

Phylogenetic placement and revision of the tropical Asian crab spider genus *Pagida* (Araneae : Thomisidae)

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Abstract. The tropical Asian crab spider genus *Pagida* Simon, 1895 has remained taxonomically unrevised and has never been subjected to phylogenetic evaluation. The present study is designed to investigate the monophyly of the genus, its placement within Thomisidae and review all species. Our cladistic analysis, based on 78 morphological characters from 34 taxa (30 ingroup and four outgroup), demonstrates the monophyly of the genus and shows that *Pagida* is sister to *Stiphropus* Gerstäcker, 1873 within Thomisidae. The monophyly of *Pagida* and *Pagida* + *Stiphropus* is well supported. *Pagida salticiformis* (O. P.-Cambridge, 1883), the type species of *Pagida*, is redescribed from a series of specimens collected recently from its type locality, Sri Lanka. *Pagida pseudorchestes* is redescribed based on nine males and seven females. A new species, *Pagida minuta*, sp. nov., is described, based on four males and one female.

Additional keywords: biodiversity, conservation, endemics, India, *Palaephatus*, taxonomy.

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Introduction

The spider family Thomisidae consists of 174 genera with over 2302 species (World Spider Catalog 2015). Thomisidae species are small to medium-sized, squat, entelegyne spiders that demonstrate sexual dimorphism. Crab spider cephalothoracic colour can range from white to yellow with red stippling in flower-dwelling species, to green, brown or black in species that reside in leaf litter. Thomisidae species, which make up the sixth largest family of the order Araneae, do not use foraging webs. Instead, they utilise signal strategies to take advantage of pollinating insects (Morse 2007). A combination of signals, strong forelegs and venom facilitates the capture of prey significantly larger than the crab spider itself (Heiling *et al.* 2005; Théry 2007).

The crab spider genus *Pagida* Simon, 1895 was erected by Eugène Simon (1895) as a replacement name for *Palaephatus*, which was named by O. P.-Cambridge (1883). This genus has remained taxonomically unrevised and has never been subjected to phylogenetic evaluation. The original specimen, an immature female, was collected by G. H. K. Thwaites in 1871 in Sri Lanka (then Ceylon). O. P.-Cambridge (1883) likened the specimen to a salticid spider, naming it *P. salticiformis*. A second species, *P. pseudorchestes*, was added by Thorell (1890). However, it is unclear whether *P. pseudorchestes* is congeneric with the type species as it is currently inadequately known. Our samples of *P. salticiformis*, newly collected, are from leaf litter from the Monaragala, Puttalam, Kandy, Ampara and Mannar districts of Sri Lanka. A collection of *Pagida* from South-east Asia made by Christa Deeleman-Reinhold and co-workers contained specimens of *P. pseudorchestes* as well as a new species.

Recent phylogenetic studies of Thomisidae (Benjamin *et al.* 2008; Benjamin 2011) did not include *Pagida*. As currently defined, *Pagida* is part of the subfamily Thomisinae (Ono, 1988). However, the placement of *Pagida* within Thomisinae or even Thomisidae has been recently questioned, with Lehtinen (2007) proposing family status for *Pagida*, *Stiphropus* Gerstäcker, 1873, *Stiphropella* Lawrence, 1952 and *Heterogriffus* Platnick, 1976. This unpublished proposal has not been accepted to date (World Spider Catalog 2015). In this paper we investigate the monophyly and the placement of the genus *Pagida* within the family Thomisidae using morphological data and re-circumscribe it in phylogenetic terms. In addition, *P. salticiformis* and *P. pseudorchestes* are redescribed and a new species, *P. minuta*, sp. nov., is described.

Materials and methods

Material examined

Types and other specimens were borrowed from the Hope Entomological Collections, Oxford University Museum, Oxford (OUMNH), the Institute of Fundamental Studies, Kandy (IFS), Museo Civico di Storia Naturale ‘Giacomo Doria’, Genova (MCSN), the National Museum of Natural History, Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), the Smithsonian Institution, Washington, DC (USNM) and the Zoological Research Museum Alexander Koenig, Bonn (ZFMK). Methodology follows Benjamin (2011). Specimens used for habitus illustrations were placed in 70% ethanol and photographed with a Zeiss AxioCam HRc camera mounted on a dissecting microscope (Zeiss Discovery V20) with top illumination

and magnification of up to 150 \times . Images were edited using the Zeiss AxioVision Rel. 4.8 software package (Carl Zeiss AG, Oberkochen, Germany). Left male palp structures are depicted unless otherwise stated. Drawings were done as described in Benjamin (2011). Setae are usually not depicted in the final drawings. All measurements are given in millimetres. Morphological features were studied and photographed at either the Amray 1810 (Amray Inc, Bedford, MA, USA) housed at the USNM scanning electron microscope (SEM) facility or the Hitachi S-2460 (Hitachi, Ibaraki, Japan) housed at ZFMK. All specimens were deposited in IFS unless otherwise stated. Coordinates are given only where known. Morphological abbreviations: ALE, anterior lateral eyes; AME, anterior median eyes; CO, copulatory opening(s); CY, cymbium; E, embolus; FD, fertilisation duct(s); PC, paracymbium; PER, posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes; PS, peg-like setae; RTA, retrolateral apical tibial apophysis; S, spermatheca; TR, tegular ridge; VTA, ventral tibial apophysis.

Characters

The character matrix used in the present study is an adapted version (one character was deleted and the matrix was supplemented with five new characters; three characters have added states) of the character matrix in Benjamin (2011), with 78 characters being assessed in total (Table 1). The new characters and deletions are as follows. Character 33 describes the presence (state 1) or absence (state 0) of a membranous copulatory sac in females. Character 38, which describes the presence (state 1) or absence (state 0) of peg-like setae on the cymbium, is used instead of describing the presence of peg-like setae on the tip of the female palp (character 37 in Benjamin (2011), which was deleted). Character 43 describes the presence (state 1) or absence (state 0) of leg microsetae in male spiders. Character 47 compares the length of the tarsus and metatarsus in the first two pairs of legs, with a longer tarsus than metatarsus being state 1 and shorter tarsus than metatarsus being state 0. Character 48 compares tarsus girth and metatarsus girth: tarsus girth same as metatarsus girth (state 0), tarsus girth smaller than metatarsus girth (state 1).

Additional states for characters used in Benjamin (2011) are as follows: state 3 (black) was added to character 66, which assesses body colouration in thomisids. Character 10 (paracymbium type) was altered to include state 3, where the paracymbium surrounds the RTA. Finally, character 71 (presence or absence of a third tarsal claw) was altered so that state 0 accounts for the presence of a third tarsal claw while state 1 is used to describe species in which the third tarsal claw is absent. This character describes the presence of the third tarsal claw in the outgroup taxa *Psechrus* and *Uduba* (Griswold *et al.* 2005). All multistate characters are treated as nonadditive.

Cladistic analysis

Mesquite (version 2.72; Maddison and Maddison 2009) was used to construct and edit the character matrix. The data matrix was analysed with TNT (version 1.1; Goloboff *et al.* 2008) under both equal and implied weights, with 1000 replications and TBR. Ten trees per iteration were kept. The default collapsing rule in TNT was left unchanged. Character

evolution was assessed using WinClada (version 1.00.08; Nixon 2002) and MacClade (version 4.08; Maddison and Maddison 2001). Symmetric resampling (Goloboff *et al.* 2003) was performed to assess branch stability using TNT (1000 replicates). Bremer support and relative Bremer support (Bremer 1994; Goloboff *et al.* 2003) was also assessed on TNT (retain trees suboptimal = 10 steps). Further, details of the phylogenetic methodology and settings used can be found in Benjamin (2011).

Results and discussion

Heuristic searches in TNT under equal weights resulted in 35 trees (best score of 244). The strict consensus of these trees is shown in Fig. 1. Traditional searches with implied weights $K = 1$ to $K = 10$, using the same parameters given above, resulted in two trees (length = 334, $Ci = 37$, $RI = 62$). These trees are shown in Figs 2 and 3. These two trees differ only in the placement of the clade *Apyretina* (*Stiphropus* + *Pagida*) within Thomisidae.

The three known species of *Pagida* form a well-supported clade (Fig. 1), validating the placement of *P. pseudorchestes* by Thorell (1890) in the genus. All trees place *Pagida* within Thomisidae as sister to *Stiphropus* (Figs 1–3). Further, *Pagida* + *Stiphropus* are placed as sister to *Apyretina*. These relationships are well supported. The monophyly of *Pagida* is well supported by the following five characters: prominent PC that surrounds the RTA (character 10), legs approximately similar in length (character 42), anterior eye region projects beyond the clypeus (character 59), joined eye tubercles (character 61) and black body colour (character 66).

Further, the monophyly of *Pagida* + *Stiphropus* is supported by the following morphological characters: oval tegulum (character 11), lack of leg spines (character 43), fused metatarsus and tarsus joint (character 44) and longer tarsus (character 47). These two genera are sister to *Apyretina*, supported by four characters (Figs 1, 2). Thus, the proposed elevation of *Pagida* and *Stiphropus* to family level cannot be accepted. Benjamin (2011) suggested that the presence of PS might be synapomorphic to a small group of Old World thomisids. This hypothesis is also supported here (Figs 1, 2). As recently shown in Benjamin (2011), none of the traditionally accepted generic groups of Thomisidae turn out to be monophyletic. It is now very apparent that thomisid taxa above genus level have been mostly defined on the basis of plesiomorphic character states. However, further work needs to be done to properly delimit generic groupings before questions around subfamilies can be addressed.

