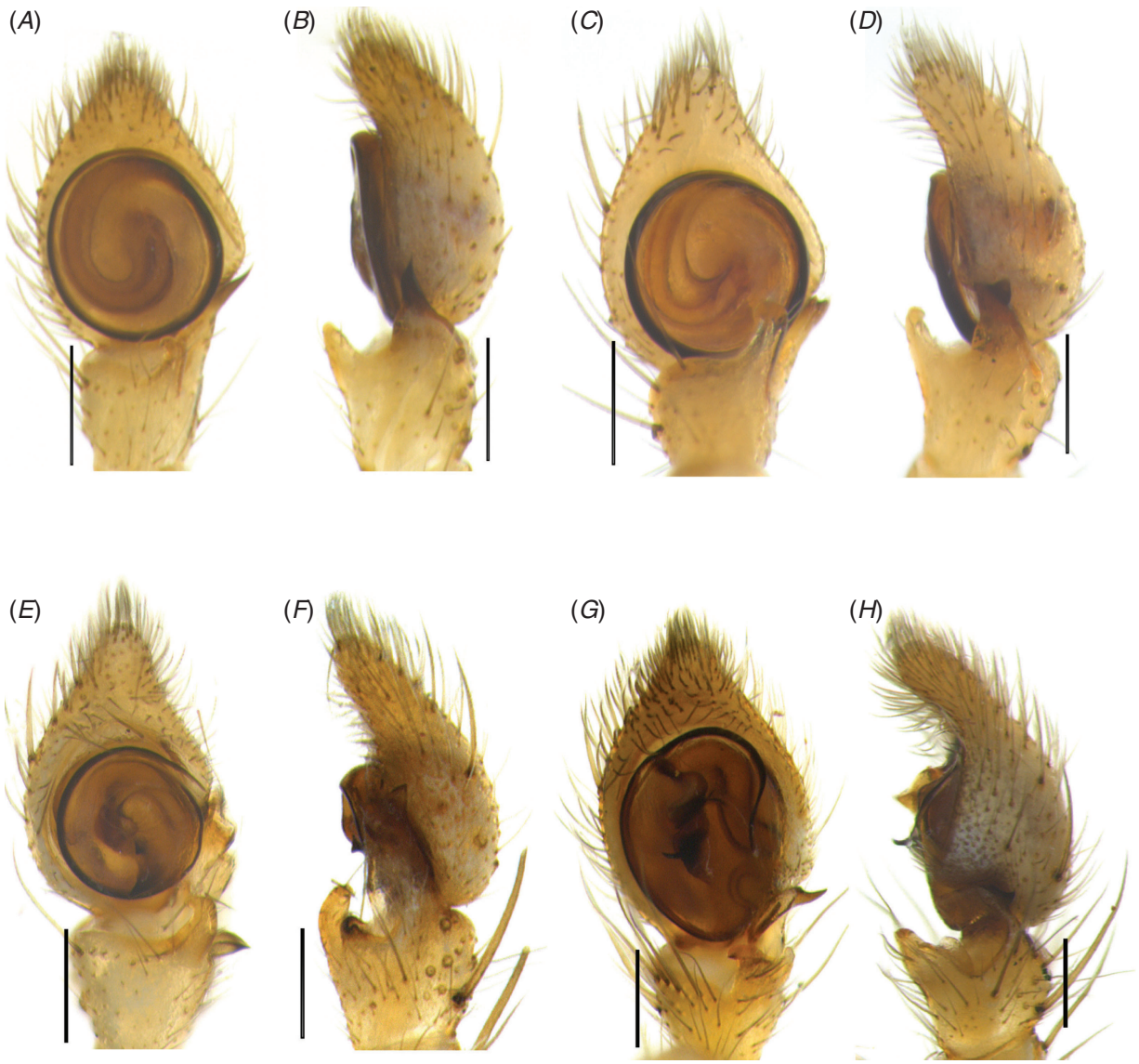

Fig. 7. Male palpal morphology of *Tmarus* species in Sri Lanka. (*A*) *Tmarus viridomaculatus*, sp. nov., ventral; (*B*) as previous, retrolateral; (*C*) *Tmarus manojkaushalyai*, sp. nov., ventral; (*D*) as previous, retrolateral; (*E*) *Tmarus hiyarensis*, sp. nov., ventral; (*F*) as previous, retrolateral; (*G*) *Tmarus hystrix*, comb. nov., ventral; (*H*) as previous, retrolateral. Scale bars: *A–H*, 0.2 mm.

and vulva with a long longitudinal epigynal ridge, copulatory ducts short, spermathecae kidney-shaped (Fig. 11*C*, *D*).

