The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2010, **159**, 711–745. With 28 figures

Revision and cladistic analysis of the jumping spider genus *Onomastus* (Araneae: Salticidae)

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Received 5 September 2008; accepted for publication 25 February 2009

The jumping spider genus *Onomastus* Simon, 1900 is revised. Four new species: ***Onomastus indra* sp. nov.**, ***Onomastus kaharian* sp. nov.**, ***Onomastus pethiyagodai* sp. nov.**, and ***Onomastus rattotensis* sp. nov.** are described. Parsimony analysis of 26 morphological characters supported the monophyly of *Onomastus*. *Lyssomanes* is sister to *Onomastus*. *Onomastus* separates into two clades: the widespread South-East Asia clade and the South Asia clade. The South Asia clade is restricted to the Sri Lanka–Western Ghats biodiversity hotspot. Species of the South Asia clade appear to be spot endemics, highly in danger of extinction because of habitat loss and climate change. Male palps are complex and species-specific, suggesting rapid divergent evolution.

doi: 10.1111/j.1096-3642.2009.00580.x

ADDITIONAL KEYWORDS: biodiversity – climate change – hotspots – India – South-East Asia – Sri Lanka.

INTRODUCTION

Our current understanding of the evolutionary relationships of jumping spiders, the largest spider family, suggest at least four major lineages: the lyssomanines, the spartaeines, the *Cocalodes* group, and the much larger Salticoida clade (Wanless, 1980a, 1984; Maddison, 1996; Maddison & Hedin, 2003; Maddison & Needham, 2006). The three non-Salticoida clades have recently been collectively termed 'basal salticids' (Maddison & Needham, 2006). Jumping spiders of the genus *Onomastus* Simon, 1900 are lyssomanines (Wanless, 1980b). They are small to medium sized spiders (2.0 to 5.2 mm total length) that live on foliage of tropical evergreen forests. They stalk for prey and do not build capture webs. They resemble other lyssomanines in coloration, general slender body shape, and by having the eyes arranged in four transverse rows (Wanless, 1980b). However, in contrast to Salticoida and other lyssomanines and spartaeines, *Onomastus* male palps are unusually complex and provide enough information to clearly distinguish amongst closely related species. Except for *Onomastus complexipalpis* sp. nov., female genitalia are less complex and more similar in most aspects.

Currently lyssomanines are defined by the presence of four rows of eyes and a tracheal system that is confined to the opisthosoma (Galiano, 1962; Wanless, 1980a). Wanless (1980a) used the eye pattern to define groupings of lyssomanine genera: *Asemonea* O. P.-Cambridge, 1869, *Goleba* Wanless, 1980, *Macopaeus* Simon, 1900, and *Pandisus* Simon, 1900 was termed group III; group III was considered by him to be related to group II, which consisted of the genera *Lyssomanes* Hentz, 1845 and *Chinoscopus* Simon, 1901. *Onomastus* was however, considered not closely allied to either of them and was thus placed in group I (Wanless, 1980a). However, these hypotheses have not been tested in a phylogenetic context.

The type species of *Onomastus, Onomastus nigricauda* Simon, 1900 is endemic to lowland evergreen rainforests of western Sri Lanka. A further two species, *Onomastus quinquenotatus* Simon, 1900 from Sri Lanka and *Onomastus patellaris* Simon, 1900 from the Western Ghats of southern India, were described by Simon (1900). The first species outside the Indian subcontinent, *O. complexipalpis* was

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described in a comprehensive treatment of the genus by Wanless (1980b). However, by 1980 only *O. nigricauda* and *O. patellaris* were known by both sexes. Recently several species from East Asia have been described: *Onomastus simoni* Zabka, 1985 from Vietnam (male unknown), *Onomastus kanoi* Ono, 1995 from Okinawa, Japan (female unknown), and *Onomastus nigrimaculatus* Zhang & Li from China (Zabka, 1985; Ono, 1995; Zhang & Li, 2005).

As part of an on-going survey of spider diversity in Sri Lanka, a large number of *Onomastus* was collected. They turned out to be of four species, two known and two new. All seem to be endemic and restricted to small patches of higher elevation rain forest. Additionally, a collection of South-East Asian *Onomastus* from the collections of Christa L. Deeleman-Reinhold has been incorporated. A further undescribed species from the Western Ghats was also discovered in the collections of the CAS. Here, I provide comprehensive accounts of all *Onomastus* from Sri Lanka and the surrounding region with descriptions of new species and updated diagnosis. Additionally, higher-level relationships of Salticidae are discussed based on a cladistic analysis of *Onomastus* plus exemplars of Wanless's group I–III (Wanless, 1980a).

MATERIAL AND METHODS

Methodology and taxonomic descriptions follow the format of Benjamin (2004, 2006). Specimens used for illustrations were placed on washed sand in 70% ethanol and photographed using a dissecting microscope (Leica MZAPO) with top illumination and a magnification of up to 50 ×. Digital images were taken with a Nikon DXM1200F camera. Images were edited using an Auto-Montage software package. Either a LEO 1430VP or an Amray 1810 scanning electron microscope (SEM) was also used to study and photograph morphological features. Prior to SEM work specimens were prepared as mentioned in Benjamin (2004) and mounted on to aluminium rivets with the help of conductive copper adhesive tape or wire. Such mounting, although rather intricate, enabled rotation of specimens in the SEM chamber. Male palps were cleared in methyl salicylate and mounted on temporary slides to observe and illustrate their internal structures. Left structures (e.g. palps, legs, etc.) are depicted unless otherwise stated. Hairs and macrosetae are usually not depicted in the final palp drawings. All measurements are given in millimetres and were made with a compound microscope (Leica MZAPO) equipped with a 10 × ocular and an ocular micrometre scale. Abbreviations used in the text and figures are given below. Leg spination is described according to the system adopted by Platnick & Shadab (1975). A complete synonymy of the species is given in Platnick (2009).

ABBREVIATIONS

Institutional

BMNH, British Museum, Natural History, London; CAS, California Academy of Sciences, San Francisco; MHNG, Muséum d'Histoire Naturelle, Genève; MNHN, Muséum National d'Histoire Naturelle, Paris; RMNH, Naturalis, National Museum of Natural History, Leiden; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Morphological structures

AEB, anterior epigynal border; ALE, anterior lateral eye; AME, anterior median eye; AP, apical plates of epigynum; B, bulbus; BH, basal haematodocha; C, conductor; CD, copulatory duct; CO, copulatory opening; CY, cymbium; E, embolus; EF, epigynal folds; EP, embolic base; F, femur; FD, fertilization duct; MA, median apophysis; MAP, mesal branch of MA; MP, mate plug; PA, patella apophysis; PLE, posterior lateral eye; PME, posterior median eye; PT, patella; RTA, retrolateral tibial apophysis; S, spermatheca; SP, spur mesal branch of C; ST, subtegulum; T, tibia; TA1, tegular apophysis 1 (Figs 4A, 10A, 17A); TA2, tegular apophysis 2 (Figs 4A, 17A); TA3, tegular apophysis 3 (Figs 4A, 9B, 28D).

CLADISTIC ANALYSIS

Outgroup choice

The primary aim of the cladistic analysis was to test the monophyly and the internal structure of *Onomastus*. Unfortunately, relationships of basal salticids are far from satisfactorily resolved, complicating the selection of the putative outgroup. The selection of outgroup taxa was based on Wijesinghe (1997), Wanless (1980a), and Maddison & Needham (2006). Thus, I have included the genera *Onomastus*, *Lyssomanes*, *Pandisus*, *Asemonea*, and *Goleba*. Further, as suggested by Maddison & Needham (2006), I have also included *Hispo* Simon, 1886, a possible sister to Lyssomaninae.

Taxa and characters scored

The taxa and characters used served the main purpose of the study, which was to test the monophyly and the internal structure of *Onomastus* and not to tackle higher-level relationships amongst salticids. As in my previous work (Benjamin, 2004), I consider all character statements to be hypotheses of homology, unless putative homology of traits of two or more taxa

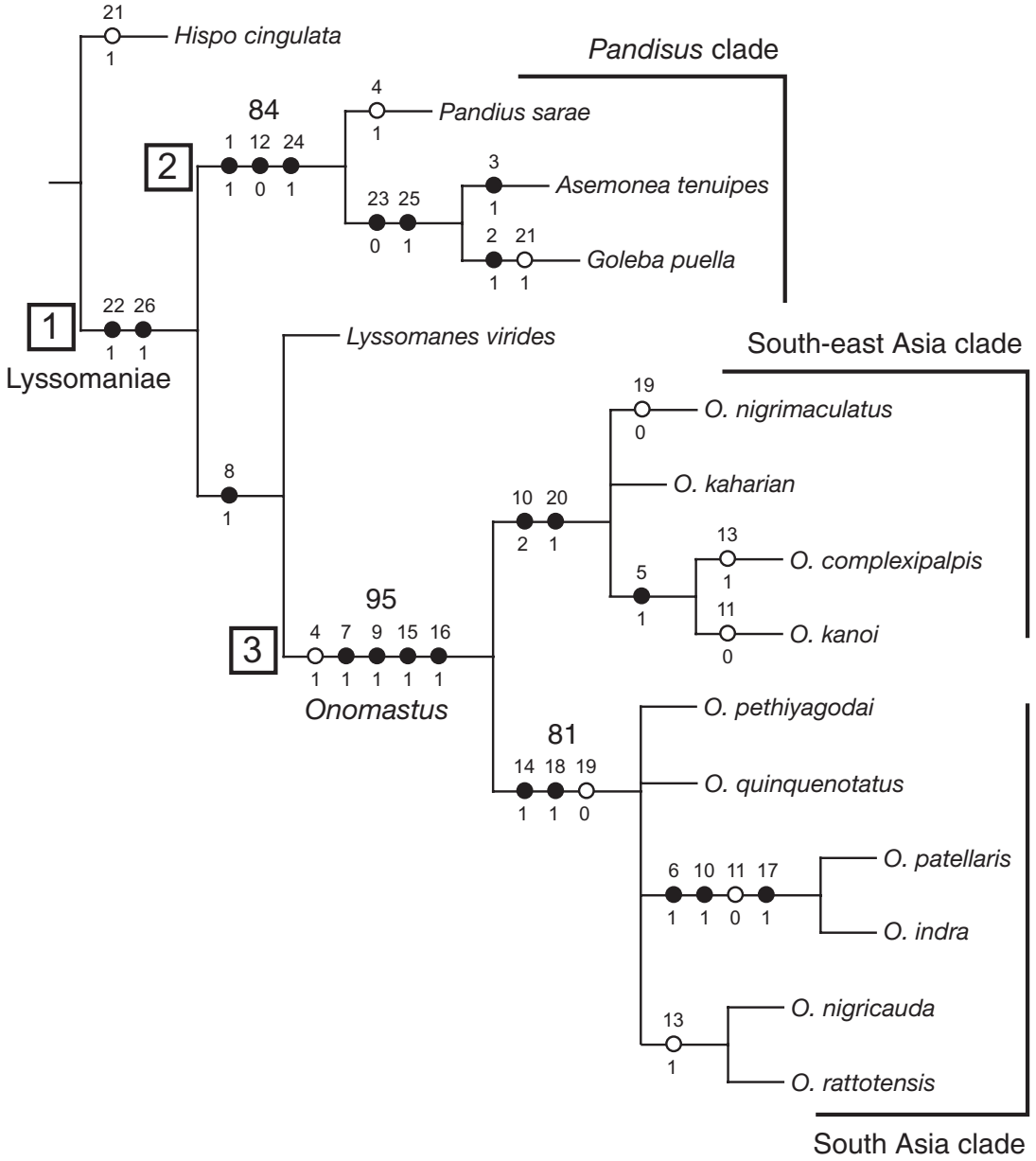

Figure 1. Preferred most parsimonious tree of *Onomastus* based on the character matrix presented in Table 1 (length = 32 steps, consistency index = 0.81, retention index = 0.89). Character state changes are mapped using Farris optimization. Closed circles represent unambiguous character changes.

are rejected by the cladistic analysis (Fig. 1). All *Onomastus* species except for *O. simoni* are included in the phylogenetic analysis (Table 1). *Onomastus simoni* is only known from a single female specimen, additional material was unavailable for study. All characters are scored directly from voucher specimens. However, as a result of a lack of material in collections and to some extent because of the reluctance of curators to lend material for SEM work, outgroup taxa were scored on the basis of published accounts.

Male palp

1. FA: absent/femora smooth, 0; present, 1.

FA is defined here as any structure projecting outwards from the surface of the femur. Present in *Asemonea*, *Pandisus*, and *Goleba* (Wanless, 1980a: figs 4e, 18c). In *Onomastus* femora are smooth and

Table 1. Distribution of characters scored for ten *Onomastus* taxa and outgroups

	0									1			
	1	2	3	4	5	6	7	8	9	0	1	2	3
Onomastus quinquenotatus	0	–	0	1	0	0	1	1	1	0	1	1	0
Onomastus nigrimaculatus	0	–	0	1	0	0	1	1	1	2	1	1	0
Onomastus nigricauda	0	–	0	1	0	0	1	1	1	0	1	1	1
Onomastus patellaris	0	–	0	1	0	1	1	1	1	1	0	1	0
***Onomastus indra* sp. nov.**	0	–	0	1	0	1	1	1	1	1	0	1	0
***Onomastus pethiyagodai* sp. nov.**	0	–	0	1	0	0	1	1	1	0	1	1	0
***Onomastus rattotensis* sp. nov.**	0	–	0	1	0	0	1	1	1	0	1	1	1
Onomastus complexipalpis	0	–	0	1	1	0	1	1	1	2	1	1	1
Onomastus kanoi	0	–	0	1	1	0	1	1	1	2	0	1	0
***Onomastus kaharian* sp. nov.**	0	–	0	1	0	0	1	1	1	2	1	1	0
*Pandisus sarae**	1	0	0	1	0	0	0	0	–	–	–	0	–
*Asemonea tenuipes**	1	0	1	0	–	0	0	0	–	–	–	0	–
*Goleba puella**	1	1	0	0	–	0	0	0	–	–	–	0	–
*Hispo cingulata**	0	–	–	0	–	0	0	0	–	–	–	1	0
*Lyssomanes viridis**	0	–	–	0	–	0	0	1	0	0	–	1	0

							2						
	4	5	6	7	8	9	0	1	2	3	4	5	6
O. quinquenotatus	1	1	1	0	1	0	0	0	1	1	0	0	1
O. nigrimaculatus	0	1	1	0	0	0	1	0	1	1	0	0	1
O. nigricauda	1	1	1	0	1	0	0	0	1	1	0	0	1
O. patellaris	1	1	1	1	1	0	0	0	1	1	0	0	1
***O. indra* sp. nov.**	1	1	1	1	1	0	0	0	1	1	0	0	1
***O. pethiyagodai* sp. nov.**	1	1	1	0	1	0	0	0	1	1	0	0	1
***O. rattotensis* sp. nov.**	1	1	1	0	1	0	0	0	1	1	0	0	1
O. complexipalpis	0	1	1	0	0	1	1	0	1	1	0	0	1
O. kanoi	0	1	1	0	0	?	?	?	1	1	0	0	1
***O. kaharian* sp. nov.**	0	1	1	0	0	1	1	0	1	1	0	0	1
*P. sarae**	–	0	0	0	0	1	0	0	1	1	1	0	1
*A. tenuipes**	–	0	0	0	0	1	0	0	1	0	1	1	1
*G. puella**	–	0	0	0	0	1	0	1	1	0	1	1	1
*H. cingulata**	0	0	0	0	0	1	0	1	0	1	0	0	0
*L. viridis**	0	0	0	0	0	1	0	0	1	1	0	0	1

Character states are scored 0 to 2, ? for unknown, – for inapplicable. Outgroup taxa are denoted with an asterisk.

unmodified, lacking any furrows or apophyses as found in *Asemonea* and *Pandisus* (Fig. 26B; Wanless, 1980b).