Taxonomy

Family Thomisidae Sundevall

Genus *Pagida* Simon

Palaephatus O. P.-Cambridge 1883: 362 [junior homonym of *Palaephatus* Butler, 1883 (Lepidoptera)].

Pagida salticiformis Simon 1895: 1000 (replacement name for *Palaephatus* Butler, 1883).

Type species: Palaephatus salticiformis O. P.-Cambridge, 1883, by monotypy.

Table 1. Phylogenetic data matrix

The first state is '0', followed by '1', etc.; '?' denotes missing data, '-' is inapplicable. Polymorphisms: A = 0/1, B = 1/3, C = 1/4, D = 1/5, E = 2/3, F = 0/4

Taxa	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	777777777
<i>Psechrus</i> sp.	0000-00000	301040-01	20-000000	10000-0010	000000???	0000200000	-2202????	01200111
<i>Uduba</i> sp.	000100000	000-11111	20-000001	14?0-0010	000000???	1000200000	-2200????	00-?11?
<i>Philodromus nifius</i>	000100000	000020-01	01000000??	02?0-0010	000001?0?	2000222000	-11000D01	1121C000
<i>Onomastus nigricauda</i>	0000-00000	201032111	3110000000	02?20-0010	0000000?0	2212111000	-000130??	11301000
<i>Borboropactus cinerascens</i>	000100000	0011110101	00-0110000	11000-0010	0100100020	1000020011	0011?0???	12?00000
<i>Borboropactus nyerere</i>	000100000	0011110101	00-0110000	11000-0010	0100100020	1100020011	0011003E0E	11001000
<i>Epidius parvati</i>	1111000000	0010411002	00-0000000	00?10-0010	0100010010	?01020001	00110100??	11011000
<i>Epidius binotatus</i>	1111000000	000-11002	10-0000000	00010-0010	01000100?0	?01020001	0011?1???	12?000?0
<i>Pharta gongshan</i>	0011000000	000-11102	00-0000010	12020-0010	0100110010	011022001?	0011101???	11011000
<i>Cebrennius rugosus</i>	0011000000	000-11115	10-1000000	00020-0010	01?01100?0	011002200?	00?11001100	11011000
<i>Cebrennius rivijaya</i>	0011000000	000-11115	10-100?001	00020-0010	01?0110011	01-02-001	001100???	11011000
<i>Stephanopsis cambridgei</i>	0001010001	000-0-00	20-100?000	01?00-0010	0100010000	?010100011	00110022??	1???B000
<i>Onocolus</i> sp.	0001000000	000-0-05	00-?000101	??0-0010	0100110000	010002001?	0?11002203	11003000
<i>Geraesta hirta</i>	0011001010	0011010101	00-0011000	10000-0010	0100110010	0101022011	00111013?1	11011000
<i>Geraesta lehtineni</i>	00011001010	0011010101	10-0011000	10000-0010	01001100?0	?0101?0001	0011?01300	11011000
<i>Aphantochilus rogersi</i>	0001100101	010-0-03	10-1000000	1000110101	1000002000	0110022101	0011001414	11000000
<i>Aphantochilus taurifrons</i>	00010100?2	110-0-00	00-0000000	1000110101	1000000200	0110022101	00110014?4	1??00000
<i>Thomisus granulifrons</i>	0001010000	110-0-00	00-0000000	03?40-0000	0100010000	0000022001	1?1100???	11110000
<i>Monaes</i> sp.	0001010000	110-0-00	00-0000000	??0-0000	0100010000	0110022001	0?1101100?	11100000
<i>Xysticus cristatus</i>	00010100?2	110-0-14	00-0000000	01000-0000	0100010200	0110022001	0?1100???	11100000
<i>Xysticus fraternus</i>	0001010002	110-0-14	00-0000001	01?00-0000	0100010200	0110022001	0??0001000	1111F000
<i>Diaca subdola</i>	0001010002	110-0-04	00-0000000	04?30-0000	0100010200	0100022001	11110010??	1120A000
<i>Strigoplus</i> sp.	00010100?1	110-0-00	00-000????	??0?110?01	0100010200	0110022001	01?1001000	11202000
<i>Strophilus</i> sp.	0001010001	110-0-00	00-0000001	0000100001	010001?000	011002200?	0?11001005	11202000
<i>Oxytate subvirens</i>	0001010000	110-0-00	00-000001?	00000-0000	0100010000	0110022001	011101???	11200000
<i>Stiphropus lugubris</i>	0001010001	001020-01	00-0000000	?4??0-1000	0111011100	0112022001	00??000000	11002000
<i>Apyretina</i> sp.	0000-00001	110-0-00	00-0000001	??000-1000	01000100?0	0112022001	0011000000	11012000
<i>Mecaphesa asperata</i>	0001010002	110-0-03	00-0000101	??0?0-0000	01000100?0	0000022001	1111001000	10-?000
<i>Stephanopsis</i> sp.	000?0000??	??00001??	??-?000101	04100-0?10	01001100?0	0102222011	00??02E13	11011000
<i>Sidymella lucida</i>	00010000??	000-0-00	00-?00???	??000-0010	010?2100?0	?01021001?	??0?00???	12?0000?
<i>Sidymella angulata</i>	00?10000?1	000-0-00	20-100???	??0?00010	0100?100?0	010122001?	??0?00???	1??0000?
<i>Phrynarache</i> sp.	0001010000	110-0-00	00-0000000	00?30-0010	0100110200	0110222001	01??002410	11001000
<i>Stephanopoides</i> sp.	00?0-00000	110-0-00	00-0000001	00?00-0010	01000100?0	?0022200?	0?0?00???	11?0000?
<i>Pagida salticiformis</i>	0001010003	010-0-00	00-0000000	00100-1000	0011011101	?112022011	11??030000	11202000
<i>Pagida pseudorchestes</i>	0001010003	010-0-00	00-000000?	22000-1000	0011011101	?112?20011	11??03???	??0?0000
<i>Pagida minuta</i> sp. n.	0001010003	010-0-00	00-000000?	20000-1000	0011011101	?112?20011	11??03???	??0?0000

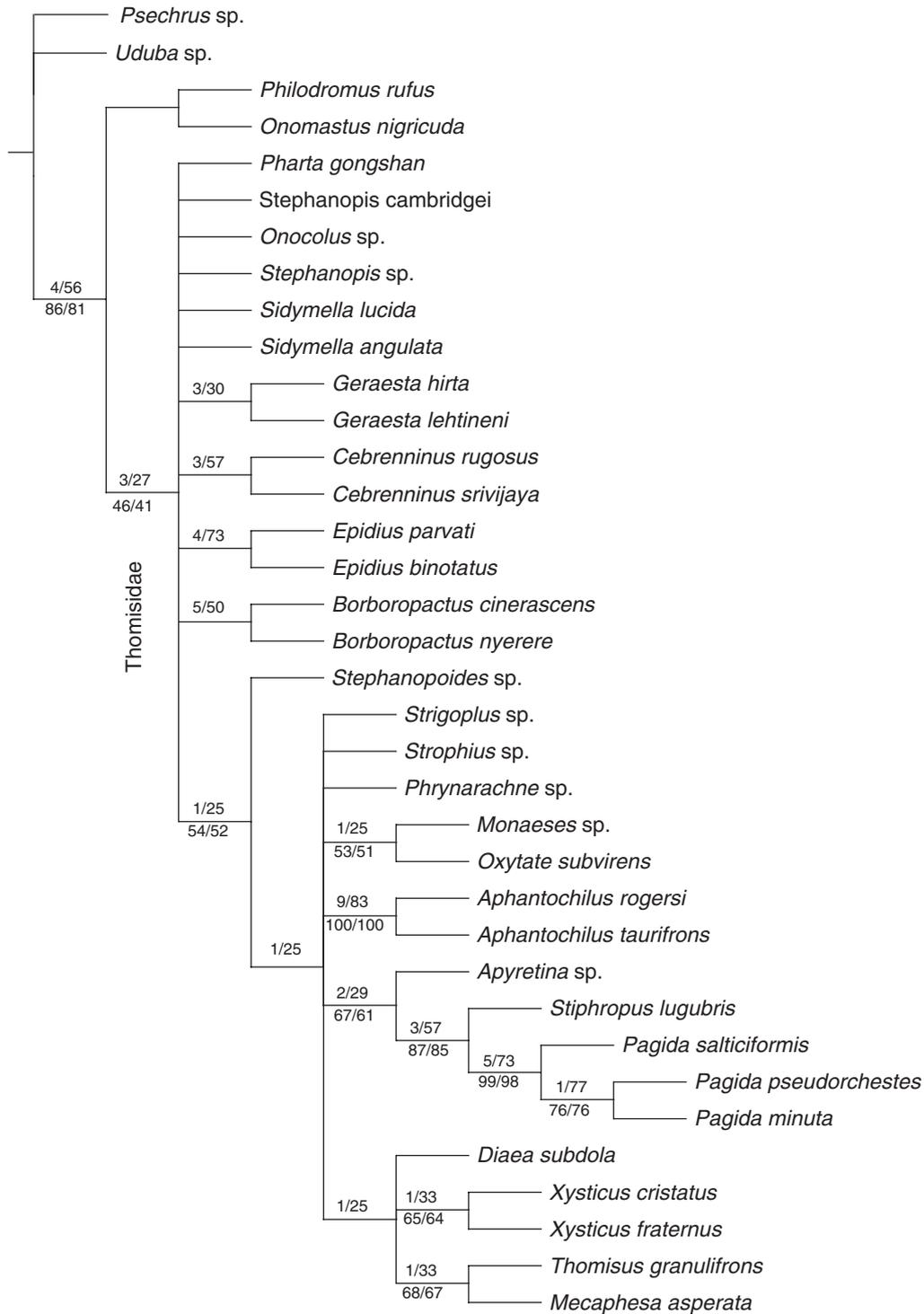


Fig. 1. Phylogenetic placement of the crab spider genus *Pagida* Simon, 1895 obtained by the analysis of 78 morphological characters under equal weights. Consensus of thirty-five most parsimonious trees (MPT) found for the Thomisidae character matrix. The values at the top of each node represent Bremer support/relative Bremer support, while the values at the bottom of nodes represent sympatric resampling frequencies/sympatric resampling frequency differences.