Intraspecific variation

Range of measurements in males ($n = 4$) and females ($n = 4$, in parentheses) in non-type series: total length: 3.1–3.3 (3.7–3.9); prosoma length 1.5–1.6 (1.6–1.7), width 1.4–1.6 (1.4–1.6); opisthosoma length 1.7–1.9 (2.3–2.6), width 1.1–1.2 (1.1–1.3).

Distribution and habitat

Specimens were collected by beating vegetation up to a height of 1 m–2 m. This species occurs in the lowland (<600 m) secondary forests of the dry and wet zones of Sri Lanka (Fig. 4). It is usually found on dry branches without or with few leaves where they seem to be well camouflaged. Found in sympatry with *T. hystrix* in several localities.

Etymology

The specific epithet is taken from the type locality.

Tmarus hystrix (Simon, 1895), comb. nov

(Figs 3*G*, *H*, 5*G*, *H*, 6*G*, *H*, 7*G*, *H*, 11*E–H*)

Peritraeus hystrix Simon, 1895: 980. (♀ syntype from Sri Lanka, deposited in MNHN; not found; species catalogue card not found).

Material examined

Neotype. ♂, Sri Lanka: Central Province, Matale District: Bowatenna FR, 07°39′37″N, 80°41′18″E, 252 m, beating, 10.ii.2016, leg. S.P. Benjamin *et al.* (IFS_Tho_455).