2. Position of FA: retrolateral/distal, 0; ventral/median, 1.
Refers to the position of the FA mentioned above. FA is more towards the ventral surface of the centre of the femur in *Goleba* (Wanless, 1980a: figs 22c, d, 24b), whereas it is in a distal retrolateral position in *Asemonea* and *Pandisus* (Wanless, 1980a: figs 4e, 18c). Wanless (1980a) described state 1 found in *Goleba* as 'ventral tubercle on the palpal femur'.

3. Femoral groove: absent, 0; present, 1.
Femoral groove is defined as a cavity of the surface of the femur. It does not project outwards as is the case in the FA. The femoral groove is only present in *Asemonea* (Wanless, 1980a: figs 10e, 13c). In *Onomastus* femora are smooth and unmodified, lacking any furrows (Fig. 26B).

4. PA: absent, 0; present, 1.
Present in all *Onomastus* and *Pandisus* (Figs 9A, 10A, 14F, 17A; Wanless, 1980a; Wanless, 1980b). *Onomastus* lack an RTA, instead the patella of the male palp is armed with an apophysis at the distal end that

probably functions as a replacement for the RTA. A PA is also present in *Pandisus*, as illustrated for *Pandisus scalaris* by Wanless (1980a: fig. 3). One would consider the PA to be homologous in both genera based on the criteria of Remane (1952). However, it appears to be otherwise (Fig. 1).

5. PA shape: tapering, 0; blunt, 1.
PA is rather tapering with a smooth rounded tip in all *Onomastus,* except *O. complexipalpis* and *O. kanoi*. In *O. complexipalpis* and *O. kanoi* the PA broadens towards the end (Figs 3A–C, 3A, 7F; Ono, 1995).

6. Relative size of patella: patella = tibia, 0; patella > tibia, 1.
The relatively elongated patella is unique to the two Indian *Onomastus*, *O. patellaris* and *Onomastus indra* (Figs 4A, B, 17A). Hence the origin of the specific name '*patellaris*', which was the first *Onomastus* species with an elongated patella to be described from India; a second is described below.

7. RTA: present, 0; absent, 1.
A RTA is absent in *Onomastus*. As mentioned above, the distal ends of the tibia of male palps of all *Onomastus* are smooth. As a member of the RTA clade one would expect to see a RTA in all *Onomastus*. However, this is not the case and it is presumed lost in all species (Wanless, 1980b).

8. Conductor: absent, 0; present, 1.
A very complex conductor is present in all known *Onomastus* species and is species-specific in size and shape (Figs 2F, G, 5A, B, 9A; Wanless, 1980b).

9. Type of conductor: hyaline, 0; sclerotized, 1.
A hyaline conductor also termed 'membraneous secondary conductor' by Wanless (1980a: fig. 2g, h), is a conductor that is transparent and very thin. A hyaline conductor is present on *Chinoscopus* Simon, 1901 and *Lyssomanes* (Galiano, 1962, 1980; Wanless, 1980a: fig. 2g, h). The presence of a hyaline conductor might turn out to be a synapomorphy that unites *Chinoscopus* and *Lyssomanes*, two exclusively New World genera.

10. Shape of conductor: filiform, 0; stout, 1; broad, 2.
Conductor shape varies from an elongated filiform-apophysis to a large disk-shaped structure. Scored as filiform for *Onomastus* of Sri Lanka (Figs 11D, 19B, E), as stout for *Onomastus* of India (Figs 4A, 17A), and as broad for the species of the South-East Asia clade (Figs 2B, 3A, 11D, E).

11. Number of hooks on the tip of C: one, 0; two, 1.
The conductor tip of *O. indra*, *O. kano*, and *O. patellaris* is furnished with a single hook (Figs 4A, 7A, E, 17A). The rest have a bifurcated tip ending with two pointed hooks (Fig. 11A–C).

12. MA: absent, 0; present, 1.
All species of *Onomastus* have a heavily sclerotized MA. They are branched and species-specific in shape (Figs 9A, B, 11D, 14D, E, 17A, 25G, H; Wanless, 1980b). MA is present in *Hispo* (Wanless, 1981) and *Lyssomanes*. However, it is absent in *Chinoscopus* (Wanless, 1980a).

13. MA distal end: bifurcate, 0; smooth/tapering, 1.
In *O. nigricauda*, *O. rattotensis*, and *O. complexipalpis*, the MA is distally bifurcated, diverging into two branches (Figs 11D, 28A). Smooth or tapering in the rest (Figs 14D, E, 17A, 25G, H).

14. MAP: absent, 0; present, 1.
The MA has a mesal branch that supports the conductor embolus complex, which is present in all known species from Sri Lanka and India (Figs 4A, 11D, 19E, 27A).

15. Origin of embolus: dorsal, 0; ventral, 1.
The embolus originates from the tegulum within the alveolus in all *Onomastus* species (Fig. 9A, 15A, B; Wanless, 1980b). The origin of the embolus is visible when male palps are cleared in methyl salicylate. It is also clearly visible in the expanded palp (Fig. 9A). This character is diagnostic for *Onomastus*.

16. TA1: absent, 0; present, 1.
Onomastus male palps possess three different tegular structures. Each originates from different positions of the tegulum. I call them TA1, TA2, and TA3, to avoid mislabelling any one of them as homologous to the tegular apophysis (or TA) found in most spider male palps. TA1 ('y' in Wanless (1980b); 'subtegular apophysis' in Zhang & Li (2005) is unique to *Onomastus* (Figs 4A, 10A, 14F, 17A, 25B, E, 28A). TA1 is not known to occur in any other Salticidae (Wanless, 1980a, b). This character is diagnostic for *Onomastus*.

17. TA2: absent, 0; present, 1.
The presence of TA2 ('x' in Wanless (1980b) is unique to the two Indian *Onomastus*, *O. patellaris* and *O. indra* (Figs 4A, 17A). In addition to TA1 the male pulps of Indian *Onomastus* carry a second tegular apophysis termed TA2 in this study. It originates from the prolateral margin of the male palp, distally to the TA1 (Figs 4A, 17A).

18. TA3: absent, 0; present, 1.
TA3 is situated distally to TA1 and TA2, on the ventral/distal surface of the tegulum (Fig. 25H, 28D).

TA3 is present in all known species from Sri Lanka and India (Figs 4A, 9B, 19E, 25E, H, 27A, 28D).

Female genitalia

19. Female copulatory ducts: absent, 0; present, 1.
Copulatory ducts are absent in *Onomastus* (Wanless, 1980b). The exceptions are *Onomastus kaharian*, *O. complexipalpis*, and *O. simoni*, all of the South-East Asia clade. It is present in all outgroup taxa (Wanless, 1980a).The female of *O. kanoi* is unknown; however, I predict that it would have copulatory ducts.

20. EF: absent, 0; present, 1.
EF, also called 'septum' in Zhang & Li (2005) are absent in most *Onomastus*, instead the CO is a simple opening in the cuticle (Wanless, 1980b). The exceptions are species of the South-East Asia clade (Fig. 5C–E; Zhang & Li, 2005). EF are also absent in the outgroup taxa (Wanless, 1980a).

21. Epigynal lip: absent, 0; present, 1.
Present only in *Goleba puella* (Wanless, 1980a).

Somatic morphology

22. Number of eye rows: three, 0; four, 1.
Three considered in *Hispo cingulata* (Wanless, 1981); four in all other taxa in the matrix (Galiano, 1962, 1980; Wanless, 1980a, b).

23. Relative size of PME: PME < PLE, 0; PME = PLE, 1.
PME = PLE in *Asemonea* and *Goleba*. PME < PLE in the rest. Outgroups are scored based on Wanless (1980a). This character might be informative in much broader cladistic studies as well.

24. Relative distance between PME–PME vs. ALE–ALE: PME–PME subequal or longer than ALE–ALE, 0; PME–PME < ALE–ALE, 1.
This character was proposed to define a grouping of genera consisting of *Asemonea*, *Goleba*, *Macopaeus*, and *Pandisus* by Wanless (1980a), which he termed group III. Group III was considered by him to be related to group II, which consisted of the genera *Lyssomanes* and *Chinoscopus*. *Onomastus* was however, considered not closely allied to either of them and was, thus placed in group I (Wanless, 1980a). This character might be informative in much broader cladistic studies as well.

25. Relative size of PLE to PME: much smaller, 0; similar in size, 1.
PME are similar in size in *Asemonea* and *Goleba*. PME are much smaller in the rest. Outgroups are scored based on Wanless (1980a).

26. Prosoma coloration: red/brown, 0; light green, 1.
Lyssomaninae are considered to be transparent green in colour (Wanless, 1980a; Maddison & Needham, 2006). However, available information in the literature on prosoma coloration is rather scanty. All *Onomastus* are clearly green (Figs 8A–D, 18A–F) and so are *Asemonea tenuipes* and *Lyssomanes viridis* (pers. observ.). The remaining taxa are scored based on the their descriptions by Wanless (1980a, 1981).

Analysis

The parsimony analyses were performed using the computer program NONA 2ed (Goloboff, 1999). WinClada version 1.00.08 (Nixon, 1999) and MESQUITE version 1.12 (Maddison & Maddison, 2006) were used to study character optimizations on the cladograms and to build and edit the character matrix, respectively. Ambiguous character optimizations were resolved so as to favour reversal or secondary loss over convergence [Farris optimization or accelerated transformation (ACCTRAN)]. All multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch, 1971). Missing characters were coded as ?, and inapplicable characters as -. Branches were collapsed if the minimum possible branch length was zero ('amb-') or if there was no character that could be optimized to support a node. Tree statistics were only calculated from phylogenetically informative characters. I also used PAUP (Swofford, 2002) to analyse the data as carried out in Benjamin (2004); see Benjamin (2004) for justification of the analytical parameters. Below, characters and states are abbreviated and in bold, e.g. character 2 becomes **2**, character 2, state 1, becomes **2-1**.

RESULTS

Onomastus relationships

The phylogenetic analysis of the above-mentioned, equally weighted characters performed in NONA (hold10000; hold/200; 1000 replicates of tree bisection-reconnection (TBR) + TBR (mult*1000) produced one tree of minimal length. Analysis of the same data set in PAUP with heuristic search methods (100 replicates of random taxon addition subjected to TBR branch swapping; 'MulTrees' set to 100000; branches collapsed if the minimum possible branch length was zero ('amb-'; ACCTRAN or Farris optimization) produced the same minimal length tree found with NONA. This tree was selected as the preferred phylogenetic hypothesis for *Onomastus* (Fig. 1). *Onomastus* is resolved at node 3 supported by four unambiguous synapomorphies. Within *Onomastus*, species are grouped into two clades, which are named here as

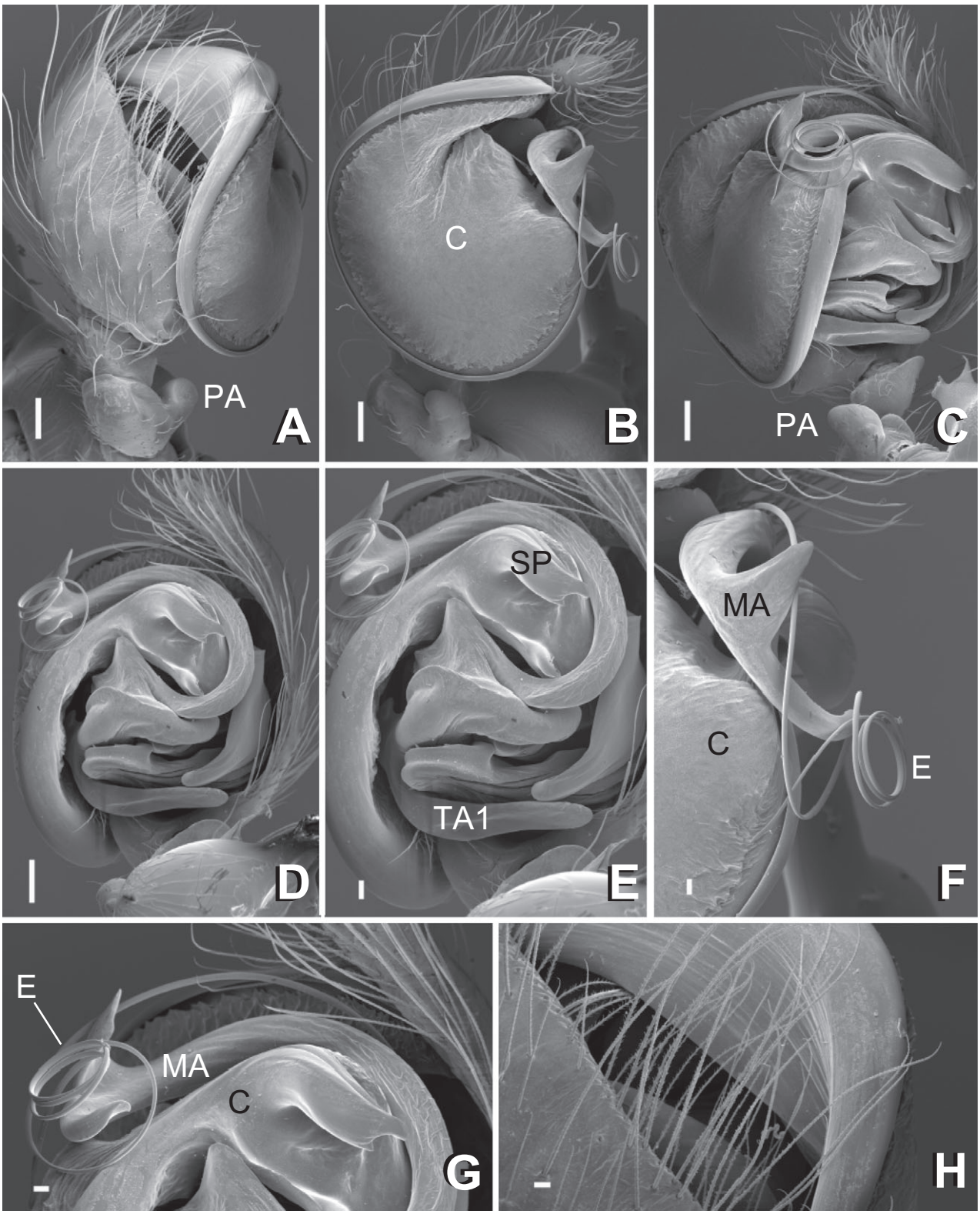

Figure 2. Scanning electron micrographs of *Onomastus complexipalpis* from South Kalimantan, right male palp (RMNH). A, H, prolateral view. B, F, ventral view. C, D, E, G, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PA, patella apophysis; SP, spur mesal branch of C; TA1, tegular apophysis 1. Scale bars = 20 μm (F, G, H), 30 μm (E), 100 μm (A, B, C, D).

the South Asia clade (SA clade) which includes species from Sri Lanka and India and the South-East Asian clade (SE clade), which includes the remaining diversity.

DISCUSSION

Onomastus is a relatively small genus of jumping spiders mostly known from Sri Lanka. This study adds four more species from Sri Lanka, India, and South-East Asia. Noteworthy is the micro endemism of species of the SA clade. In contrast, species of the SE clade seem to be widespread. This study indicates that *Onomastus* of Sri Lanka and India may have originated from a common ancestor and subsequently evolved independently of each other. This is not unusual and has been reported for several faunal groups from Sri Lanka (Bossuyt *et al.*, 2004). Species of the SA clade are spot endemics found mostly in higher elevation habitats. They may be highly in danger of extinction because of habitat loss and climate change.