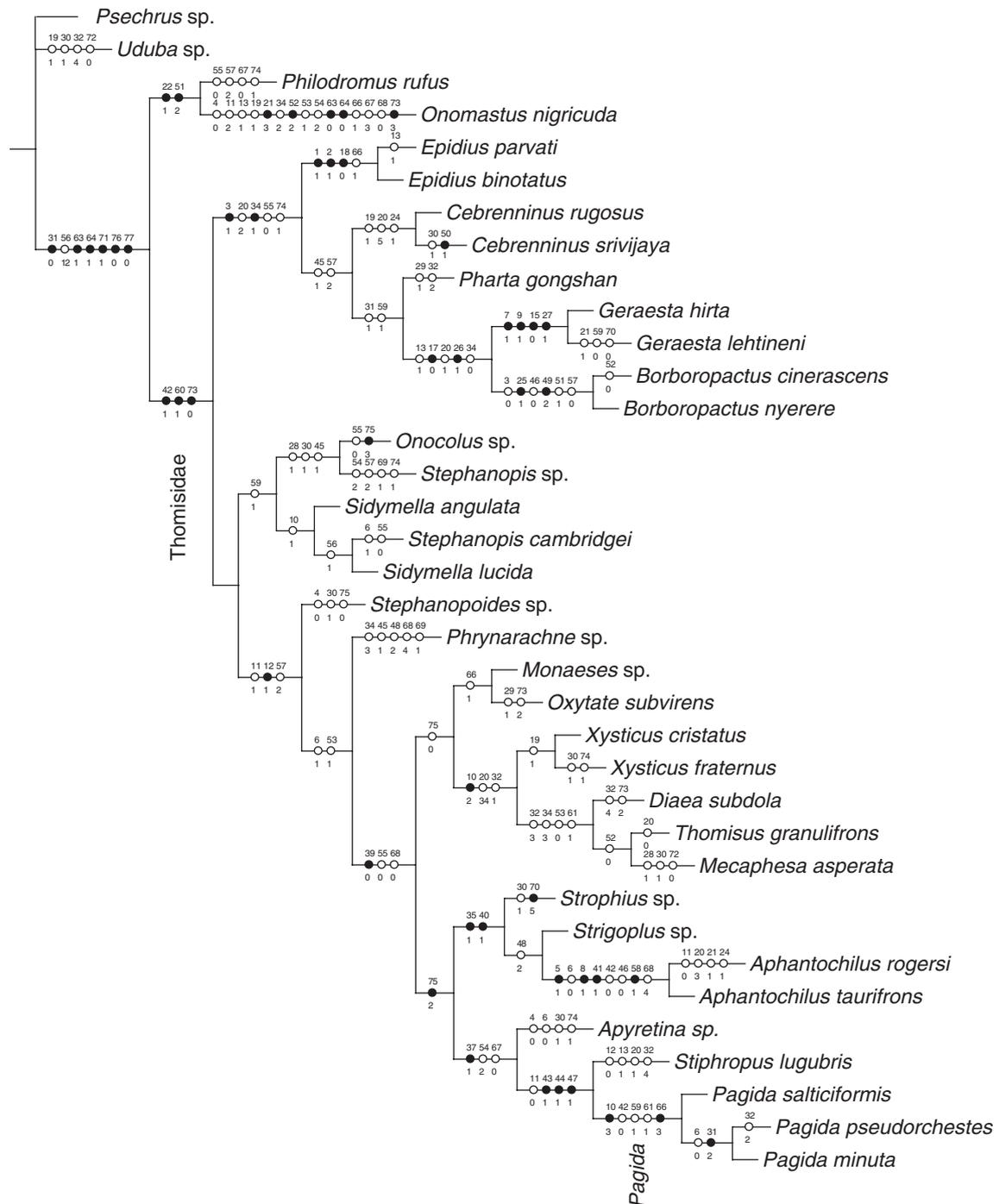


Fig. 2. Phylogenetic placement of the crab spider genus *Pagida* Simon, 1895 obtained by the analysis of 78 morphological characters. The first of the two MPT trees found when the character matrix was analysed using implied weights ($K = 1$ to 10, $L = 334$, $Ci = 37$, $RI = 62$). Unambiguous character state changes were mapped using Farris optimisation.

Diagnosis

Male and female *Pagida* are distinguished by the following combination of characters: prominent paracymbium that surrounds the RTA (character 10); legs approximately similar

in length (character 42); anterior eye region projects beyond the clypeus (character 59); joined eye tubercles (character 61); black body colour (character 66). Further, *Pagida* can be separated from *Stiphropus* by the smooth tegulum and fine embolus.

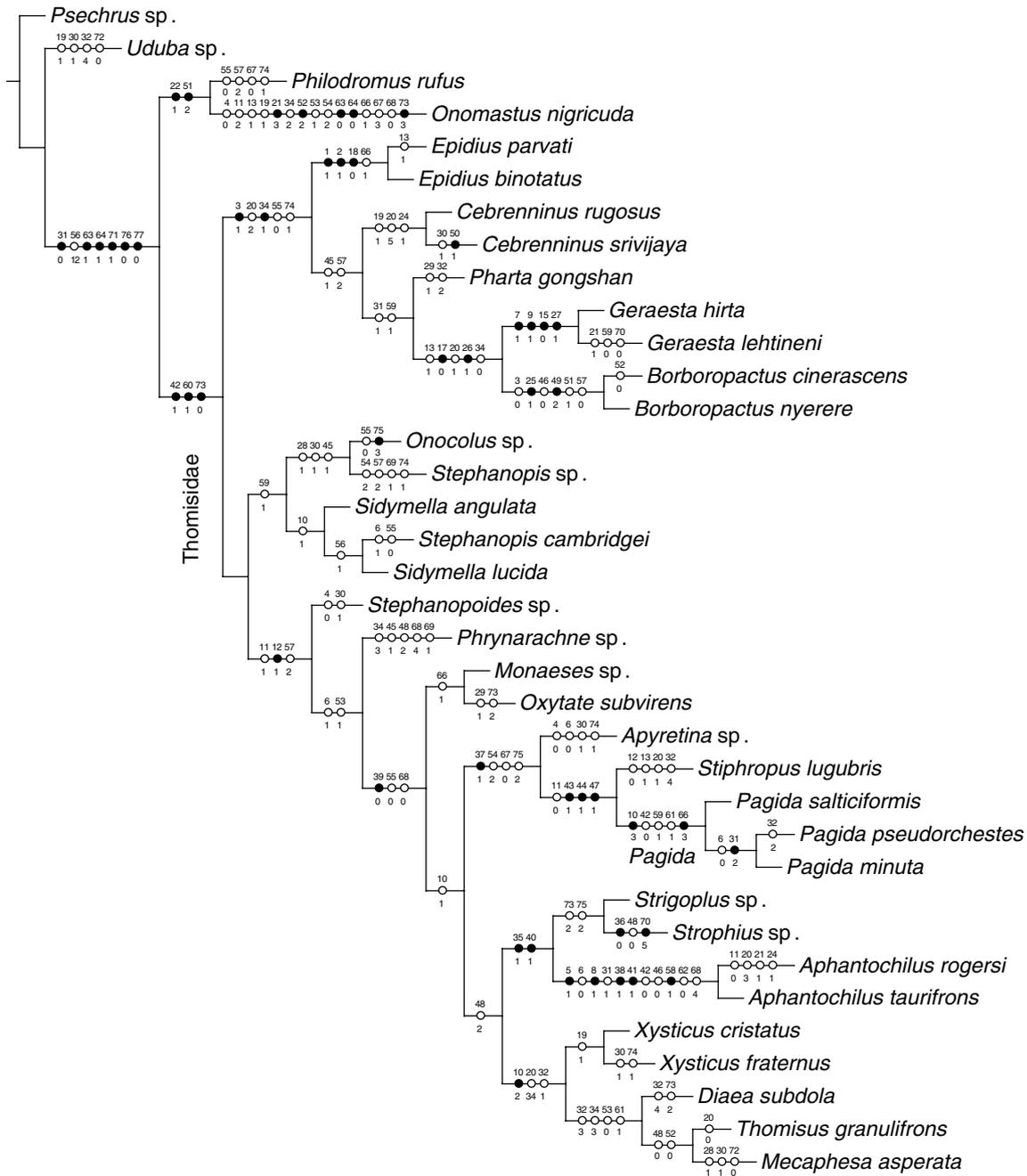
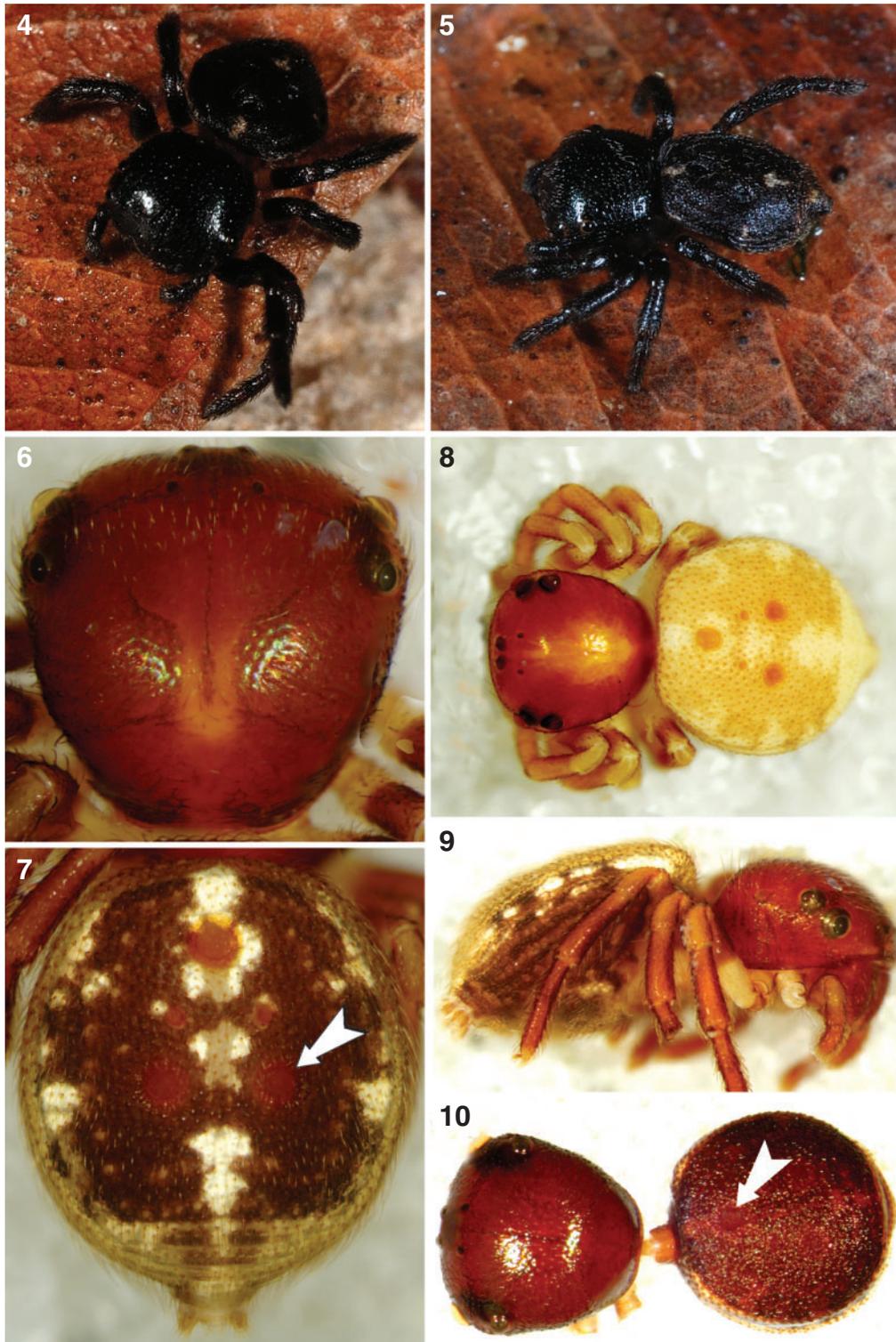