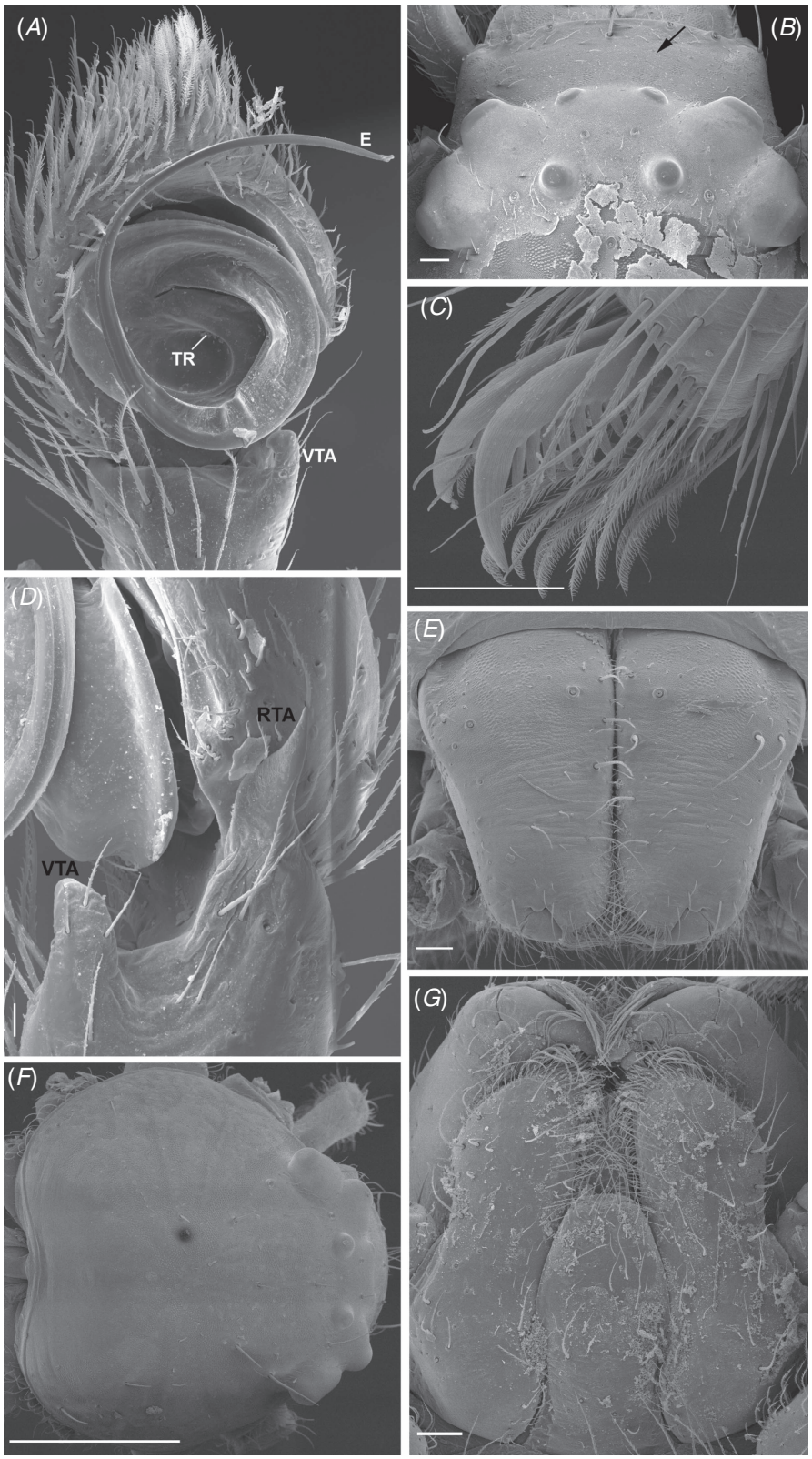

Fig. 8. Scanning electron micrographs of *Tmarus viridomaculatus*, sp. nov., male. (*A*) Left palp; (*B*) ocular area (arrow head shows the protruded clypeus); (*C*) claws and claw tufts of male; (*D*) retrolateral view; (*E*) chelicerae, front view; (*F*) prosoma, dorsal view; (*G*) endites and labium. Abbreviations: E, embolus; RTA, retrolaeral tibial apophysis; TR, tegular ridge; VTA, ventral tibial apophysis. Scale bars: *A*, 30 µm; *B*, *C*, *E*, *F*, 100 µm; *D*, 20 µm; *G*, 1 mm.