Wanless (1980b) considered *Onomastus* distinct from any other Lyssomaninae, although no clear arguments were provided. However, this study suggests that it is a genus within a monophyletic Lyssomaninae (node 1), which is supported by two unambiguous synapomorphies (**22-1**, **26-1**). The inclusion of *Onomastus* within Lyssomaninae is in agreement with results of Wijesinghe (1997). However, although the monophyly of Lyssomaninae is widely accepted (Wijesinghe, 1997; Maddison & Hedin, 2003; Maddison & Needham, 2006), further assessments with the addition of more outgroup taxa are considered necessary.

This study suggests that *Onomastus* is sister to the New World genus *Lyssomanes* (Fig. 1). Interestingly *Onomastus* and *Lyssomanes* occupy similar ecological niches. However, this result is in contrast to that of Wijesinghe (1997) who suggested that *Onomastus* is sister to rest of the lyssomanines. Together, *Onomastus* and *Lyssomanes* come out as sister to a grouping of three Old World genera, *Pandisus*, *Asemonea*, and *Goleba* informally termed here as the *Pandisus* clade (node 2), which is essentially 'group lll' proposed by Wanless (1980a). The monophyly of the *Pandisus* clade is supported by three unambiguous synapomorphies (**1-1**, **12-0**, **24-1**). This study sheds more light on the phylogenetic position of *Goleba*, which was unclear in Maddison & Needham (2006). They did not include *Onomastus, Pandisus*, or *Asemonea* in their molecular study, which might have affected placement of *Goleba*. However, these hypotheses of relationships need to be further tested as the present cladistic analysis was designed to test the monophyly and the internal structure of *Onomastus* and not that of Lyssomaninae.

The tracheal system has been widely used in the classification of spiders (Hormiga, 1994 and references). The Lyssomaninae have been characterized as a group that possess a tracheal system that terminates in the opisthosoma (Wanless, 1980a and references) as is the case in *Hispo* (Wanless, 1981). *Onomastus* seem to be an exception (Fig. 27D, E). However, careful preparation of specimens seems to be critical to observing the fine tracheae that enter the prosoma.

SYSTEMATICS

ONOMASTUS SIMON, 1900

Type species: Onomastus nigricauda by original designation.

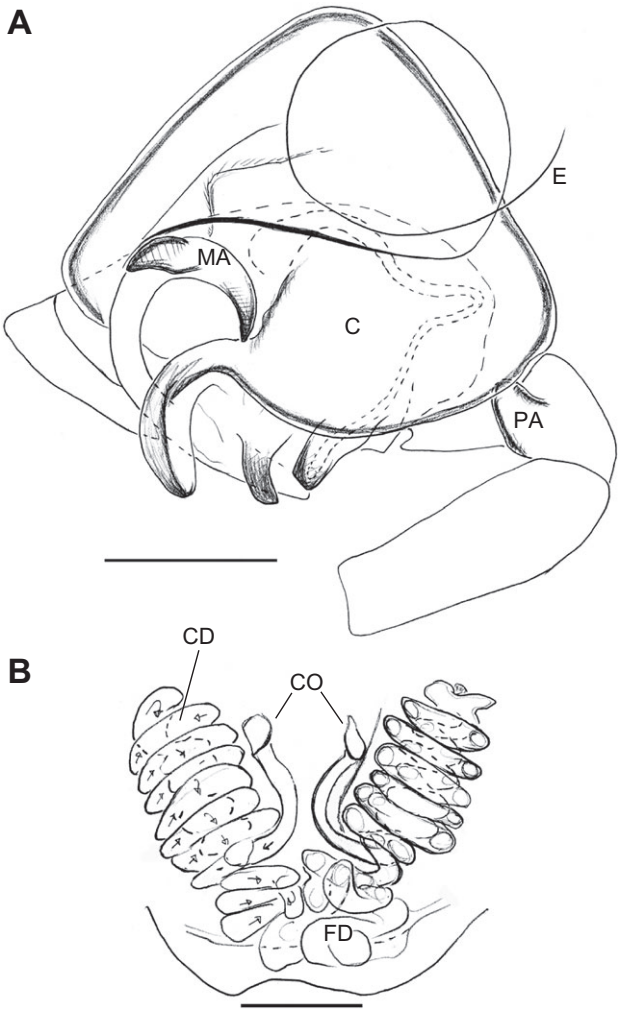

Figure 3. *Onomastus complexipalpis* from South Kalimantan (RMNH). A, left male palp (BMNH 1979.7.4.1). B, vulva, ventral view. Abbreviations: C, conductor; CD, copulatory duct; CO, copulatory opening; E, embolus; FD, fertilization duct; MA, median apophysis; PA, patella apophysis. Scale bars = 0.1 (B), 0.5 (A).

KEY TO MALE *ONOMASTUS* (*O. SIMONI* IS EXCLUDED FOR LACK OF MATERIAL)

1 Male palp with TA2 (Figs 4A, 17A); endemic to India.....2
– Male palps without TA2.....3
2(1) TA2 with upward hook, relatively longer (Fig. 17A).....*Onomastus patellaris*
– TA2 otherwise, TA1 and TA2 shorter (Fig. 4A).....***Onomastus indra* sp. nov.**
3(1) Male palps with a broad, in some cases, disk-shaped C (Figs 2B, 6B, 7C), female epigynum with folds, vulva with clearly defined CD (3B, 5D).....7
– Male palp with filiform C, female epigynum without folds, vulva without CD, all species endemic to Sri Lanka 4
4(3) MA deeply bifurcate, prolateral section with pleats (Figs 27A, 28B, C).....***Onomastus rattotensis* sp. nov.**
– MA without pleats.....5
5(4) MA less strongly bifurcated (Fig. 10A).....*Onomastus nigricauda*
– MA tip bulb like (Figs 20D, 23A).....6
6(5) Tip of MA pointed, spermatheca oval (Figs 23A, 24C, D.....*Onomastus quinquenotatus*
– Tip of MA stout, spermatheca relatively round (Figs 20D, 21B, C).....***Onomastus pethiyagodai* sp. nov.**
7(3) C broad, partly covers the tegulum, conductor with SP (Figs 2G, 7D) 8
– C filiform resting between MA and tegulum.....9
8(7) C large, covers most of the tegulum, MA tapering with a bifurcated tip (Figs 2A, 3A)..... .....*Onomastus complexipalpis*
– C smaller, MA stout (Fig. 7C, D).....*Onomastus kanoi*
9(7) MA chisel-shaped, CD absent (Figs 14E, 16D).....*Onomastus nigrimaculatus*
– MA scoop like, CD C-shaped (Figs 5D, 6D).....***Onomastus kaharian* sp. nov.**

KEY TO FEMALE *ONOMASTUS* (FEMALES OF *O. KANOI* REMAIN UNKNOWN)

1 CD absent or very short, endemic to Sri Lanka and India.....5
– CD clearly visible, epigynal folds present 2
2(1) CD characteristically long, coiled (Fig. 3B).....*Onomastus complexipalpis*
– CD relatively shorter or absent, epigynal folds present (Fig. 5D–E).....3
3(2) CD absent, S round (Fig. 16C–E).....*Onomastus nigrimaculatus*
– CD present, epigynal folds present.....4
4(3) CD inverted 'C'-shaped (Fig. 5D, E).....***Onomastus kaharian* sp. nov.**
– CD inverted 'L'-shaped, running partly parallel to each other.....*Onomastus simoni*
5(1) S round, endemic to South India.....*Onomastus patellaris*, ***Onomastus indra* sp. nov.**
– S elongated endemic to Sri Lanka.....*Onomastus nigricauda*, ***Onomastus pethiyagodai* sp. nov.**, *Onomastus quinquenotatus*, ***Onomastus rattotensis* sp. nov.**

Remarks: Listed as *O. nigricaudus* in Platnick (2009). However, nigri-cauda is a substantive and thus needs no gender adjustment.

Diagnosis: Onomastus is separated from all other Salticidae by the presence of TA1 ('y' in Wanless, 1980b) in the male palp (**16-1**). The following additional characters support the monophyly of *Onomastus* and may serve to separate it: loss of the RTA (**7-1**), presence of a hyaline conductor (**9-1**), the dorsal origin of the embolus (**15-1**). Further, *Onomastus* is separated from all other Salticidae except for *Lyssomanes* and *Chinoscopus* by the presence of a conductor (**8-1**) and the lack of CD (**19-0**; gained in *O. kaharian*, *O. kanoi*, and *O. complexipalpis*). The lack of a clearly defined fovea might also serve to characterize *Onomastus*. See also Wanless (1980b) for a detailed diagnosis.

Description: Male palp: complex and species-specific, suggesting that they have undergone rapid divergent evolution. Femur lacks any form of modification such as apophysis or furrows (Figs 3A, 26B). Patella with a retrolateral apophysis (Figs 3A, 4A, 6F). Tibia with a reduced retrolateral apophysis, hardly visible in most cases. Cymbium distally tapering ('finger-like extension' in Wanless, 1980b), proximal promargin sclerotized and fringed with setae (Figs 2H, 11C, 15C, 28G). Embolus broad based (EP in Fig. 9A), tapering, slender, moderate to long in length, originates from the dorsal parts of the tegulum within the alveolus (Figs 5B, 9A). It may be used in some species as a mating plug (Fig. 11F, G). Tegulum large, makes up to half of the copulatory bulb. Distal tegular end tapers to an apophysis unique to *Onomastus* (TA1; 'Y' in Wanless, 1980b). The prolateral tegular margin of *O. patellaris* and *O. indra* holds an additional apophysis

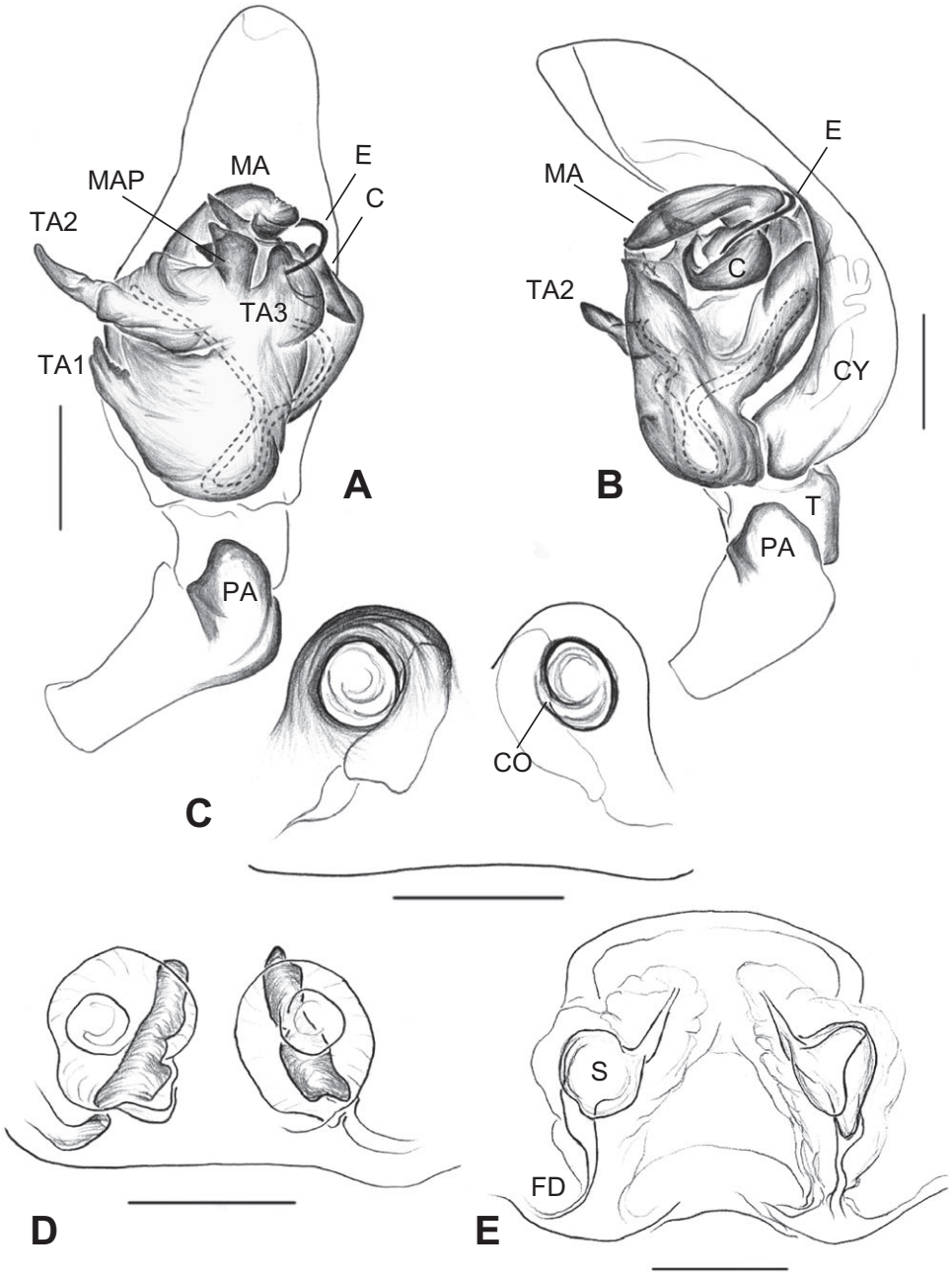

Figure 4. ***Onomastus indra*** **sp. nov.** (CAS). A, left male palp, ventral view. B, ditto, retrolateral view. C, epigynum, ventral view. D, vulva, ventral view. E, ditto, dorsal view. Abbreviations: C, conductor; CO, copulatory opening; CY, cymbium; E, embolus; FD, fertilization duct; MA, median apophysis; MAP, mesal branch of MA; PA, patella apophysis; S, spermatheca; T, tibia; TA1, tegular apophysis 1; TA2, tegular apophysis 2; TA3, tegular apophysis 3. Scale bars = 0.05 (E), 0.1 (C, D), 0.2 (A, B).

unique to them [TA2; 'X' in Wanless (1980b)]. A third tegular apophysis is present in some species (Figs 4A, 10A, 19E, 27A), but absent or reduced in others. The apical half of the copulatory bulb constitutes the MA and conductor–embolus complex. The conductor originates from in between the tegulum, which is grooved on the peripheral margin to form an embolic guide (e.g. in Wanless, 1980b). Its tip is species-specifically modified (spur in Wanless, 1980b). Except for *O. rattotensis*, which has three distal branches, the MA is well sclerotized and distally bifurcate. The distal branches are species-specifically modified. In the South Asian species the base of the MA possesses an apophysis (MAP) that serves as a rest for the apical