Fig. 3. Phylogenetic placement of the crab spider genus *Pagida* Simon, 1895 obtained by the analysis of 78 morphological characters. The second of two MPT trees found when the character matrix was analysed using implied weights ($K = 1$ to 10 ; $L = 334$, $Ci = 37$, $RI = 62$). Unambiguous character state changes were mapped using Farris optimisation.

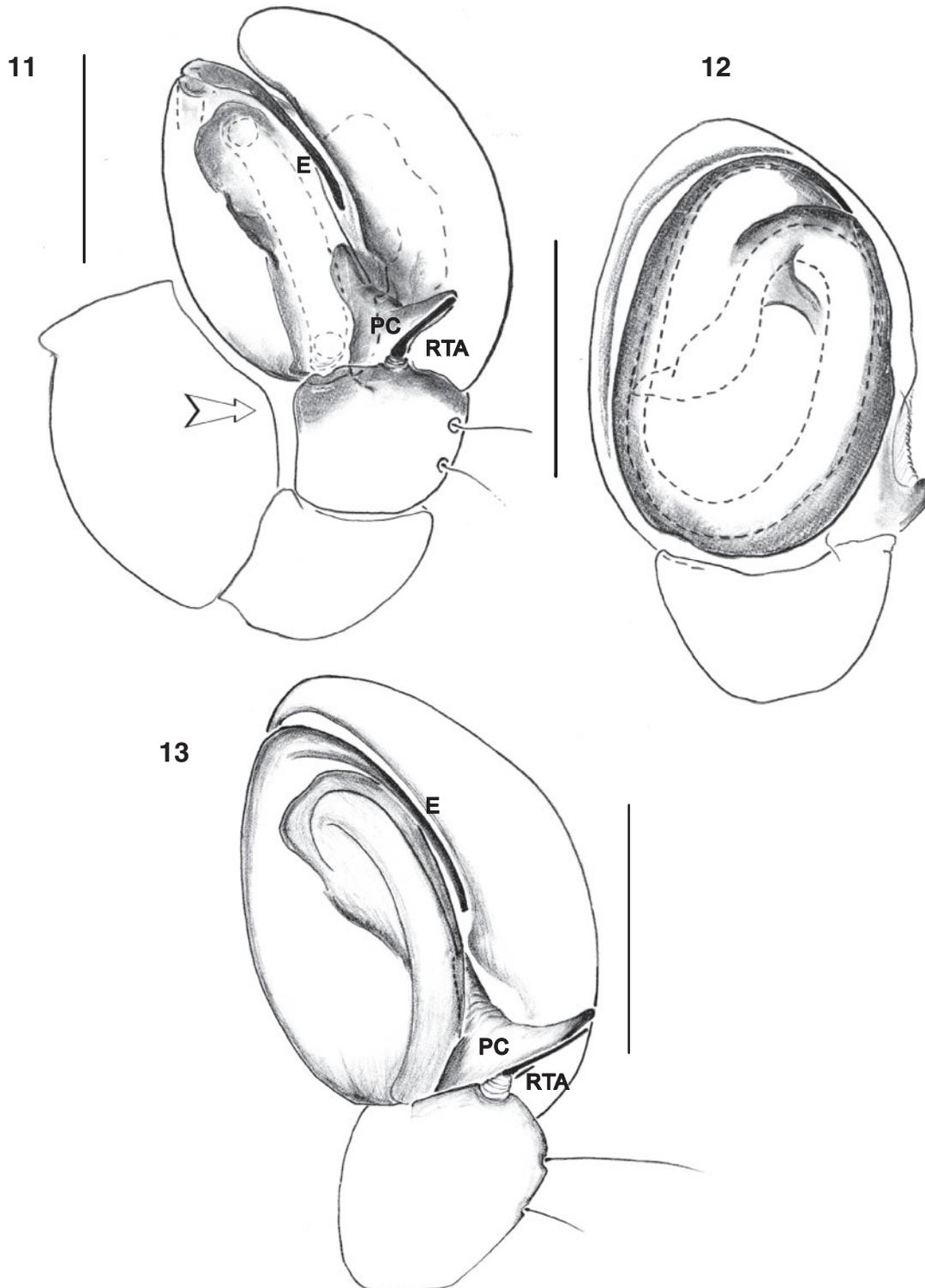
Description

Small spider, 3.3–2.4 mm. Prosoma of alcohol-preserved specimens dark reddish brown. Prosoma widest at the lateral eyes and tapered posteriorly, covered with sub-erect weak setae. Opisthosoma rounded, covered with sub-erect weak setae, lighter than the prosoma, lateral surfaces whitish, surrounded by white lines, a central folium of white patches in the form of

a cross present in some species. Muscle spots clearly visible. Eyes with black tubercles, both rows recurved. Eye formula: ALE > PLE > AME > PME. Chelicerae promargin with peg-like setae. Leg formula 4–3–2–1 (minimal length differences present). All legs lack spines. Metatarsi and tarsi of all legs are fused and darker coloured than the rest of the leg. Metatarsi shorter than tarsi. Palp: femur longer than tibia, cymbium modified to accommodate the stout RTA (Figs 11, 13). Bulb oval, embolus



Figs 4–10. *Pagida salticiformis*. 4, 5, Female from Wanatha Villu, in life. 6–9, Female syntypes (OUMNH b.1241 t.97). 10, Male from Wilpattu National Park (USNM). Arrows points to muscle spots.



Figs 11–13. *Pagida salticiformis* from Wilpattu National Park (USNM). *11*, Retrolateral view of left male palp; *12*, ventral view of same. *13*, Male from Padiathalawa, retrolateral view of left male palp. E, embolus; PC, paracymbium; RTA, retrolateral apical tibial apophysis. Arrow points to the enlarged femur. Scale bars = 0.2 mm.

short (Figs 11, 12). Epigynum: simple with an anterior hood, copulatory openings clearly visible. Sclerotised copulatory openings lead to multi-chambered spermatheca.

Composition

Three species: *Pagida salticiformis* (O. P.-Cambridge, 1883), *P. pseudorchestes* (Thorell, 1890) and *P. minuta*, sp. nov. A further undescribed species from India is also known (P. T. Lehtinen, pers. comm.).

Distribution

Sri Lanka, India, Thailand, Indonesia and Malaysia.