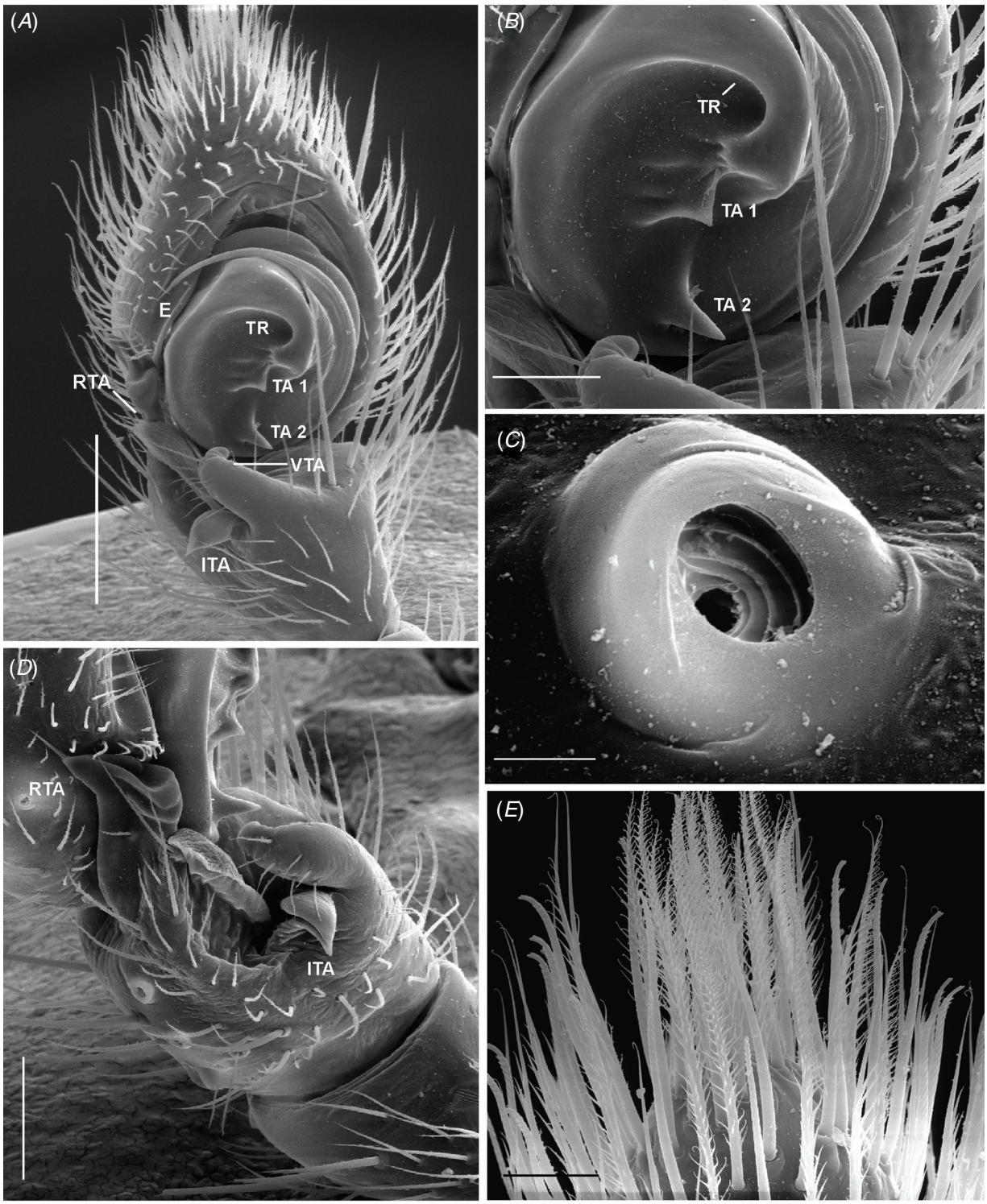

Fig. 9. Scanning electron micrographs of *Tmarus hiyarensis*, sp. nov., male. (*A*) Right palp; (*B*) tegular apophyses; (*C*) base of tricobothrium; (*D*) right palp, detail of RTA and ITA, retrolateral view; (*E*) palpal setae. Abbreviations: E, embolus; ITA, intermediate tibial apophysis; RTA, retrolaeral tibial apophysis; TA, tegular apophysis; TR, tegular ridge; VTA, ventral tibial apophysis. Scale bars: *A*, 200 μm; *B*, 60 μm; *C*, 6 μm; *D*, 100 μm; *E*, 30 μm.