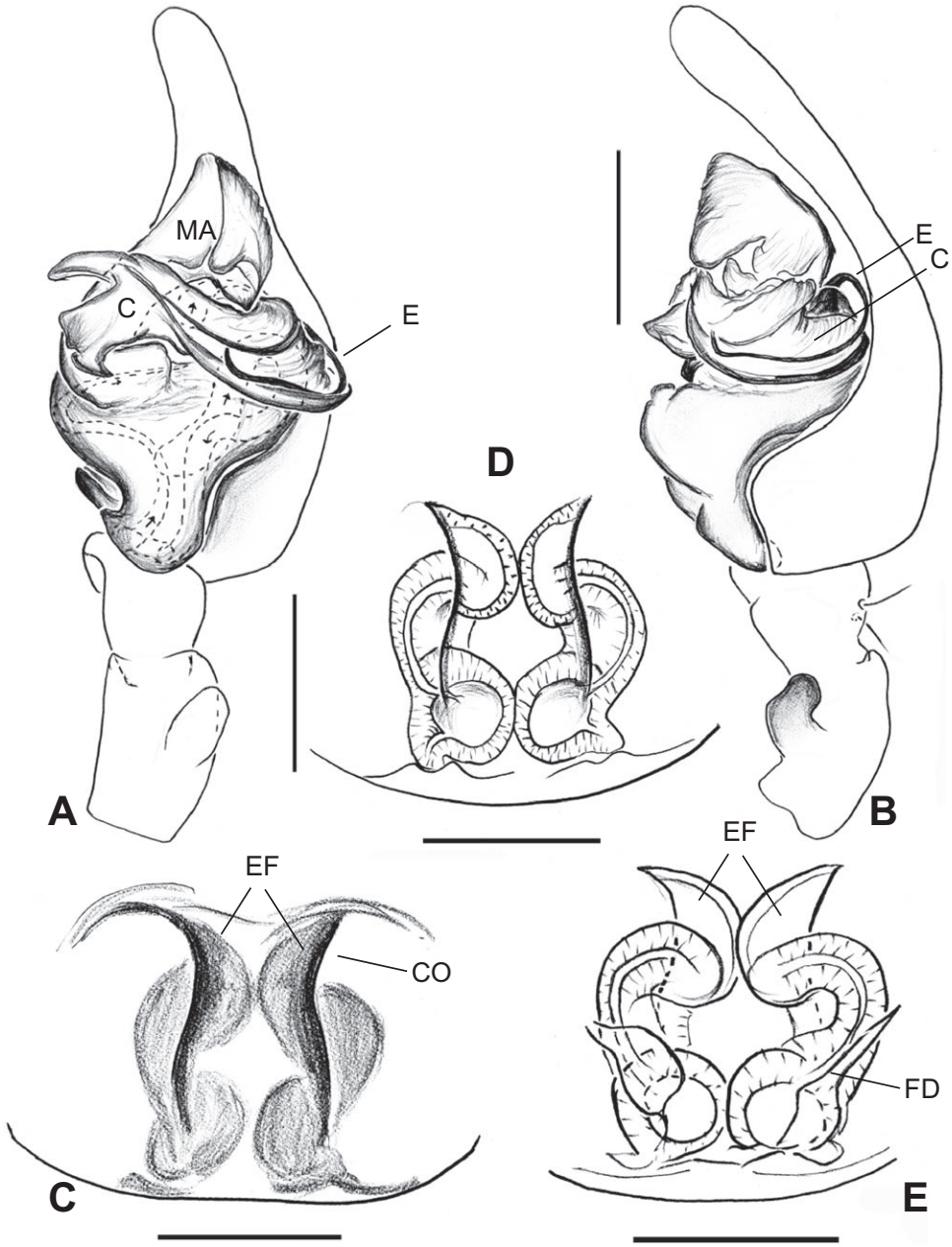

Figure 5. ***Onomastus kaharian*** **sp. nov.** from Central Kalimantan (RMNH). A, left male palp, ventral view. B, ditto, retrolateral view. C, epigynum, ventral view. D, vulva, ventral view. E, ditto, dorsal view. Abbreviations: C, conductor; CO, copulatory opening; E, embolus; EF, epigynal folds; FD, fertilization duct; MA, median apophysis. Scale bars = 0.1 (C–E), 0.2 (A, B).

portion of the embolus–conductor complex (Figs 4A, 11D, 19E). Epigynum: simple to absent. The CO leads directly to the spermathecae. CD lacking in most species. Spermathecae are large and well sclerotized. See also Wanless (1980b) for a detailed description.

Distribution: Oriental region, from Sri Lanka to Japan. However, 55% of the species are endemic to the Sri Lanka–Western Ghats biodiversity hotspot. The Sri Lankan endemics are restricted to small patches of rain forest and are highly endangered as a result of habitat loss.

Composition: Eleven species: *Onomastus complexipalpis* Wanless, 1980, *O. indra* sp. nov., *O. kaharian* sp. nov., *O. kanoi* Ono, 1995, *O. nigricauda* Simon, 1900, *Onomastus nigrimaculatus* Zhang & Li, 2005, *O. patellaris* Simon, 1900, *O. pethiyagodai* sp. nov., *O.*

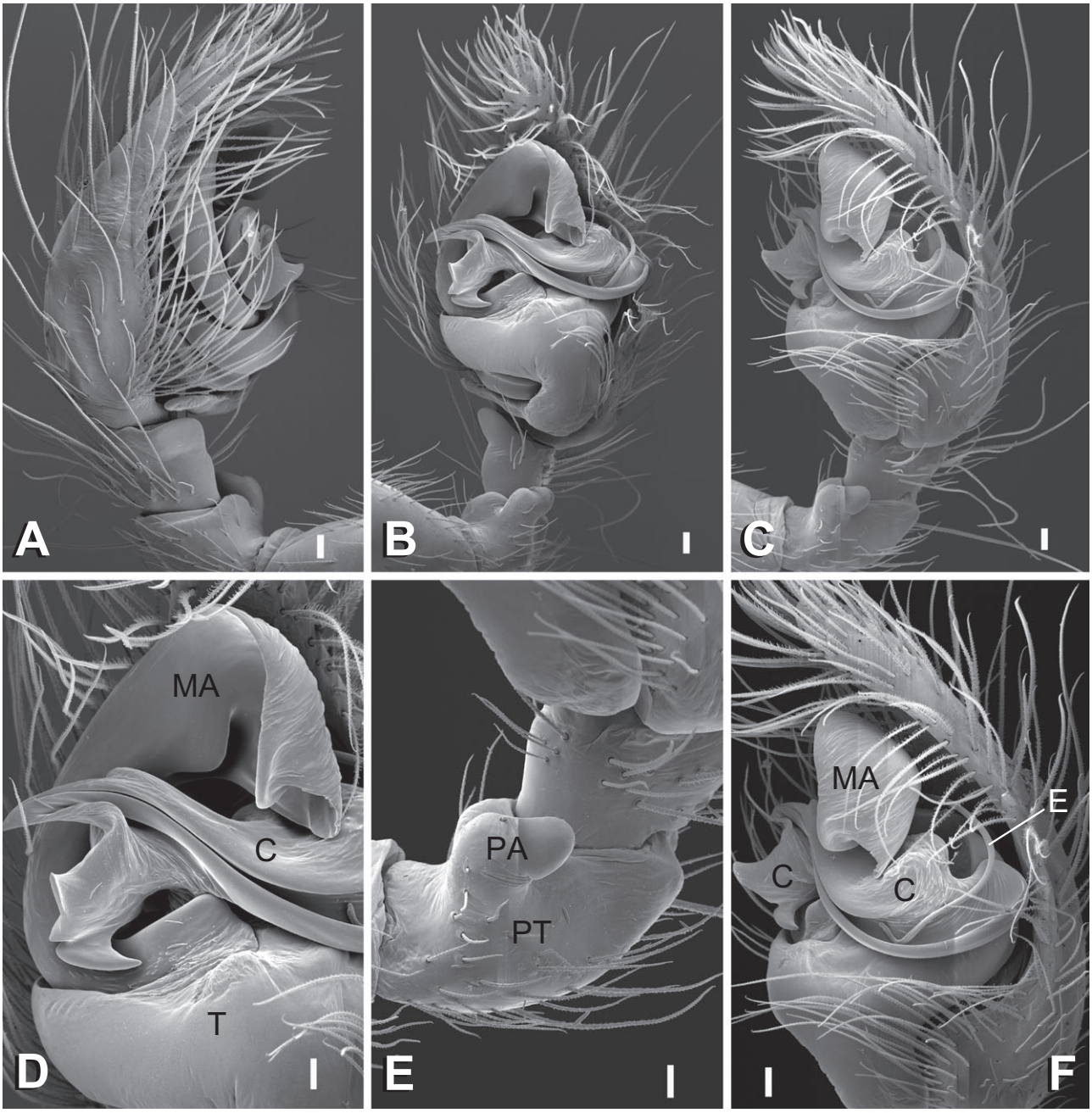

Figure 6. ***Onomastus kaharian*** **sp. nov.** from Central Kalimantan (RMNH). A, left male palp, prolateral view. B, D, ditto, ventral view. C, E, F, Ditto, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PA, patella apophysis; PT, patella; T, tibia. Scale bars = 20 μm (D, E), 30 μm (A, B, C, F).

quinquenotatus Simon, 1900, *O. rattotensis* sp. nov., and *O. simoni* Zabka, 1985.

Onomastus complexipalpis Wanless, 1980 (Figs 2A–H, 3A–B)

Holotype: 1♂ from Indonesia: Borneo, Santan, Kalimantan, 03.vii.1976. Leg. R. Thompson, BMNH 1979.7.4.1, examined.

Diagnosis: Onomastus complexipalpis is readily distinguished from all known species of *Onomastus* by the large palpal conductor in the males and the long coiled copulatory ducts in the females (Figs 2A–H, 3A–B).

Male from South Kalimantan: Total length: 3.9 mm; prosoma length: 1.8, width: 1.3. Leg I: femur 1.2, patella 0.5, tibia 1.3, metatarsus 1.0, tarsus 0.5.

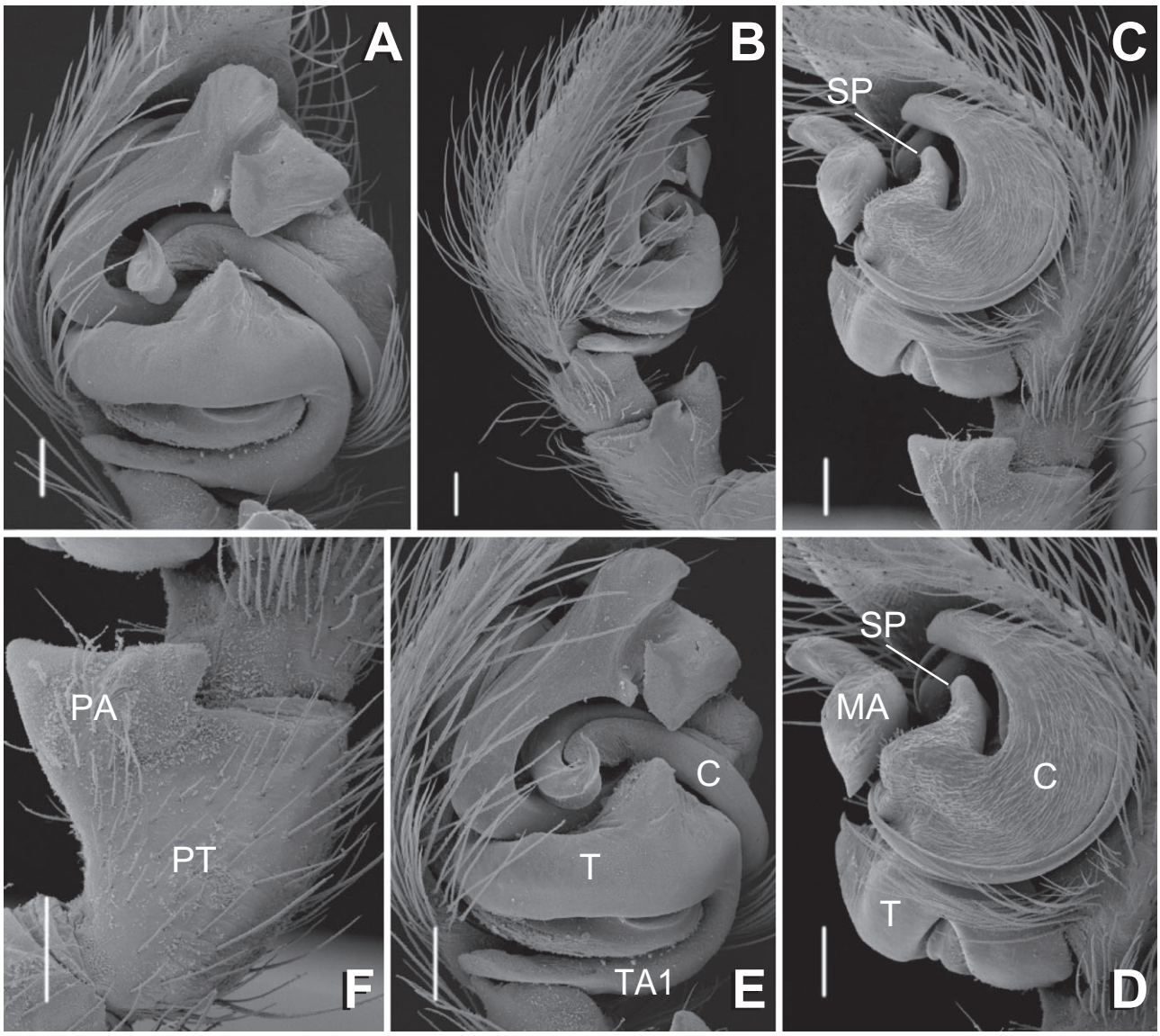

Figure 7. *Onomastus kanoi* from Okinawa Prefecture (USNM). A, E, left male palp, ventral view. B, ditto, prolateral view. C, D, ditto, retrolateral view. F, profile of PA, retrolateral view. Abbreviations: C, conductor; MA, median apophysis; PA, patella apophysis; PT, patella; SP, spur mesal branch of C; T, tibia; TA1, tegular apophysis 1. Scale bars = 100 μm.

Prosoma oval, almost as wide as long. Opisthosoma oval, longer than wide. All legs laterally without dark markings. All eyes except AME surrounded by dark rings. Chelicerae with pro- and retromarginal teeth, number not examined. Leg formula 4132. Leg spination: leg 1: metatarsus D 1-0-0, V 2-2-2; tibia D 1-1-0, V 2-2-2; femur D 1-1-2, P 0-0-1, R 0-0-1. Palps as in Figures 2A–H and 3A. A detailed description of the male is provided by Wanless (1980b).

Female from South Kalimantan: Total length: 3.3; prosoma length: 1.1, width: 0.9. Leg 1: femur 1.5, patella 0.5, tibia 1.4, metatarsus 1.0 tarsus 0.4. Morphology as above, except for the lighter coloured prosoma and opisthosoma. Leg formula 4132. Leg spination: leg 1: metatarsus V 2-1-2; tibia V 2-2-3; femur D 1-0-1, P 0-0-1, R 0-0-1. Epigynum and vulva as in Figure 3B.

Other material examined: Indonesia, Central Kalimantan, Kaharian, 20°2′S, 113°40′E. Swampy primary forest, in leaf litter, 2–16.ix.1985. Leg. Suharto Djojosudharmo. 1♂, 1♀; South Kalimantan, 40 km north-west of Palangkaraya, secondary forest, 1♂, 2♀ (right palp on a sputter-coated SEM stub). Deposited in RMNH.