Pagida salticiformis (O. P.-Cambridge)

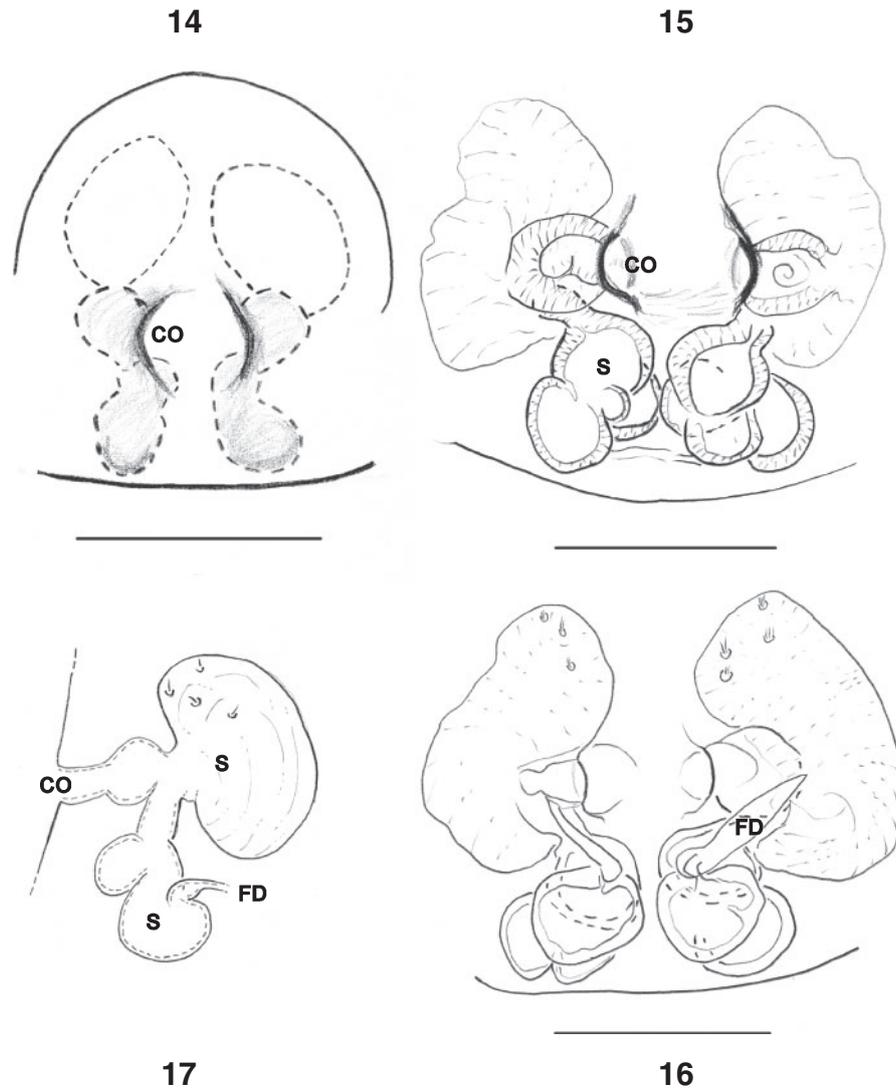
(Figs 4–16, 18–30, 34–37)

Palaephatus salticiformis O. P.-Cambridge 1883: 362, plate 37, fig. 7.
Pagida salticiformis (O. P.-Cambridge): Simon 1895: 1000, figs 1064–1065.

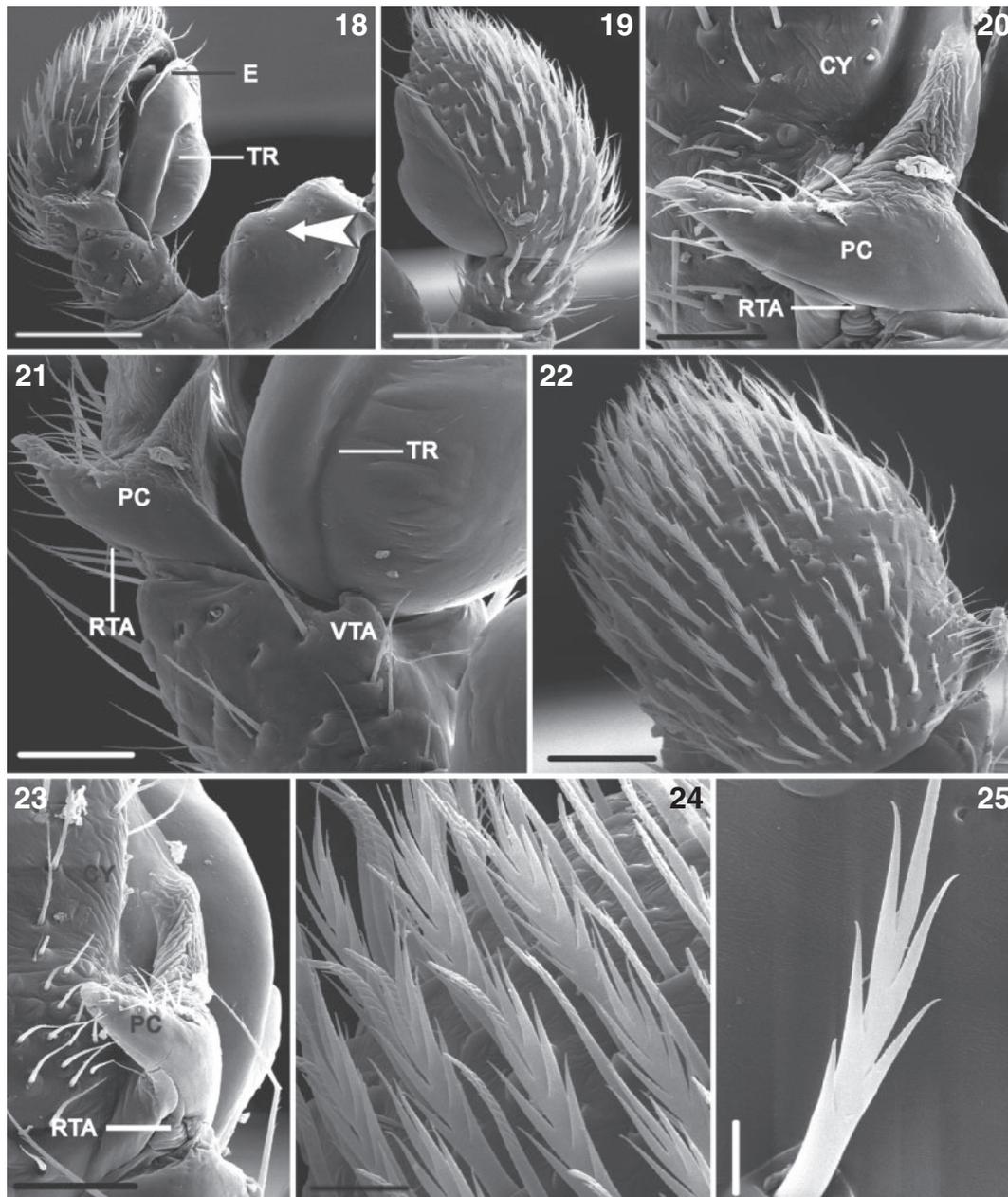
Material examined

Syntypes. 1 ♀, 1 juvenile, Sri Lanka, leg. G. H. K. Thwaites (OUMNH b.1241 t.97).

Non-type material. **Sri Lanka:** Uva Province: 1 ♀, Monaragala District, Mau Ara (USNM); Eastern Province: 1 ♂, Ampara District, 18 km from Padiathalawa (IFS); 1 ♂, 1 ♀, Kokagala (IFS); Central Province: 1 juvenile, Kandy District, Randenigala (IFS); 1 ♂, Matale District, IFS Arboretum (IFS); North Western Province: 1 ♂, Wilpattu National Park (USNM) (IFS);



Figs 14–17. *Pagida salticiformis*. 14–16, Female syntype (OUMNH b.1241 t.97). 14, Epigynum, ventral view. 15, Vulva, ventral view; 16, vulva, dorsal view. 17, Schematic representation of the internal genitalia, lateral view. CO, copulatory opening; FD, fertilisation duct; S, spermatheca. Scale bars = 0.2 mm.



Figs 18–25. Scanning electron micrographs of *Pagida salticiformis*. Right male palp (18, 20, 21, 23, retrolateral view; 18, prolateral view; 22, 24, 25, dorsal view). 20, Paracymbium; 21, 23, paracymbium, more detail. 22, 24, Cymbium, with branched setae. 25, Branched seta. CY, cymbium; E, embolus; PC, paracymbium; RTA, retrolateral tibial apophysis; TR, tegular ridge; VTA, ventral tibial apophysis. Arrow points to the enlarged femur. Scale bars = 10 μm (25); 20 μm (24); 40 μm (20), 50 μm (23), 60 μm (21), 100 μm (22), 200 μm (18, 19).

1 sub-adult ♂ (IFS); 1 sub-adult ♂, 2 ♀, same locality and data (IFS); Northern Province: 1 ♂, Mannar District, along Madu Road (IFS).