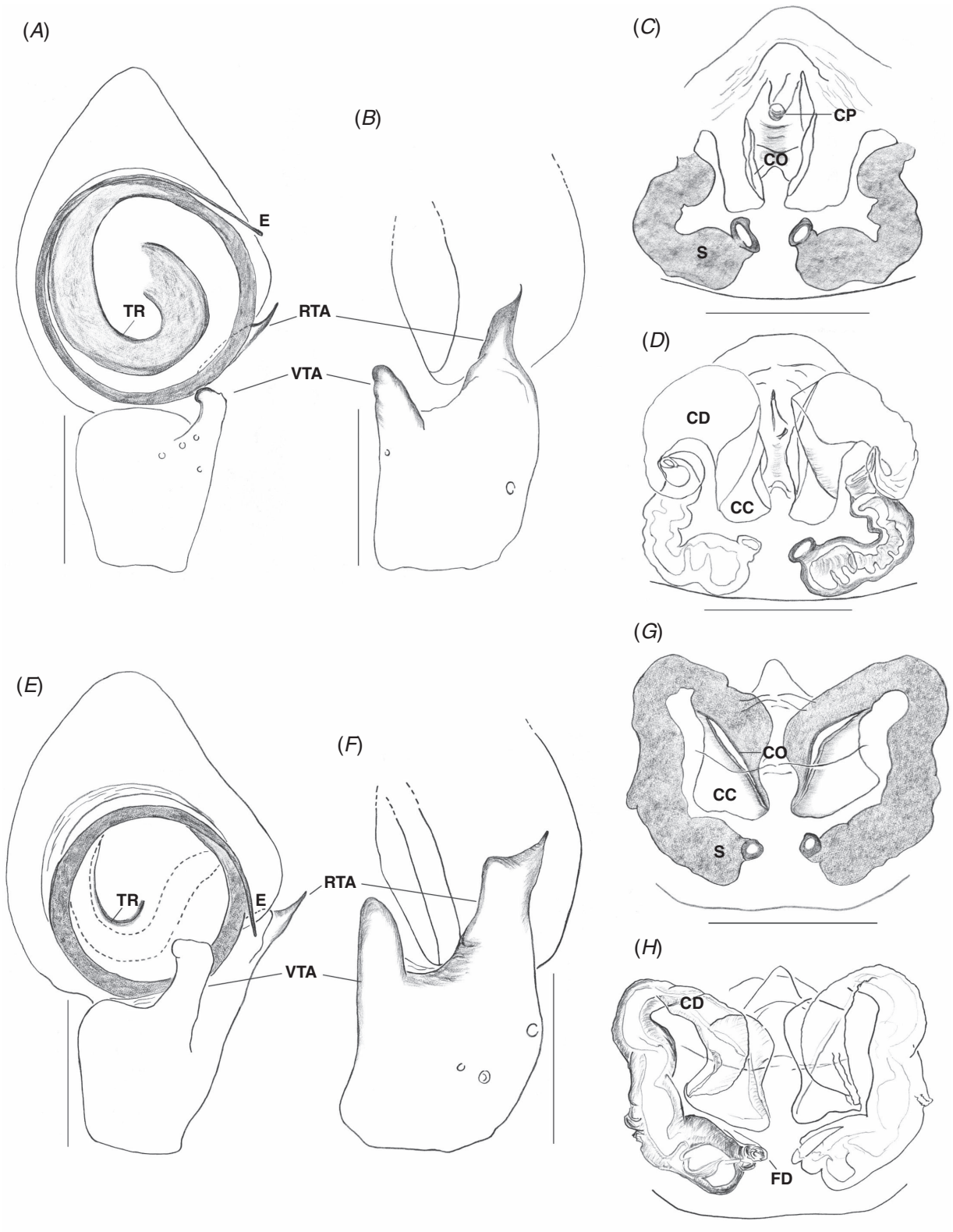

Fig. 10. (*A–D*) Genital morphology of *Tmarus viridomaculatus*, sp. nov. (*A*), Male palp, ventral view; (*B*) same, retrolateral view; (*C*) epigynum, ventral view; (*D*) vulva, dorsal view. (*E–H*) Genital morphology of *Tmarus manojkaushalyai*, sp. nov.; (*E*) Male palp, ventral view; (*F*) same, retrolateral view; (*G*) epigynum, ventral view; (*H*) vulva, dorsal view. Abbreviations: CC, copulatory chamber; CD, copulatory duct; CO, copulatory opening; CP, copulatory pouch; E, embolus; FD, fertilisation duct; RTA, retrolateral tibial apophysis; S, spermatheca; TR, tegular ridge; VTA, ventral tibial apophysis. Scale bars: *A–H*, 0.2 mm.

Non-type materials. 1♀, same data as above (IFS_Tho_456); 1♀, same data as above (IFS_Tho_624); 1♀, Dambulla, IFS Arboratum; 1♂ 1♀, same data (IFS_Tho_201, IFS_Tho_202); Kandy District: 1♂, Dunumadalawa FR (IFS_Tho_340); 1♀, same data as above (IFS_Tho_625); 1♂, Knuckles Range (IFS_Tho_449); North Western Province: Kurunegala District: 3♂ 2♀, Ethagala FR (IFS_Tho_425, IFS_Tho_426, IFS_Tho_287, IFS_Tho_171, IFS_Tho_427); 2♂, Badagamuwa Forest Reserve (IFS_Tho_548 and IFS_Tho_554); 1♀, Nikaweratiya (IFS_Tho_314).

Diagnosis

Males of *T. hystrix* can be separated from other congeners by their hook-shaped median aphophysis, and the slender, long and folded embolus (Figs 7*G*, *H*, 11*E*, *F*). Females are distinguished by the elliptical and broad epigynal hood, short and curved copulatory ducts and oval to irregular spermathecae with intricate folds (Fig. 11*G*, *H*).

Description

Male (neotype)

Total length 3.6; prosoma length 1.4, width 1.5; opisthosoma length 1.9, width 0.9. Prosoma brown, mottled dull yellow patches, covered sparsely with long setae. Chelicerae, clypeus, ocular area and middle section of carapace, white with brown spots. Prominent 'V'-shaped marking, outlined in white lines, extends up to posterior border of prosoma (Fig. 3*G*). Opisthosoma is reddish brown mottled with grey, pale yellow, white patches, covered with sparsely distributed setae. Eye tubercles pale yellowish white. Eye measurements: AME 0.05; ALE 0.16; PME 0.09; PLE 0.16; AME–AME 0.14; AME–ALE 0.16; PME–PME 0.23; PME–PLE 0.36. MOA length 0.34 with front width 0.25 and back width 0.39. Legs pale yellowish brown with black spots and brown colour patches. Leg measurements: I: 9.4 (2.9, 0.8, 2.6, 0.9, 2.2); II: 9.3 (2.9, 0.8, 2.6, 0.9, 2.1); III: 4.9 (1.7, 0.5, 1.2, 0.5, 0.9); IV: 4.1 (1.3, 0.5, 1.1, 0.5, 0.7). Palp: RTA is bifid with a membranous blunt broad apex and triangular pointed sclerotised section attached behind it, VTA hook-like, with an inwardly folded membraneous section retrolaterally. Median apophysis is hook-like and pointed forward. Embolus long and slender, end resting on the tegulum. A twisted sperm duct is visible through the tegulum at the base of retrolateral margin (Figs 7*G*, 11*E*, *F*).