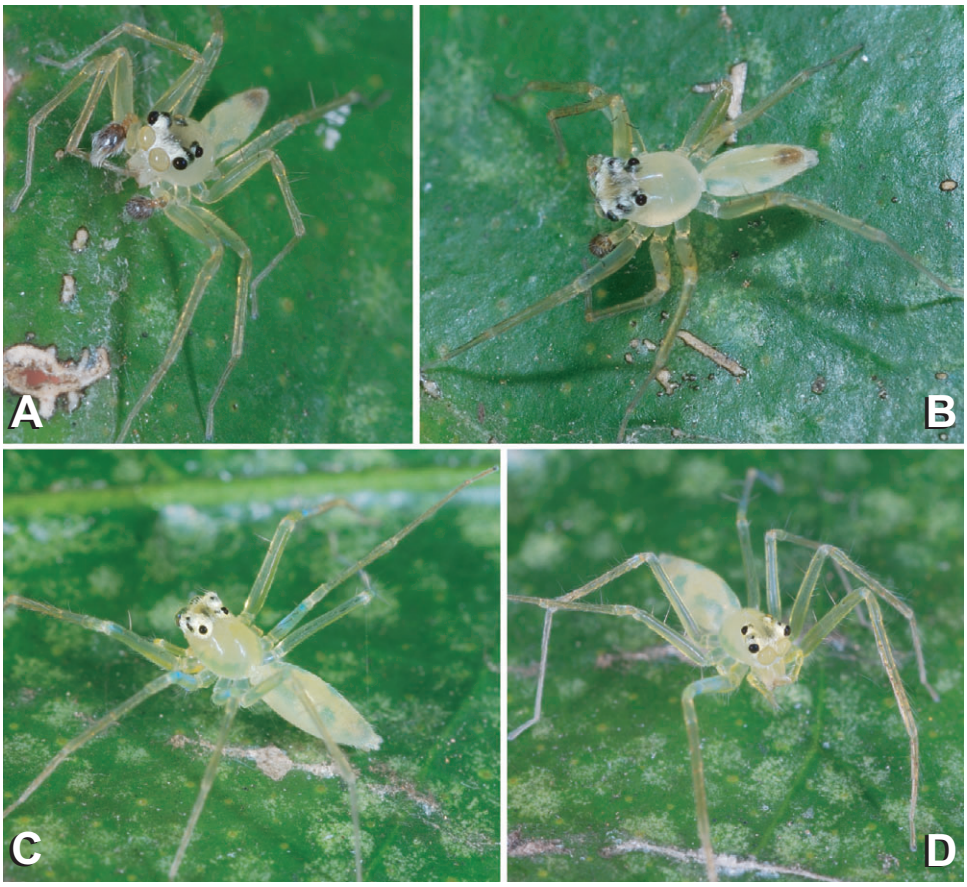

Figure 8. Photographs of live *Onomastus nigricauda* from Bodinagala, Sri Lanka (MHNG). A, B, male. C, D, female.

ONOMASTUS INDRA SP. NOV.
(FIG. 4A–E)

Holotype: ♂ from India, Kodaikanal, Grade, 1600 m, 30.iii.1962, leg. E. S. Ross and D. Q. Cavagnaro. Deposited in CAS.

Paratypes: 2♀ from the same locality as the holotype. Label data as above. Deposited in CAS.

Etymology: Indra is the deity of war in the Hindu religion. I use the species epithet as a noun in apposition.

Diagnosis: Separated from all other species except for *O. patellaris* by the occurrence of TA2 in males. Separated from *O. patellaris* by the shorter, stouter TA1 and TA2 (Fig. 4A, B); further, the end of TA2 is in the shape of an upward hook in *O. patellaris* (Fig. 17A).

Male holotype: Total length: 3.8; prosoma length: 2.0, width: 1.3. Leg I: femur 1.6, patella 0.3, tibia 0.8, metatarsus 0.7, tarsus 0.3. All spiders are whitish to pale yellow in alcohol, no markings. Prosoma oval, almost as wide as long, laterals darker. Opisthosoma oval, longer than wide, lighter in colour. Legs pale yellow, laterally without dark markings; might be a result of preservation. All eyes except AME surrounded by dark rings. Chelicerae with pro- and retromarginal teeth, number not examined. Leg formula 4132. Leg spination: leg 1: metatarsus V 2-1-2; tibia V 2-2-3; femur D 0-0-1, P 0-1-2. Palps as in Figure 4A and B.

Female paratype: Total length: 4.4; prosoma length: 2.0, width: 1.3. Leg 1: femur 1.6, patella 0.6, tibia 1.4, metatarsus 1.2, tarsus 0.6. Morphology as above, except for the lighter coloured prosoma and opisthosoma and leg spination given below. Leg spination: leg 1: metatarsus V 2-1-2; tibia V 3-2-2; femur D 1-1-1. Epigynum and vulva as in Figure 4C–E.

Other material examined: None.

ONOMASTUS KAHARIAN SP. NOV.
(FIGS 5A–E, 6A–F)

Holotype: ♂ from Indonesia, Central Kalimantan, Kaharian, 20°2′S, 113°40′E. Swampy primary forest,

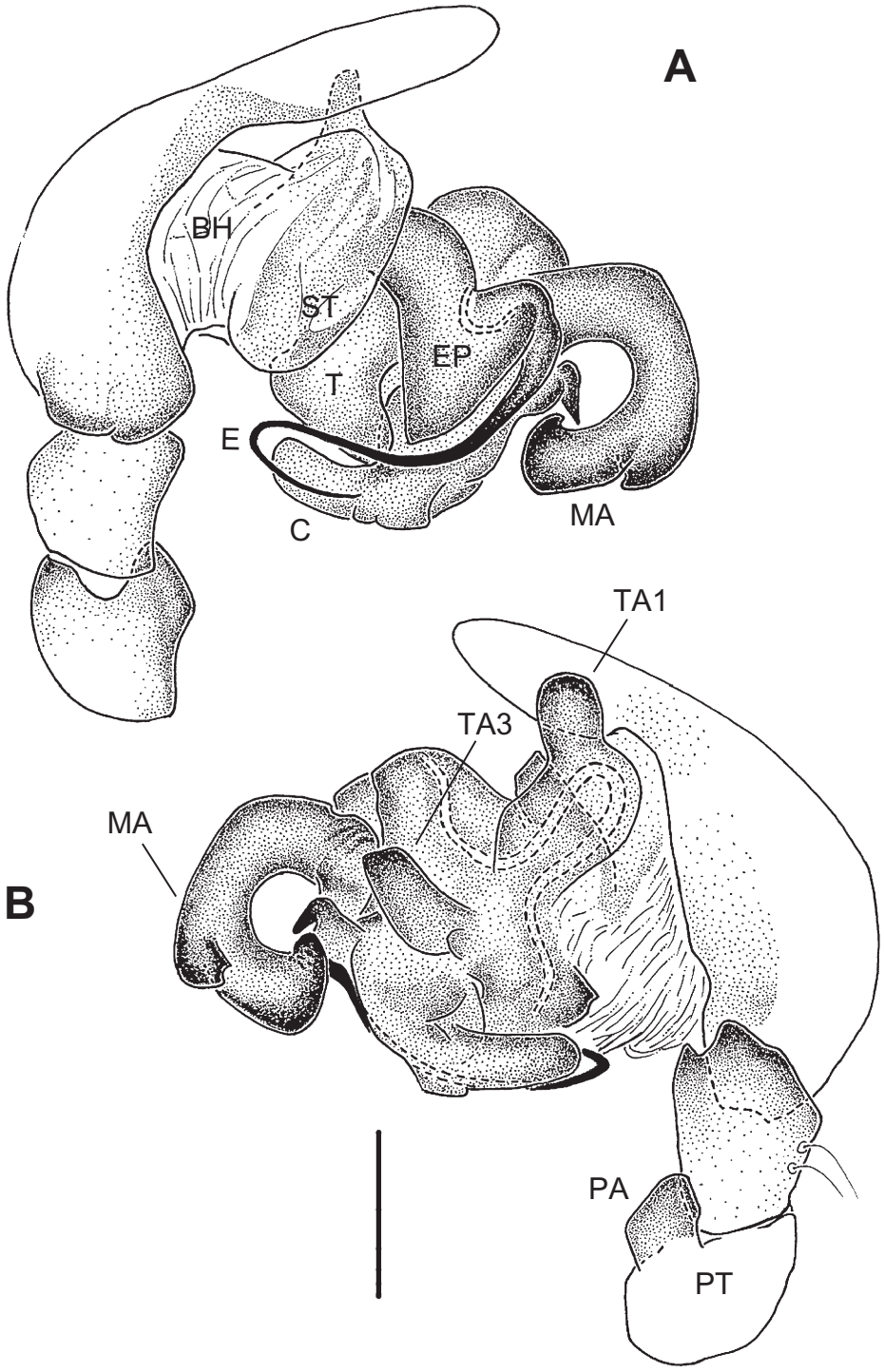

Figure 9. *Onomastus nigricauda* from Bodinagala (MHNG). A, expanded left male palp, prolateral view. B, ditto, retrolateral view. Abbreviations: BH, basal haematodocha; C, conductor; E, embolus; EP, embolic base; MA, median apophysis; PA, patella apophysis; PT, patella; ST, subtegulum; T, tibia; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bar = 0.2 mm.

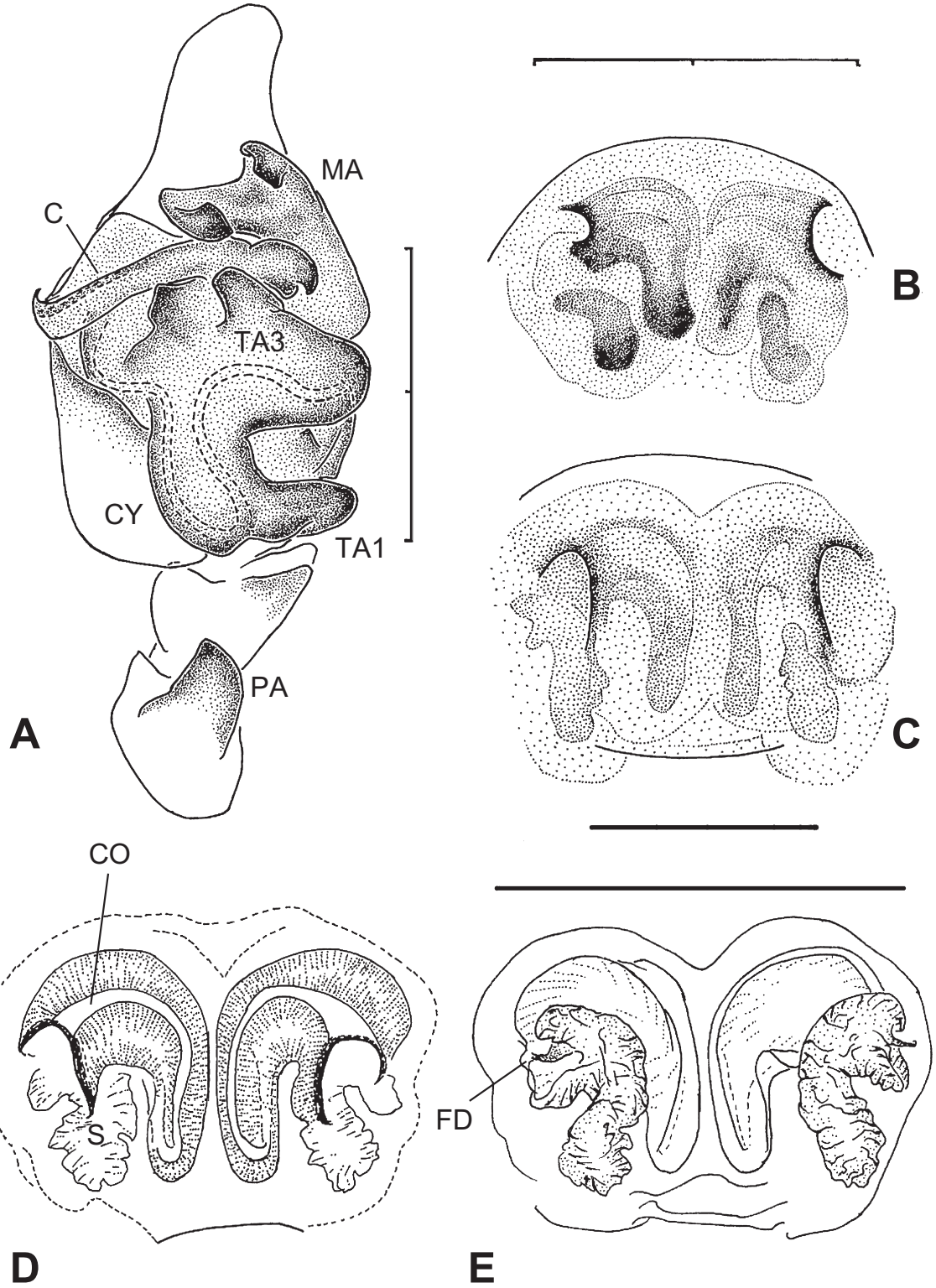

Figure 10. *Onomastus nigricauda*. A, male lectotype (MNHN 20404/1-3), right palp, ventral view. B, female (found in the same vial as the lectotype). C, female from Bodinagala, epigynum, ventral view. D, ditto, vulva, ventral view. E, ditto, dorsal view. Abbreviations: C, conductor; CO, copulatory opening; CY, cymbium; FD, fertilization duct; MA, median apophysis; PA, patella apophysis; S, spermatheca; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 0.1 mm (C), 0.2 mm (A, B, D, E).

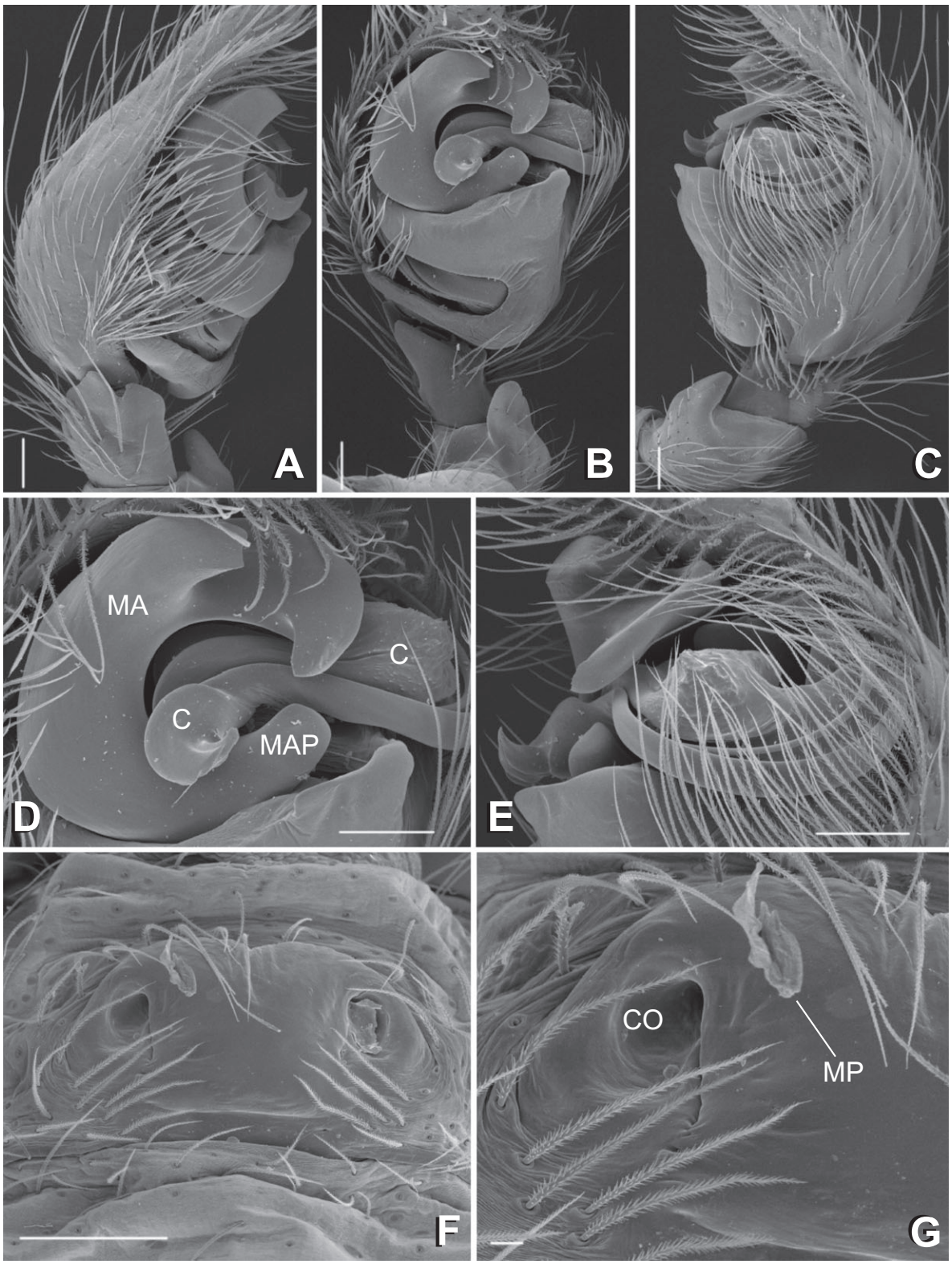

Figure 11. Scanning electron micrographs of *Onomastus nigricauda* from Bodinagala (MHNG). A, left male palp, prolateral view. B, D, ditto, ventral view. C, E, ditto, retrolateral view. F, G, epigynum, ventral view. Note the mating plug in F and G. Abbreviations: C, conductor; CO, copulatory opening; MA, median apophysis; MAP, mesal branch of MA; MP, mate plug. Scale bars = 10 μm (G), 100 μm (A–F).