Diagnosis

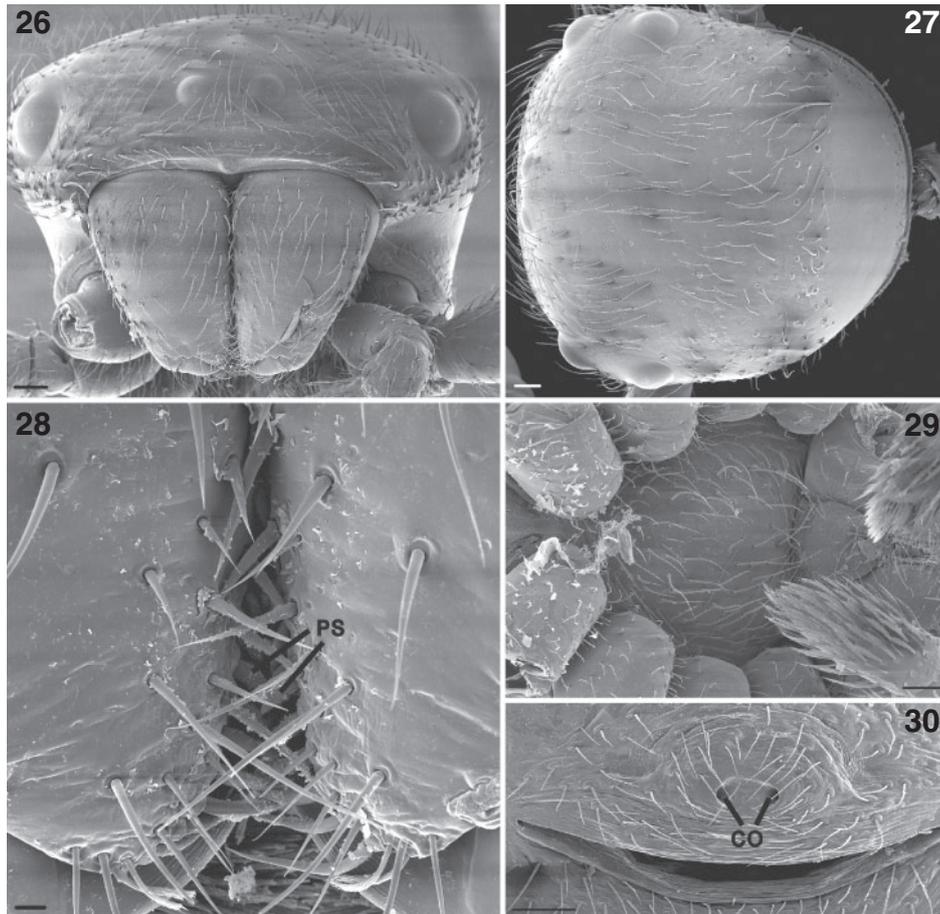
Males of *P. salticiformis* are distinguished from other described *Pagida* species by the short tibia, stout RTA and stout embolus (Figs 11–13). Further, males can be separated by the enlarged femur as shown in Fig. 11. Females are distinguished by the membranous copulatory sac and conical copulatory ducts

(Figs 14–16). Further, females can be separated by the presence of a folium of white patches in a straight line as in Fig. 7.

Description

Male

Total length 2.9; prosoma length 1.2, width 1.5; leg I 2.2, femur 0.4, patella 0.3, tibia 0.4, metatarsus 0.3, tarsus 0.6. Black spiders in life, preserved specimens reddish brown.



Figs 26–30. Scanning electron micrographs of *Pagida salticiformis*. 26, Female prosoma, front view; 27, same, dorsal view. 28, Chelicerae, front view. 29, Sternum, ventral view. 30, Epigynum, ventral view. PS, peg-like setae; CO, copulatory opening. Scale bars = 10 μm (28); 100 μm (26, 27, 29, 30).

Prosoma widest at the lateral eyes and tapered posteriorly, no visible markings dorsally (Figs 4, 5, 10). Opisthosoma rounded, lateral surfaces surrounded by faint white lines. Muscle spots clearly visible. Eyes with black tubercles, both rows recurved. Eye formula: ALE = PLE > AME > PME. Chelicerae promargin with peg-like setae (Fig. 28). Leg formula 4–3–2–1 (minimal length differences present). All legs lack spines. Metatarsi and tarsi of all legs are fused. Metatarsi shorter than tarsi (Figs 34, 35). Palp: femur and tibia enlarged, femur longer than tibia, cymbium modified to accommodate the spine-like RTA (Figs 11–13, 20, 21, 23). Bulb oval, embolus short (Figs 12, 18).

Female

Total length 3.3; prosoma length 1.6, width 1.55; leg I femur 0.6, patella 0.5, tibia 0.6, metatarsus 0.3, tarsus 0.6. Somatic morphology as above except for the pale brown colour and white patches dorsally (Figs 6–9). The white patches form a median line. Epigynum and vulva: sclerotised copulatory opening leads to a membranous copulatory sac, which then leads to spermatheca as in Figs 14–16.

Natural history

All spiders were found living in leaf litter in dry seasonal forest.

Distribution

This species occurs in Sri Lanka.

Remarks

The original description makes no mention of the mature female specimen found in the same vial. Simon's (1895) material has not been examined.

Pagida pseudorchestes (Thorell)

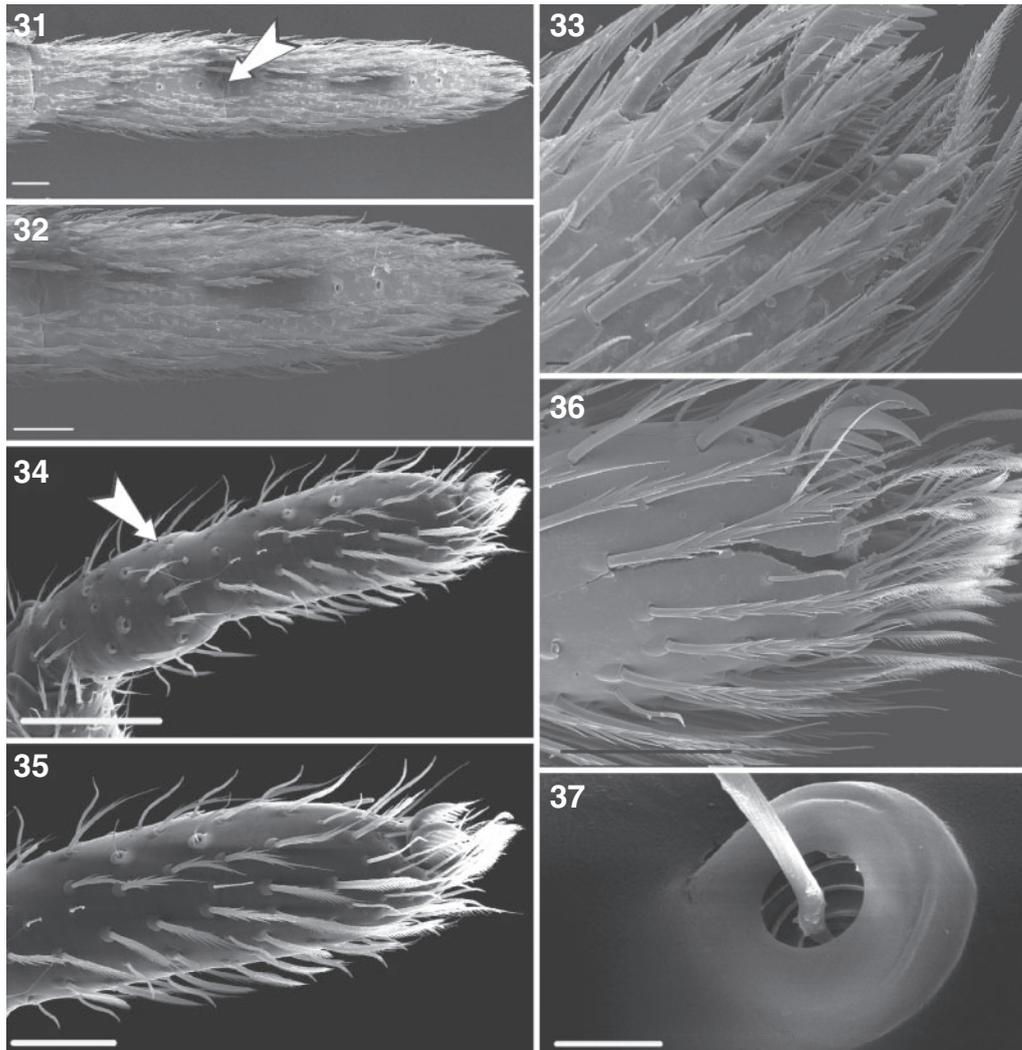
(Figs 38, 39, 42, 45, 47–50)

Palaephatus pseudorchestes Thorell 1890: 155.

Pagida pseudorchestes (Thorell): Simon 1895: 1000.

Non-type material examined

Indonesia: Bohorok: 1 ♂, Gunung Leuser National Park (RMNH, ARA.17144); 1 ♂, same locality (RMNH, ARA.17131); 2 ♀, same locality (RMNH, ARA.17143); 1 ♂, same locality (RMNH, ARA.17140); 1 ♂,



Figs 31–37. Scanning electron micrographs of: (31–33) *Stiphropus lugubris* and (34–37) *Pagida salticiformis*. 31, 32, Leg I of male depicting the fused metatarsus-tarsus joint (ZFMK Ar. 092). 33, Same, tip of tarsus. 34, 35, Leg I of female depicting the fused metatarsus-tarsus joint; 36, same, tip of tarsus. 37, Base of trichobothrium; 31, 32, 34, 35, 37, same, dorsal view; 33, same, lateral view. Arrows point to the fused metatarsus-tarsus joint. Scale bars = 6 μm (37); 10 μm (33), 90 μm (35), 100 μm (31, 32, 36), 200 μm (34).