Female

Total length 4.8; prosoma length 1.8, width 1.5; opisthosoma length 3.1, width 1.9. Somatic characters are same as above except for the white and light yellow patches on both prosoma and opisthosoma (Fig. 3*G*, *H*). Eye measurements: AME 0.07; ALE 0.19; PME 0.09; PLE 0.18; AME–AME 0.16; AME–ALE 0.18; PME–PME 0.25; PME–PLE 0.39. MOA length 0.32 with front width 0.29 and back width 0.41. Leg measurements: I: 6.9 (2.0, 0.8, 1.9, 0.8, 1.4); II: 6.9 (2.0, 0.8, 1.9, 0.8, 1.4); III: 3.7 (1.2, 0.6, 1.0, 0.4, 0.5); IV: 3.5 (1.2, 0.5, 1.0, 0.3, 0.6). Epigynum and vulva: broad epigynal hood, sclerotised copulatory opening, opens to short bent copulatory duct, spermathecae oval to irregular, with intricate folds (Fig. 11*G*, *H*).

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). Further, the shape of the sclerotised section of the RTA and the position of the tegular aphophyses seems to be variable among the observed specimens. In females the shape of the spermathecae and intricate folds were variable. The palpal variations are mainly observed in male specimens collected from the Knuckels and Badagamuwa forest areas (IFS_Tho_449, IFS_Tho_548). In addition, a few specimens were observed to be lighter or darker than most other specimens.

Range of measurements in males ($n = 6$) and females ($n = 4$, in parentheses) in non-type series: total length: 3.6–4.2 (4.4–4.8); prosoma length 1.4–1.7 (1.7–1.8), width 1.3–1.5 (1.5–1.6); opisthosoma length 1.9–2.8 (2.8–3.1), width 0.9–1.3 (1.3–1.9).

Remarks

Our identification is based on Simon's (1895) description of the female syntype. The transfer of *Peritraeus hystrix* to *Tmarus* results in a homonym: *Tmarus hystrix* Caporiacco, 1954 from French Guiana. *Tmarus hystrix* (Simon, 1895), comb. nov. has precedence. To maintain the connection with Caporiacco, we rename the species in his honour, *Tmarus caporioccoi* Ileperuma Arachchi & Benjamin, replacement name. The specimen from Dunumadalawa, Kandy, is designated as the neotype to define *Tmarus hystrix* (Simon, 1895), comb. nov.

The median apophysis of *T. hystrix* is extremely fragile, and easily broken even when handled with extra care. Thus, it is not depicted in drawings as it was broken while imaging; it is clearly visible in Fig. 7*G*, *H*.

Distribution and habitat

This species was collected by beating vegetation up to a height of 1–2 m in dry-, intermediate- and wet-zone forests of Sri Lanka (Fig. 4). *T. hystrix* and *T. hiyarensis* were found to be sympatric in Dambulla, IFS arboretum.

Tmarus viridomaculatus, sp. nov

(Figs 3*A*, *B*, 5*A*, *B*, 6*A*, *B*, 7*A*, *B*, 8*A*–*G*, 10*A*–*D*)

Material examined

Holotype. ♂, Sri Lanka, Central Province: Nuwara Eliya District: Upcot, 06°46′N, 80°36′E, 1199 m, beating, 14.ii.2012, leg. S.P. Benjamin (IFS_Tho_130).

Paratype. ♀, same data as holotype (IFS_Tho_131).

Non-type material. **Sri Lanka**: Central Province: Nuwara Eliya District: 1♂, Upcot (IFS_Tho_419); 1♀, same locality (IFS_Tho_623); 1♀, Hakgala Strict Nature Reserve (IFS_Tho_113); 1♂, same locality (IFS_Tho_267); 1♂ 5♀, same locality data (IFS_Tho_540, IFS_Tho_543, IFS_Tho_549, IFS_Tho_550, IFS_Tho_571, IFS_Tho_572), 2♀, Agrabopath Forest Reserve (IFS_Tho_298, IFS_Tho_323); 1♀, Hortain Plains NP (IFS_Tho_329); 2♂, Mandaram Nuwara (IFS_Tho_660, IFS_Tho_661); Kandy District: 1♀, Deenston, Dothalugala (IFS_Tho_109); 1♀, Delthota, Forest adjacent to Loolkandura estate (IFS_Tho_118); 1♂, Gomaraya, B205 Road, near 26 km post (IFS_Tho_429), Matale District: 1♂, Riverston (IFS_Tho_002), 1♀, Gammaduwa, Knuckles FR (IFS_Tho_024), 3♂ 3♀, Rattota, Knuckles FR, along Rattota-Illukkumbura Road (IFS_Tho_168, IFS_Tho_168_173).