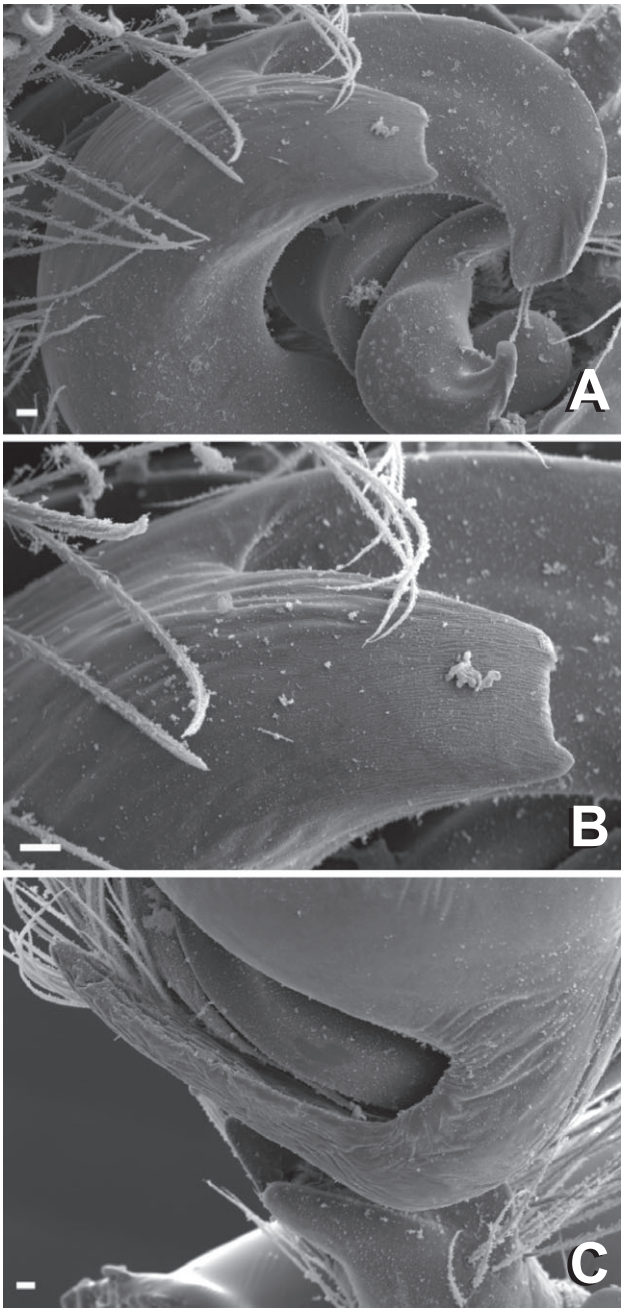

Figure 12. Scanning electron micrographs of *Onomastus nigricauda* from Bodinagala (MHNG). A, profile of MA. B, ditto, detail. C, profile of TA1. Scale bars = 5 μm (B), 10 μm (A, C).

in leaf litter, 2–16.ix.1985. Leg. Suharto Djojosudharmo. Deposited in RMNH.

Paratype: ♀ from Indonesia, locality and label data as above. Deposited in RMNH.

Etymology: The species name is a noun in apposition, taken from the type locality.

Diagnosis: Males are readily separated from *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. rattotensis*, *O. nigricauda*, *O. quinquenotatus*, and *O. pethiyagodai* by the presences of a broad conductor (Fig. 6D). Separated from *O. complexipalpis*, *O. kanoi*, and *O. nigrimaculatus* by the scoop-like MA and shape of C (Fig. 6D). Females could be separated from all other *Onomastus* by the presence of semicircular epigynal fold and C-shaped CD (Fig. 5D, E).

Remarks: Onomastus simoni appears to be closely related to *O. kaharian*. They may be separated from each other by the parallel course of CD in *O. simoni*.

Male holotype: Total length: 3.4; prosoma length: 1.5, width: 1.0. Leg I: femur 1.6, patella 0.5, tibia 1.7, metatarsus 1.1, tarsus 0.5. All spiders are whitish to pale yellow in alcohol, no markings. Prosoma oval, almost as wide as long, laterals darker. Opisthosoma oval, longer than wide, lighter in colour. Legs pale yellow, laterally without dark markings; might be a result of preservation. All eyes except AME surrounded by dark rings. Chelicerae with pro- and retromarginal teeth, number not examined. Leg formula 4132. Leg spination: leg 1: metatarsus V 2-1-2; tibia V 2-2-3; femur D 0-0-1, P 0-1-2. Palp as in Figures 5A, B and 6A–F.

Female paratype: Total length: 3.5; prosoma length: 1.4, width: 1.0. Leg 1: femur 1.4, patella 0.4, tibia 1.5, metatarsus 1.1, tarsus 0.4. Morphology as above, except for the lighter coloured prosoma, opisthosoma and leg spination given below. Leg spination: leg 1: metatarsus V 2-1-2; tibia V 3-2-2; femur D 1-1-1. Epigynum and vulva as in Figure 5C–E.

Distribution: Thailand and Indonesia.

Other material examined: Indonesia: Central Kalimantan, Kaharian, 20°2′S, 113°40′E. Swampy primary forest, in leaf litter, 2–16.ix.85, 2♂ (a single left palp on a sputter-coated SEM stub), 5♀, leg. Suharto Djojosudharmo, deposited in RMNH. Thailand: Nakhon Si Thammarat Prov. Khao Luang NP, 8°43′25.2″ N, 99°40′7.7″E, 355 m, 10–12.x.2003 (ATOL expedition 2003), 1♂ 1♀, deposited in USNM.

ONOMASTUS KANOI ONO, 1995 (FIG. 7A–E)

Diagnosis: Onomastus kanoi is readily distinguished from all known species of *Onomastus* except for *O. complexipalpis* by the large disk-shaped palpal conductor in the males (Fig. 7A–D). The conductor of *O. kanoi* is relatively smaller than that of *O. complexi-*

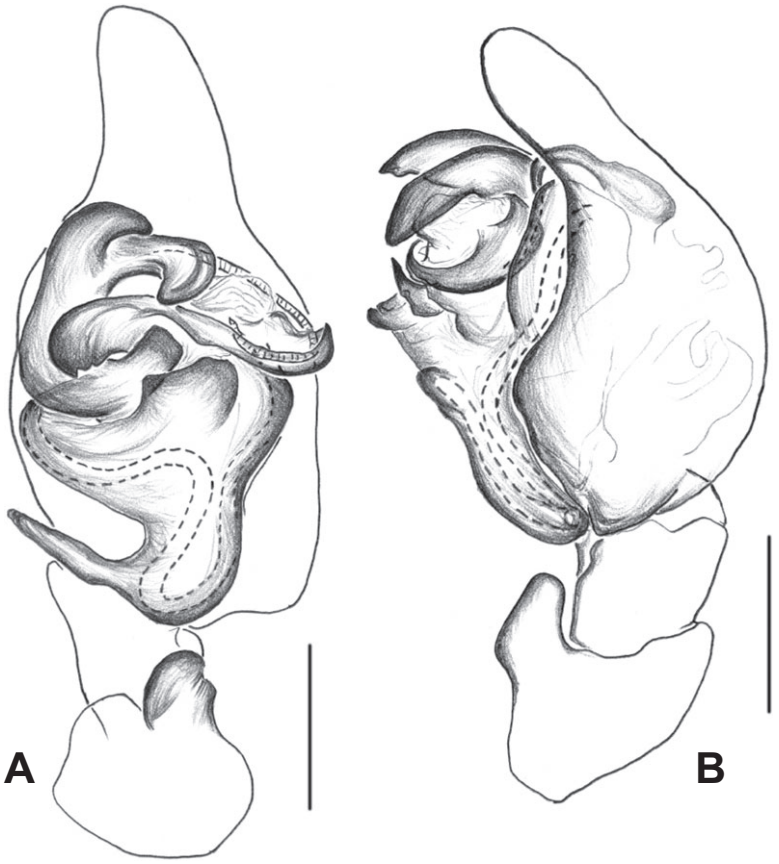

Figure 13. *Onomastus nigricauda* from Morningside (MHNG). A, left male palp, ventral view. B, ditto, retrolateral view. Scale bars = 0.2 mm.

palpis (Fig. 7D). The female of *O. kanoi* is unknown. However, I predict that the CD of *O. kanoi* females would be longer than that of all other *Onomastus*, but shorter than that of *O. complexipalpis*.

Male: Total length: 5.2; prosoma length: 2.0, width: 1.5. Leg I: femur 2.0, patella 0.6, tibia 2.0, metatarsus 2.0, tarsus 0.6. For a detailed description see Ono (1995).

Female: Unknown.

Distribution: Endemic to Okinawa Island of Japan.

Material examined: Japan, Okinawa Prefecture, Okinawajima Island, Kijoka. 01.iv.1997. 1♂; Japan, Okinawa Prefecture, Okinawajima Island, Zutsun. 01.iv.2000, 1♂. All leg. Akio Tanikawa.

ONOMASTUS NIGRICAUDA SIMON, 1900
(FIGS 8A–D, 9A–B, 10A–E, 11A–G, 12A–C, 13A–B)

Onomastus nigricauda Simon, 1900: 29. ♂ lectotype and 2♀ from Sri Lanka, Galle, in MNHN (20404/1-3), examined.

Onomastus nigricauda Simon, 1901: 400, fig. 398.

Onomastus nigricauda Wanless, 1980: 181, fig. 1A–G. Initial description of the female and designation of types.

Diagnosis: Males are readily separated from *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. complexipalpis*, *O. kanoi*, *O. kaharian*, and *O. nigrimaculatus* by the filiform conductor. Separated from *O. pethiyagodai* and *O. quinquenotatus* by the shape of the MA. *Onomastus nigricauda* seems to be most closely related to *O. rattotensis*, but may be separated by the large partly pleated MA in *O. rattotensis* (Figs 27A, 28A–C).

Male (from Bodinagala): Total length: 3.0; prosoma length: 1.5, width: 1.1. Leg I: femur 1.4, patella 0.4, tibia 1.5, metatarsus 0.9, tarsus 0.5. The spiders are green in nature. They turn whitish to pale yellow in alcohol. Prosoma oval, longer than wide. Opisthosoma longer than wide, lighter in colour. Leg I yellowish brown, leg II–IV light yellow. Legs are laterally without dark markings. All eyes except AME surrounded by dark rings. Chelicerae are

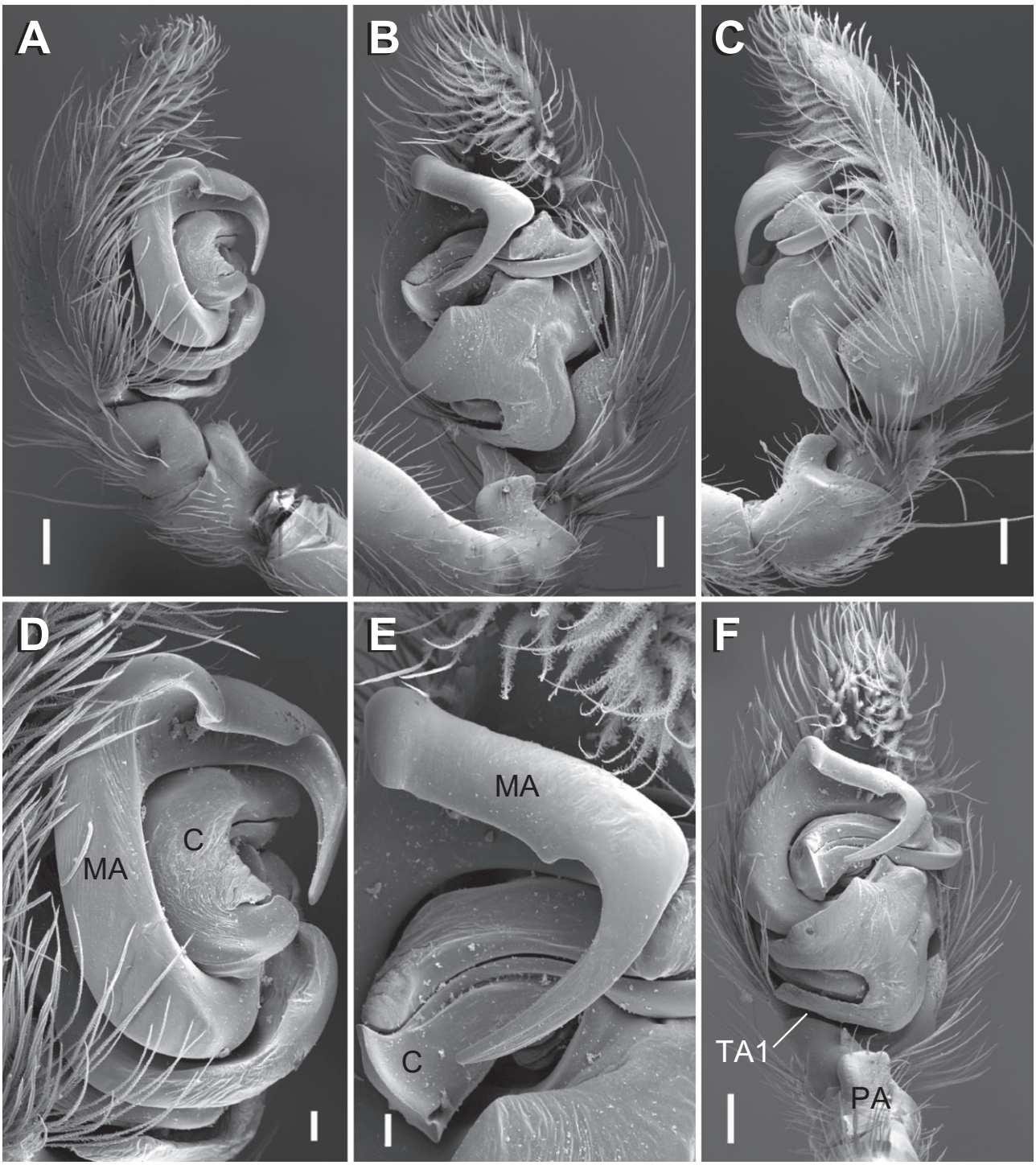

Figure 14. Scanning electron micrographs of *Onomastus nigrimaculatus* from Thailand (RMNH). A, D, left male palp, prolateral view. B, E, F, ditto, ventral view. C, ditto, retrolateral view. Abbreviations: C, conductor; MA, median apophysis; PA, patella apophysis; TA1, tegular apophysis 1. Scale bars = 10 μm (E), 30 μm (D), 100 μm (A–C, F).