1 juvenile, same locality (RMNH, ARA.17141); 1 ♀, same locality (RMNH, ARA.17132); 1 ♂, Sumatra, Mt Singalang (Bukittingi), Anai (RMNH, ARA.17133); 1 ♀, 1 juvenile, same locality (RMNH, ARA.17134); 1 ♀, West Sumatra, Kerinci Seblat National Park (RMNH, ARA.17135); 1 ♂, same locality (RMNH, ARA.17136); 1 ♂, West Sumatra, Rimba Panti Reserve (Lebuksikapung) (RMNH, ARA.17138); **Malaysia:** Borneo, 2 ♀, Sabah, Danum Valley Research Center (RMNH, ARA.17137); 1 ♀, Sarawak, Matang (Kuching), Mt Serapi (RMNH, ARA.17145); Selangor: 1 ♂, 2 juvenile, Genting Highlands (RMNH, ARA.17142); 1 ♀, Templer's Park (RMNH, ARA.17139); **Thailand:** 1 juvenile, Erawan Waterfalls National Park (RMNH, ARA.17130).

Diagnosis

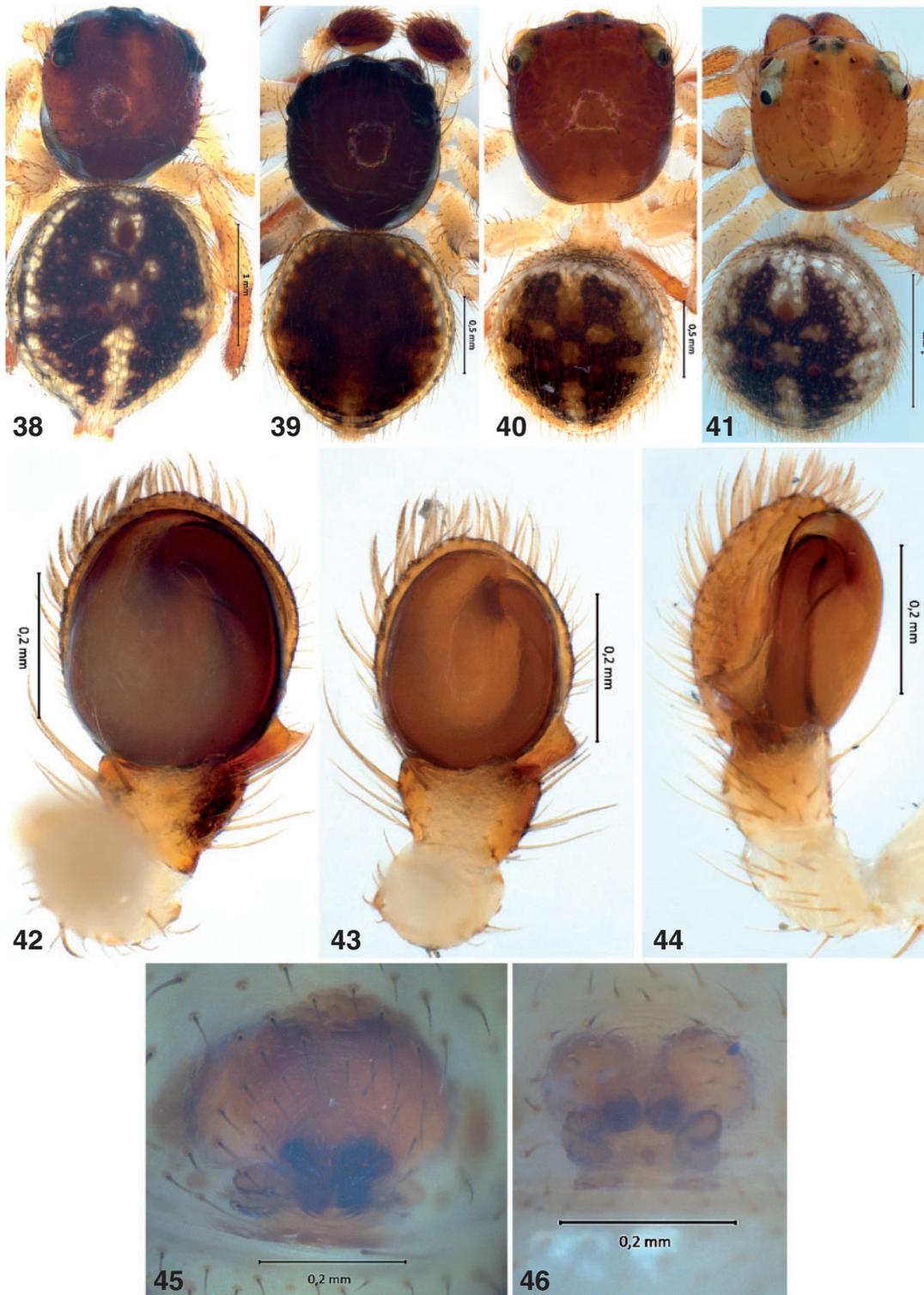
Males of *P. pseudorchestes* differ from other described *Pagida* species by the globular bulbus, shorter RTA and filiform

embolus; females differ by the oval, thin-walled spermatheca and elongated copulatory ducts (Figs 47, 48).

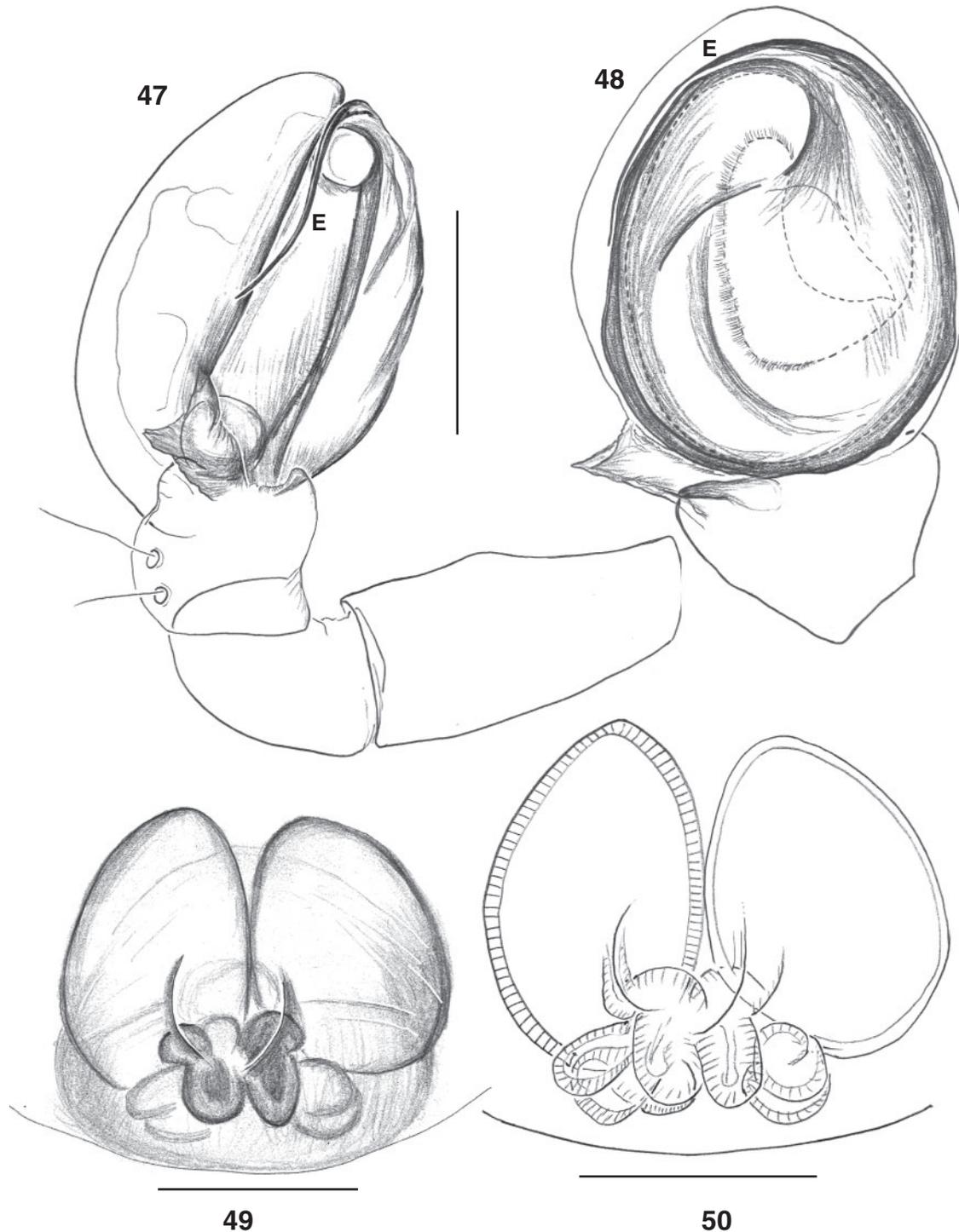
Description

Male

Total length 2.4; prosoma length 1.1, width 1.1; leg I femur 0.6, patella 0.2, tibia 0.6, metatarsus 0.3, tarsus 0.6. Prosoma of alcohol-preserved specimens dark reddish brown (Fig. 39). Prosoma widest at the lateral eyes and tapered posteriorly, covered with sub-erect weak setae, no visible markings dorsally (Fig. 39). Opisthosoma rounded, covered with sub-erect weak setae, lighter than the prosoma, lateral surfaces whitish, surrounded by white lines. Eyes with black tubercles, both rows recurved. Eye formula:



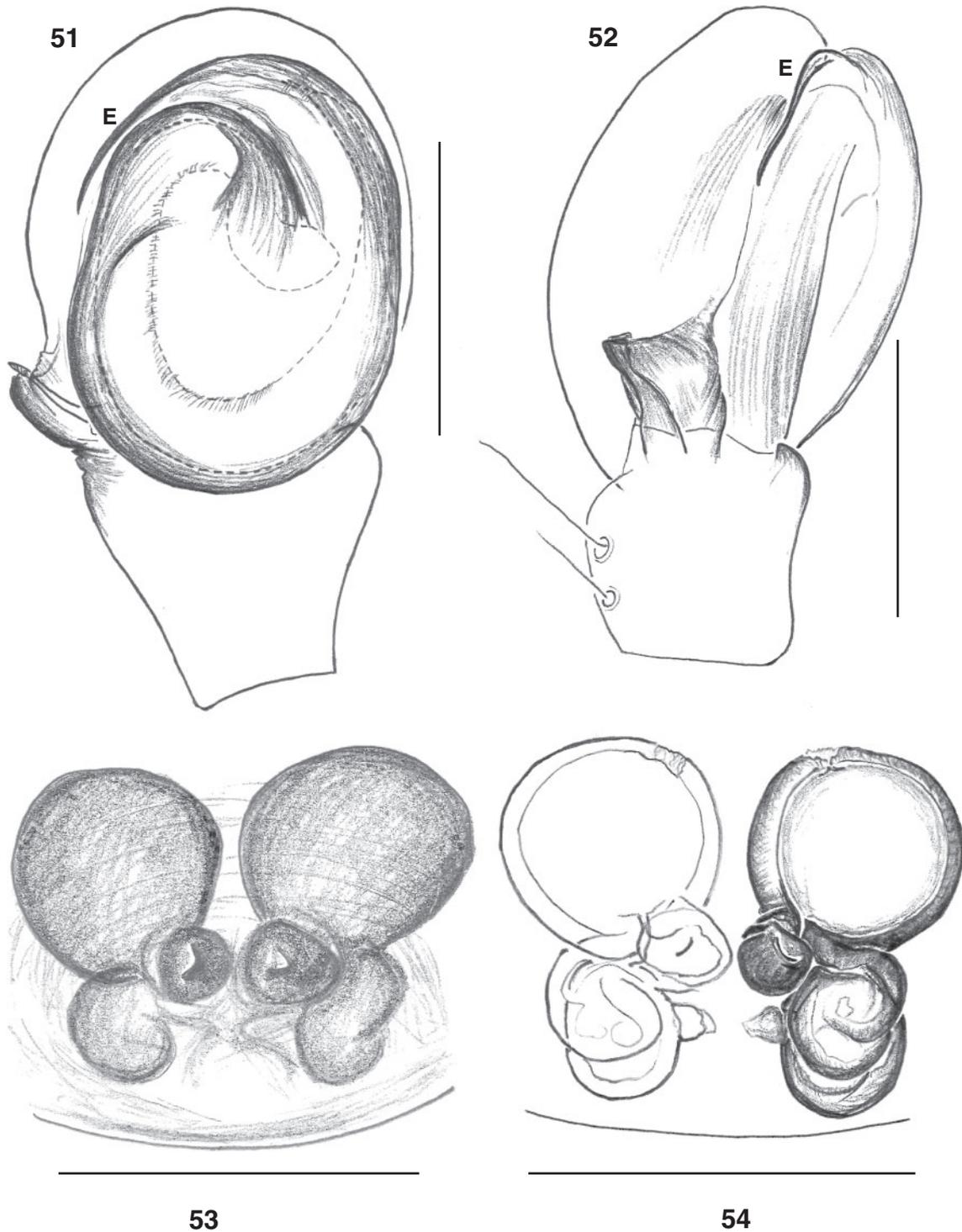
Figs 38–46. 38, 39, 42, 45, *Pagida pseudorchestes*. 40, 41, 43, 44, 46, *Pagida minuta*, sp. nov. 39, 40, Male, dorsal view. 38, 41, Female, ventral view. 42, 43, Left palp, ventral view. 44, Left palp, retrolateral view. 45, 46, Epigynum, ventral view. Scale bars = 0.2 mm (42–46), 0.5 mm (39, 40), 1.0 mm (38, 41).



Figs 47–50. *Pagida pseudorchestes*. 47, Left male palp, retrolateral view; 48, same, ventral view. 49, Epigynum, ventral view. 50, Vulva, ventral view. E, embolus. Scale bars = 0.2 mm.

ALE > PLE > AME > PME. Chelicerae promargin with peg-like setae. Leg formula 4–3–2–1 (minimal length differences present). All legs lack spines. Metatarsi and tarsi of all legs are fused and darker coloured than the rest of the leg. Metatarsi

shorter than tarsi. Palp: femur and tibia not visibly enlarged, femur longer than tibia, cymbium modified to accommodate the stout RTA (Figs 47, 48). Bulb oval, embolus short (Figs 47, 48).



Figs 51–54. *Pagida minuta*, sp. nov. 51, Ventral view of left male palp; 52, same, retrolateral view. 53, Epigynum, ventral view. 54, Vulva, ventral view. E, embolus. Scale bars=0.2 mm.

Female

Total length 3.3; prosoma length 1.5, width 1.4; leg I femur 0.6, patella 0.3, tibia 0.7, metatarsus 0.5, tarsus 0.6. Somatic

morphology as above except for the following: prosoma of alcohol-preserved specimens reddish brown (Fig. 38). Opisthosoma lighter than the prosoma, central folium of white patches in the form of a cross present. Lateral surfaces whitish,

surrounded by lines formed by white patches. Epigynum and vulva as in Figs 49 and 50.

Distribution

This species is known from several localities in Indonesia and Malaysia and from one locality in Thailand.

Natural history

In contrast to the type species, *P. salticiformis*, specimens of this species were collected on foliage. Some specimens have been observed sitting on the underside of green leaves, usually on the edges of holes and moving to the top for prey capture (C. L. Deeleman, pers. comm.). Other specimens have been collected with large ants as prey.

Remarks

The type specimen has been misplaced (M. Tavano (MCSN), pers. comm.); however, it was examined and drawn by C. L. Deeleman during a visit to MCSN in 1987. These drawings were compared with our specimens. The probable type locality is Sumatra, Mt Singalang (C. L. Deeleman, pers. comm.). Material from that locality has been examined for this study.

Pagida minuta, sp. nov.

(Figs 40, 41, 43, 44, 46, 51–54)

<http://zoobank.org/urn:lsid:zoobank.org:act:85AE8E96-28D2-46F6-BE91-BB25B7242143>

Material examined

Holotype. ♂, Malaysia: Borneo, West Sabah, Kinabalu National Park H.Q. (6°04'N, 116°33'E), at 1550 m, primary rainforest, leaf litter, 1–5. v.1991, C.L. Deeleman, P.R. Deeleman (RMNH, ARA.17147).

Paratype. **Malaysia**: 1 ♀, same locality as above, 23.vii.1980, C.L. Deeleman, P.R. Deeleman (RMNH, ARA.17148).

Non-type material. **Malaysia**: 1 ♂, 1 juvenile (damaged), same locality and data as holotype (RMNH, ARA.17149); 2 ♂, same locality and data as holotype (RMNH, ARA.17150); 1 ♂, 1 juvenile (damaged), same locality and data as holotype, (RMNH, ARA.17151); 1 juvenile (damaged), Poring Hot Springs (RMNH, ARA.17152) (specimen tentatively identified).

Diagnosis

Males of *P. minuta*, sp. nov. differ from other described *Pagida* species by the oval bulbus, longer, filiform RTA and filiform embolus; females differ by the globular, thick-walled spermatheca and globular copulatory ducts (Figs 51, 52). Further, males differ by the presence of a central folium of white patches in the form of a cross and whitish lateral surfaces.

Description

Male

Total length 2.9; prosoma length 1.3, width 1.1; leg I femur 0.6, patella 0.3, tibia 0.6, metatarsus 0.4, tarsus 0.6. Prosoma of alcohol-preserved specimens dark reddish brown (Fig. 40). Prosoma rounded, covered with sub-erect weak setae, broadest behind the PER, tapering backwards, no visible markings

dorsally (Fig. 40). Opisthosoma rounded, covered with sub-erect weak setae, light black, central folium of white patches in the form of a cross present, lateral surfaces whitish. ALE and PLE on white tubercles, both rows recurved. Eye formula: ALE>PLE>AME>PME. Chelicerae promargin with peg-like setae. Leg formula 4–3–2–1 (minimal length differences present). All legs lack spines. Metatarsi and tarsi of all legs are fused and darker than the rest of the leg. Metatarsi shorter than tarsi. Palp: femur and tibia not visibly enlarged, femur longer than tibia, cymbium modified to accommodate the stout RTA (Figs 43, 44, 51, 52). Bulb oval, embolus short (Figs 51, 52).

Female

Total length 3.0; prosoma length 1.4, width 1.2; leg I femur 0.6, patella 0.3, tibia 0.5, metatarsus 0.4, tarsus 0.6. Somatic morphology as above. Epigynum and vulva as in Figs 46, 53 and 54.

Distribution

This species is known only from the type locality on the island of Borneo.

Natural history

The female specimen was found sitting on edge of a hole in a leaf of a *Mazadella* tree, shifting from the upper to the underside of the leaf.

Etymology

The species name refers to the smaller size of the spiders.

Other non-*Pagida* material examined

Stiphropus lugubris Gerstäcker

Kenya: 3 ♂, Kakamega Forest, 0°22'N, 34°50'E, 2001–03, canopy fogging, W. Freund (ZFMK, Ar. 092).

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