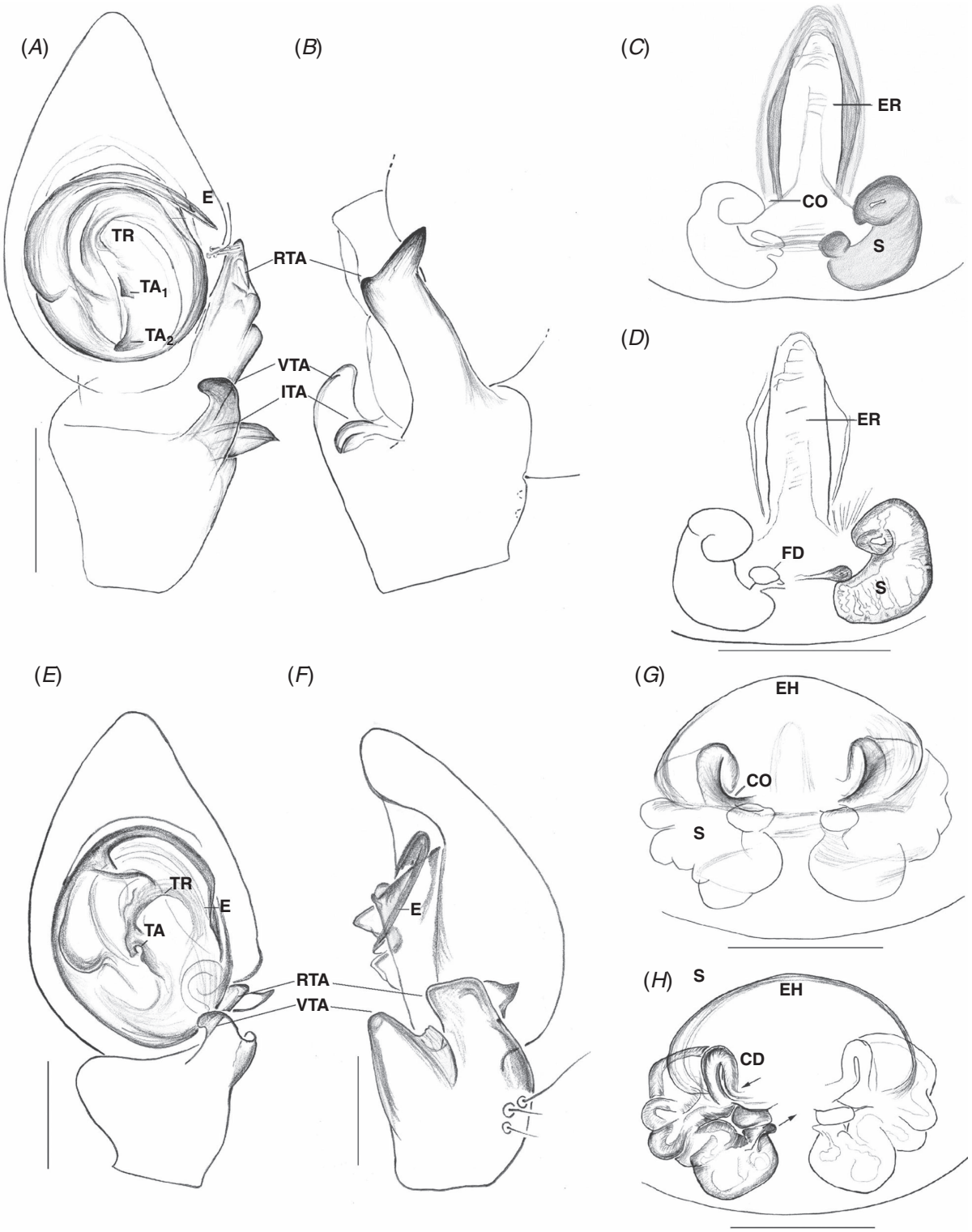

Fig. 11. (*A–D*) Genital morphology of *Tmarus hystrix*, sp. nov. (*A*) Male palp, ventral view; (*B*) same, retrolateral view; (*C*) epigynum, ventral view; (*D*) vulva, dorsal view. (*E–H*) Genital morphology of *Tmarus hiyarensis*, sp. nov. (*E*) Male palp, ventral view; (*F*) same, retrolateral view; (*G*) epigynum, ventral view; (*H*) vulva, dorsal view. Abbreviations: CD, copulatory duct; CO, copulatory opening; E, embolus; FD, fertilisation duct; EH, epigynal hood; ER, epigynal ridge; ITA, intermediate tibial apophysis; RTA, retrolateral tibial apophysis; S, spermathecae; TA, tegular apophysis; TR, tegular ridge; VTA, ventral tibial apophysis. Scale bars: *A–H*, 0.2 mm.