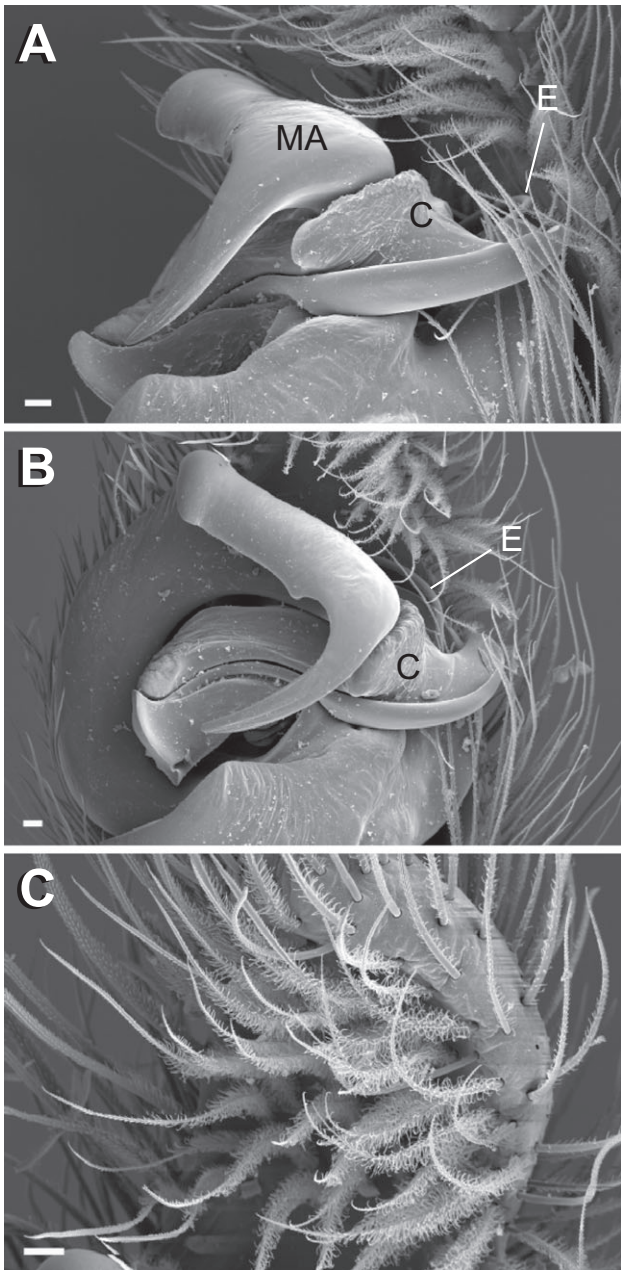

Figure 15. Scanning electron micrographs of *Onomastus nigrimaculatus* from Thailand (RMNH). A, profile of MA and C, retrolateral view. B, ditto, retrolateral-apical view. C, serrated setae of the cymbium, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis. Scale bars = 10 μm.

yellow, with seven retromarginal and three promarginal teeth. Leg formula 1432. Leg spination, metatarsus D 1-0-0, V 2-2-2; tibia D 0-0-1, P 1-0-0, V 4-4-2, R 1-0-0; patella D 0-1-0; femur D 2-1-0, P 0-0-1, R 0-0-1. Palp: (Figs 9A–B, 10C, 11A–E, 12A–C, 13A–B). Tegulum as in Figure 9A, projecting outwards, path of sperm duct with two loops as in Figure 9A and B, embolus as in Figure 9A. A detailed description of the male lectotype is also provided by Wanless (1980b).

Female (from Bodinagala): Total length: 4.0; prosoma length: 1.5, width: 1.2. Leg 1: femur 1.4, patella 0.5, tibia 1.5, metatarsus 1.1, tarsus 0.5. Morphology as above, except for the lighter coloured prosoma and opisthosoma. Leg spination, metatarsus V 4-2-2, P 1-0-0, R 1-0-0; tibia D 1-1-0, V 4-4-2; patella P 1-0-0, R 1-0-0; femur D 1-1-1, P 0-0-1, R 0-0-1. Epigynum and vulva as in Figures 10B–E and 11F–G. A detailed description of the female is provided by Wanless (1980b).

Variation: The male specimen from Morningside has a bifurcate MA in which both branches taper towards the end. Live male spiders of *O. nigricauda* from Bodinagala tend to also have a much darker palp than that of Morningside.

Distribution: Endemic to Sri Lanka; Bodinagala forest reserve is a remaining fragment of the once vast rain forest that covered the south-west of the island. It is not far from the type locality, Galle.

Other material examined: SRI LANKA: Western province, Kalutara district, Horane, Bodinagala, 19.vii.1996, 1♂ 2♀, leg. Suresh. P. Benjamin. Same locality, 10.ii.2007, 5♂ 6♀, leg. Suresh. P. Benjamin and Ziyard Jaleel. Sabaragamuwa province, Ratnapura District, Morningside section. In primary forest, 23.ii.2007, 1♂, leg. Suresh P. Benjamin and Ziyard Jaleel. All specimens deposited in MHNG.

ONOMASTUS NIGRIMACULATUS ZHANG & LI, 2005 (FIGS 14A–F, 15A–B, 16A–E)

Holotype: Male from China, Mingfeng Valley, Jianfengling National Park, Hainan Province. Deposited in the Raffles Museum of Biodiversity Research (ZRC-ARA-494). As this species was adequately illustrated in its original description, I have not examined any type material.

Diagnosis: Males of *O. nigrimaculatus* are readily separated from those of *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. rattotensis*, *O. nigricauda*, *O. quinquenotatus*, and *O. pethiyagodai* by the presence of a broad conductor and chisel-shaped MA. Separated from *O. complexipalpis*, *O. kanoi*, and *O. kaharian* by the chisel-shaped MA and details of C. Female *O. nigrimaculatus* could be separated from all other *Onomastus* by the combined presence of C-shaped epigynal fold and lack of CD.

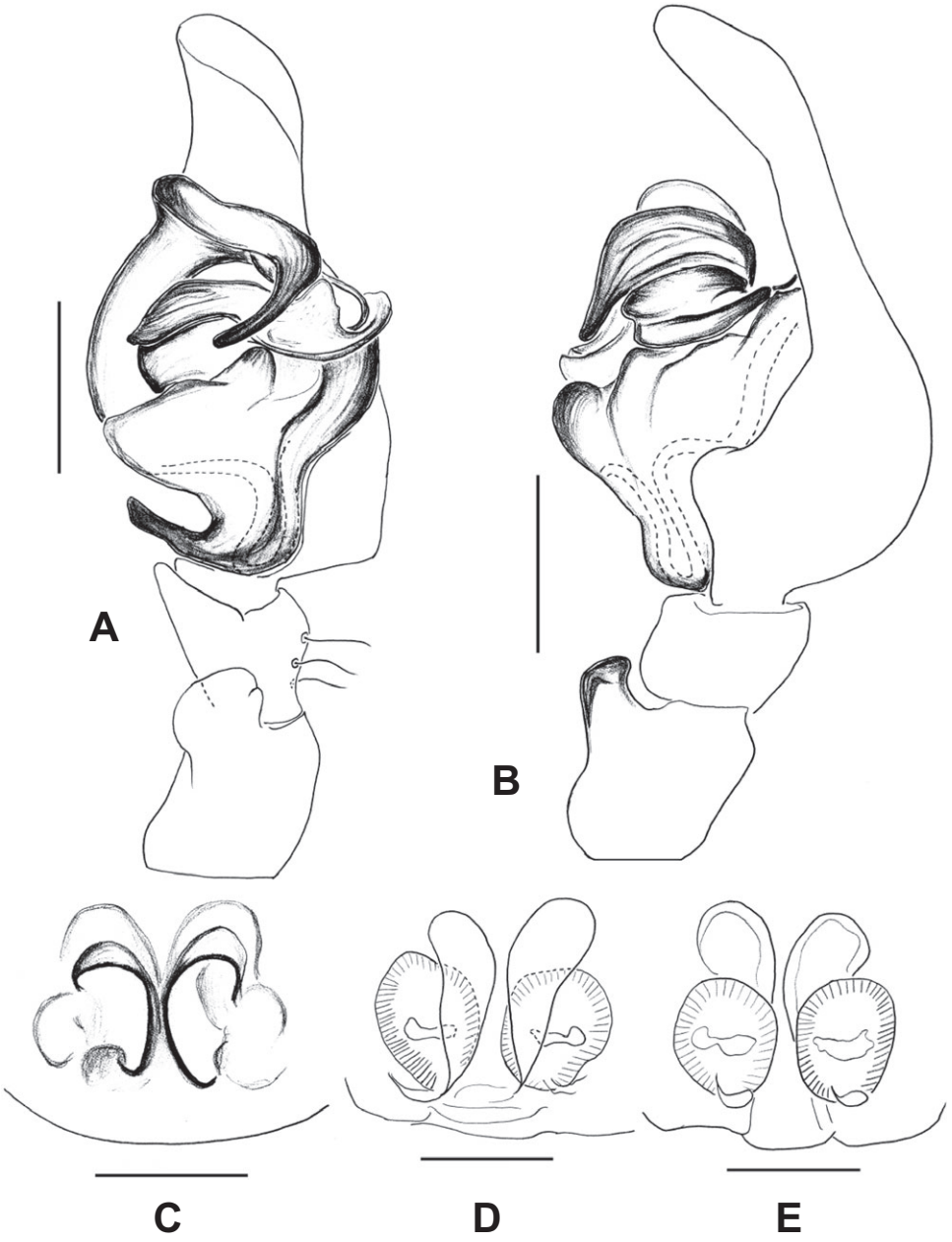

Figure 16. *Onomastus nigrimaculatus* from Thailand (RMNH). A, left male palp, ventral view. B, ditto, retrolateral view. C, female from the same locality, epigynum, ventral view. D, ditto, vulva, ventral view. E, ditto, dorsal view. Scale bars = 0.2 mm (C–E), 0.5 mm (A, B).

Male: Total length: 4.0; prosoma length: 1.8, width: 1.3. Leg I: femur 1.4, patella 0.5, tibia 1.7, metatarsus 1.4, tarsus 0.8. Prosoma oval, almost as wide as long, laterals with a faint black border. Opisthosoma oval, longer than wide, lighter in colour, four to six dark black spots on dorsum. Legs light yellow, leg 1 laterally with dark black spots, legs II–IV do not have similar spots. All eyes except AME surrounded by dark rings. Chelicerae with pro- and retromarginal teeth, number not examined. Leg formula 4132. Leg spination: leg 1: metatarsus D 1-0-0, V 2-2-2; tibia D 1-0-1, V 2-4-2, P 1-0-0, R 1-0-0; patella D 1-0-0, V 1-0-0; femur D 1-1-2, P 0-0-1, R 0-0-1. Palp as in Figures 14A–F, 15A–C, 16A–B.

Female: Total length: 5.0; prosoma length: 2.2, width: 1.5. Leg 1: femur 2.0, patella 0.7, tibia 2.4, metatarsus 1.5, tarsus 0.6. Morphology as above. Leg formula 4132. Leg spination: leg 1: metatarsus V 2-2-2, P

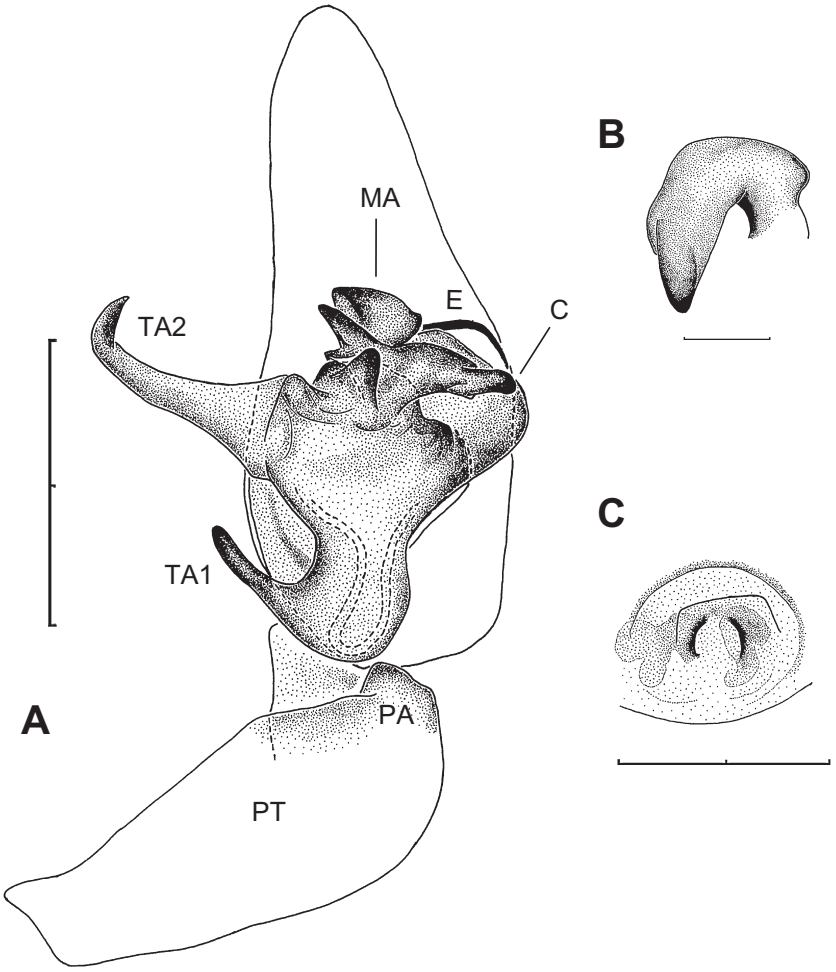

Figure 17. *Onomastus patellaris* from Kodaikanal, India (MNHN 14858). A, left male palp, ventral view. B, MA, ventral view. C, epigynum, ventral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PA, patella apophysis; PT, patella; TA1, tegular apophysis 1; TA2, tegular apophysis 2. Scale bars = 0.1 mm (B), 0.2 mm (C) 0.4 mm (A).

1-0-0, R 1-0-0; tibia D 1-0-0, V 2-2-2; Patella D 1-0-0, P 0-1-0, R 0-1-0. Epigynum and vulva as in Figure 16C–E.

Distribution: Hainan province, China (Zhang & Li, 2005) and primary rain forest of the Khao Yai National Park, Thailand.

Other material examined: Thailand, Khao Yai N.P, 3–7.iii.1986, leg. CL and PR Deeleman, 4♂. Same locality as above, 23.x.1985, leg. PR Deeleman, 4♀. Same locality, 5.x.1987, leg. CL and PR Deeleman, 1♂ 1♀. Same locality, 19–24.x.1985, leg. CL and PR Deelema, 4♀. All specimens deposited in RMNH.

ONOMASTUS PATELLARIS SIMON, 1900 (FIG. 17A–C)

Onomastus patellaris Simon, 1900: 29.

Lectotype: Single male from India, Kodaikanal, MNHN 14858, examined.