Diagnosis

Males of *T. viridomaculatus*, sp. nov. can be separated from *T. manojkaushalyai* in having shorter VTA, the tapering RTA and its pointed apex (Figs 7*A*, *B*, 10*A*, *B*). Females are separated by the tube-like epigynal opening that lies below the epigynal hood and copulatory openings placed bilaterally on the copulatory chambers (Fig. 10*C*, *D*).

The tube-like epigynal opening is absent in *T. manojkauhalyai*. The copulatory openings are placed diagonally on the copulatory chambers in *T. manojkauhalyai.* The species is separated from *Tmarus hystrix* and *Tmarus viridomaculatus* by the absences of TA.

Description

Male (holotype)

Total length 2.6: prosoma length 1.5, width 1.4; opisthosoma length 2.1, width 1.1. Overall body colour is dull green. Prosoma dull green mottled with light yellow and white patches, oval marking, light yellow outlines (Fig. 3*A*, *B*). Dorsum of opisthosoma greenish yellow mottled with white patches. Eye tubercles black. Eye measurements: AME 0.07; ALE 0.14; PME 0.09; PLE 0.16; AME–AME 0.18; AME–ALE 0.12; PME–PME 0.23; PME–PLE 0.28. MOA length 0.36, front width 0.31, back width 0.39. Legs dull green, yellow, black patches, tarsus black. Leg measurements: I: 7.6 (2.3, 0.9, 2.1, 1.5, 0.8); II: 7.4 (2.3, 0.8, 2.1, 1.5, 0.7); III: 4.3 (1.4, 0.6, 1.2, 0.6, 0.5); IV: 4.3 (1.5, 0.6, 1.2, 0.6, 0.4). Palp: VTA hook-like, short, apex curved, RTA broad based, tapering, sharply curved, apex pointed, tegulum flat, embolus long and filiform with a slightly bifurcated end (Figs 7*A*, *B*, 8*A*, *D*, 10*A*, *B*).

Female (paratype)

Total length 4.0: prosoma length 1.4, width 1.5; opisthosoma length 2.3, width 1.8–1.9. Somatic morphology as above except fewer greener and whiter and reddish brown patches on opisthosoma (Fig. 3*A*, *B*). Eye measurements: AME 0.05; ALE 0.14; PME 0.07; PLE 0.12; AME–AME 0.14; AME–ALE 0.14; PME–PME 0.25; PME–PLE 0.34. MOA length 0.36, front width 0.27, back width 0.39. Leg measurements: I: 7.0 (2.2, 0.7, 1.8, 1.5, 0.8); II: 6.8 (2.1, 0.7, 1.8, 1.5, 0.7); III: 4.6 (1.4, 0.6, 1.3, 0.7, 0.6); IV: 4.9 (1.5, 0.6, 1.4, 0.8, 0.6). Epigynum and vulva: epigynum with an epigynal hood, epigynal opening tunnel-like, copulatory openings bilateral, opening to pocket-like copulatory chambers, and copulatory ducts, copulatory ducts broad at the base, membranous, gradually tapering, bent at the opening of spermathecae, spermathecae C-shaped, duct-like (Fig. 10*C*, *D*).

Intraspecific variations

Variations in the length of the embolus and the shape of the RTA were observed in one specimen collected from Hakgala SNR. However, given the available data we consider splitting the species into two to be premature.

Range of measurements in males ($n = 6$) and females ($n = 5$, in parentheses) in non-type series: total length: 2.5–3.7 (4.0–4.3); prosoma length 1.5–1.6 (1.4–1.7), width 1.3–1.5 (1.4–1.5); opisthosoma length 2.2–2.4 (2.3–2.5), width 1.1–1.7 (1.8–1.9).

Distribution and habitat

This species occurs in the montane and submontane forests in the central highlands of Sri Lanka (Fig. 4). Unlike *T. hystrix* and *T. hiyarensis*, *T. viridomaculatus* lives on green foliage, greenish bark, branches covered with green lichens and ephiphytes and twigs of shrubs where it seems to be well camouflaged. Specimens were collected by beating vegetation up to a height of 0.5 to 2 m. This species is found in sympatry with *T. manojkaushalyai*, sp. nov. in Upcot, Hakgala SNR and Horton Plains NP.

Etymology

The specific epithet is derived from a combination of Latin words; ‘macula’ meaning ‘spots’ or ‘patch of colour’ and ‘virido’ meaning ‘green’ collectively denotes ‘green colour patches’, referring to its mottled greenish body colour.

Conflict of interest

The authors declare no conflicts of interest.

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