Diagnosis: Separated from all other species of *Onomastus* except *O. indra* by the presence of TA2 in male palps (Fig. 17A). TA1 and TA2 in *O. patellaris* are filiform. Further, the end of TA2 is in the shape of an upward hook in *O. patellaris* (Fig. 17A).

Description: See Wanless (1980b).

Distribution: India, Madras, Kodaikanal. Probably endemic to India.

Other material examined: Four ♀ from India, Trichinopoly, leg. R. P. Malat, MNHN 14898.

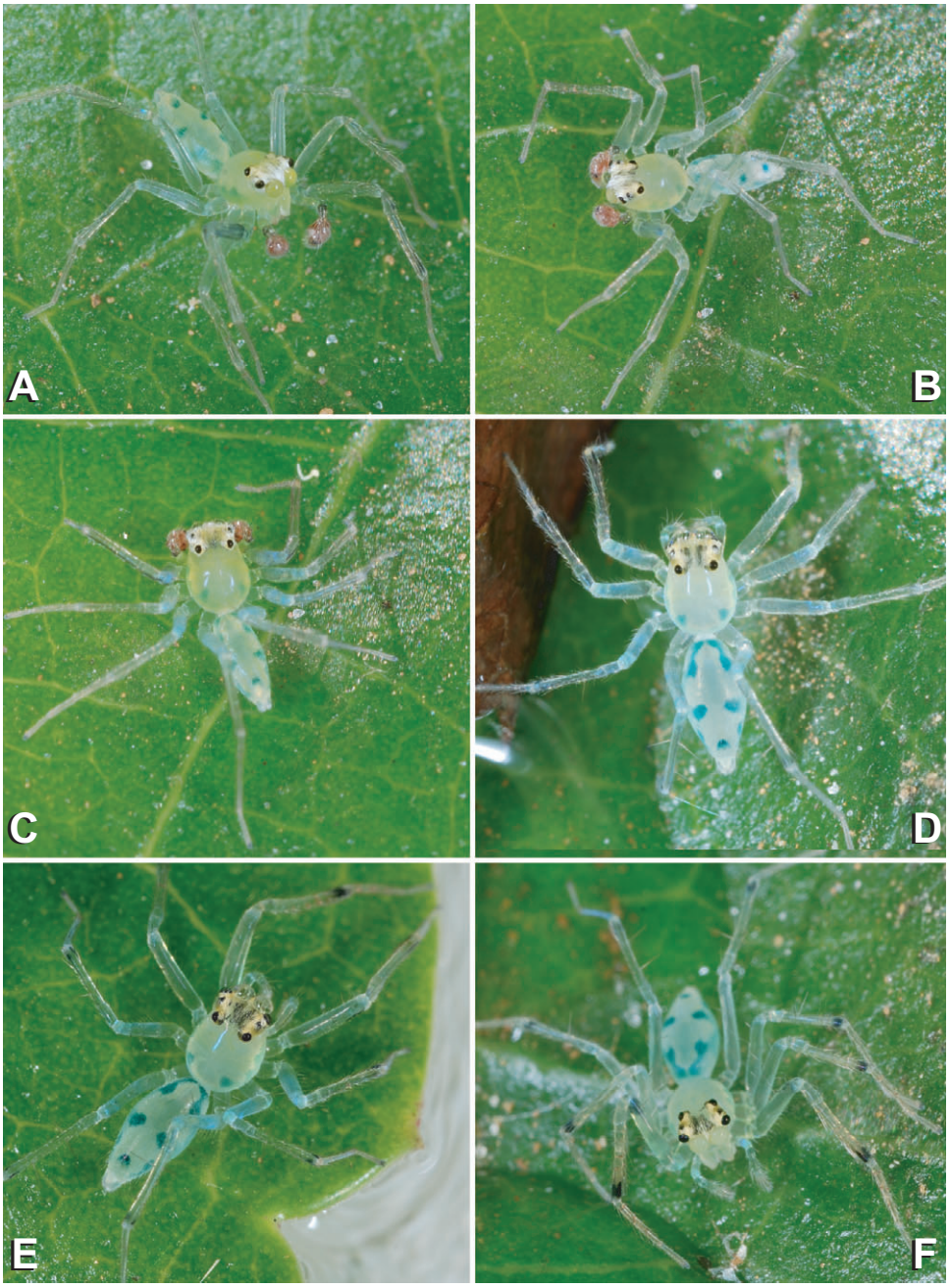

Figure 18. Photographs of live ***Onomastus pethiyagodai* sp. nov.** from Agrapathana, Sri Lanka (MHNG). A–C, male. D–F, female.

ONOMASTUS PETHIYAGODAI SP. NOV.

(FIGS 18A–F, 19A–F, 20A–E, 21A–D, 22A–B)

Holotype: 1♂, Sri Lanka: Central Province, Nuwara Eliya District, Agrapathana, Agrabopath forest, 1100 m, 08.iii.2000. Deposited in MHNG.

Paratype: 3♀, label data as above. Deposited in MHNG.

Diagnosis: Males of *O. pethiyagodai* are readily separated from that of *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. complexipalpis*, *O. kanoi*, *O. kaharian*, and *O. nigrimaculatus* by the presence of a filiform conductor. *O. pethiyagodai* is most closely related to *O. quinquenotatus*, and may be separated by the shape of the conductor and MA (Figs 19E, 20D, 22A). Females are difficult to diagnose, but may be separated by details of internal genitalia.

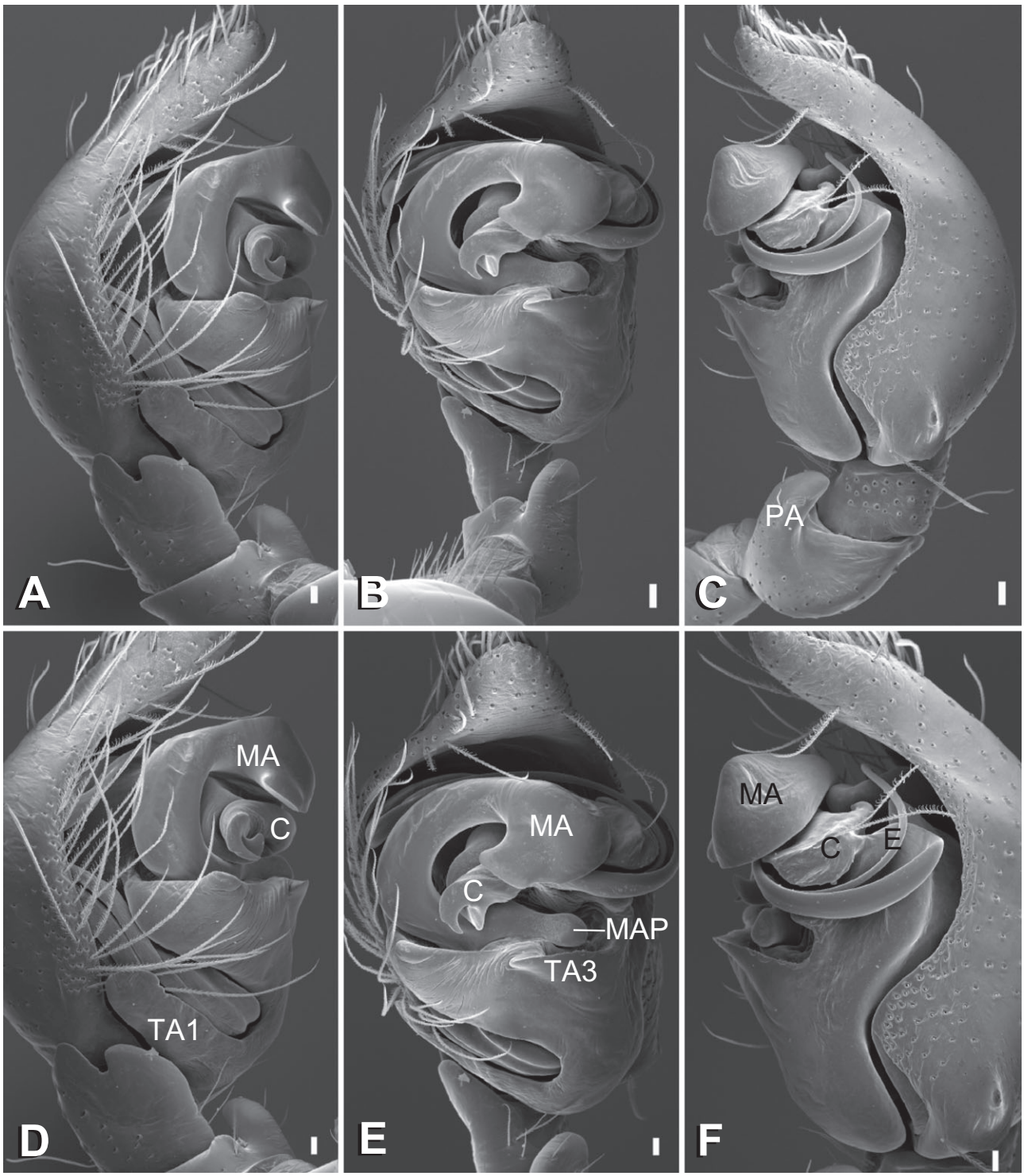

Figure 19. Scanning electron micrographs of ***Onomastus pethiyagodai* sp. nov.** from Agrapathana, Sri Lanka (MHNG). A, D, left male palp, prolateral view. B, E, ditto, ventral view. C, F, ditto, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; MAP, mesal branch of MA; PA, patella apophysis; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 20 μm (A, D, E, F), 30 μm (B, C).

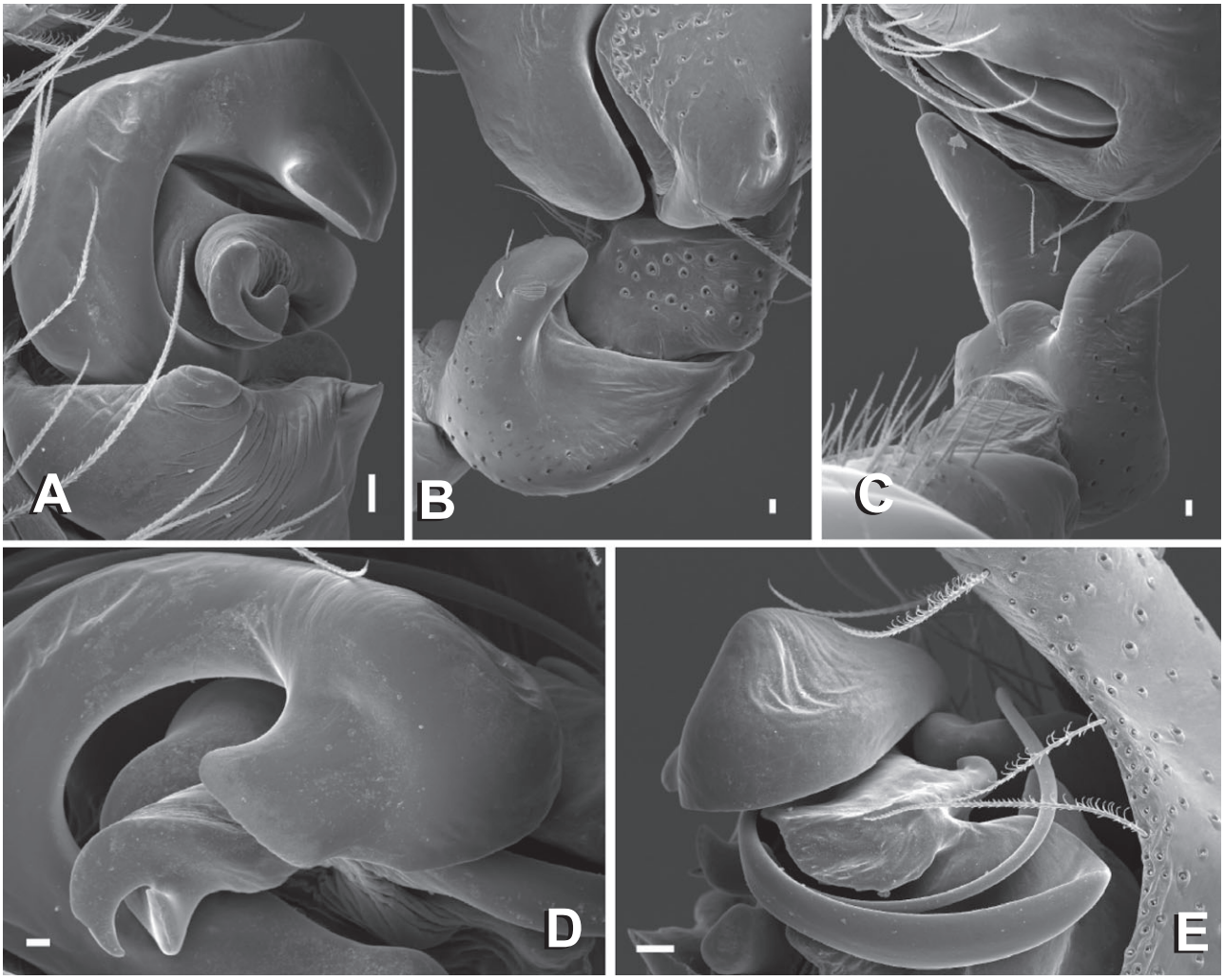

Figure 20. Scanning electron micrographs of ***Onomastus pethiyagodai*** **sp. nov.** from Agrapathana, Sri Lanka (MHNG). A, MA, prolateral view. B, PA, retrolateral view. C, ditto, ventral view. D, MA, ventral view. E, C and E prolateral view. Scale bars = 10 μm (B, C, D), 20 μm (A, E).

Male holotype: Total length: 2.9; prosoma length: 1.5, width: 1.1. Leg I: femur 1.4, patella 0.2, tibia 1.2, metatarsus 1.0, tarsus 0.4. The spiders are green in nature. They turn whitish to pale yellow in alcohol. Prosoma oval, longer than wide. Opisthosoma longer than wide, lighter in colour. Leg I yellowish brown, leg II–IV light yellow. Legs are laterally marked with dark black blobs. All eyes except AME surrounded by dark rings. Chelicerae with pro- and retromarginal teeth, number not examined. Leg formula 4132. Leg spination: metatarsus V 4-2-2; tibia P 1-0-0, V 2-4-2, R 1-0-0; patella V 2-0-0; femur D 0-1-1, P 0-0-1, R 0-0-1. Palp as in Figures 19A–F, 20A–E, 22A–B.

Female paratype: Total length: 2.9; prosoma length: 1.2, width: 1.1. Leg 1: femur 1.0, patella 0.3, tibia 1.0, metatarsus 0.8, tarsus 0.4. Morphology similar to the male except for the following. Prosoma and opisthosoma lighter in colour. Legs with lateral black blobs. Leg spination: metatarsus V 2-2-2; tibia P 1-0-0, V 2-4-4, R 1-0-0; patella P 1-0-0, R 1-0-0; femur D 0-2-1, P 0-0-1, R 0-0-1. Epigynum and vulva as in Figure 21A–D.

Distribution: Endemic to the central highlands of Sri Lanka. Known from Agrapathana, Agrabopath forest and Horton Plains National Park.

Other material examined: SRI LANKA: Central Province, Nuwara Eliya District, Agrapathana, Agrabopath forest, 1100 m, 07.iii.2000, 1♂ 2♀; 1–30.vi.2003, 7♂ 7♀ (a single left palp on a sputter-coated SEM stub), all leg. Suresh P. Benjamin. Same locality, 08.iii.2000, 1♂ leg. Sudath Nanayakkara. Same local-

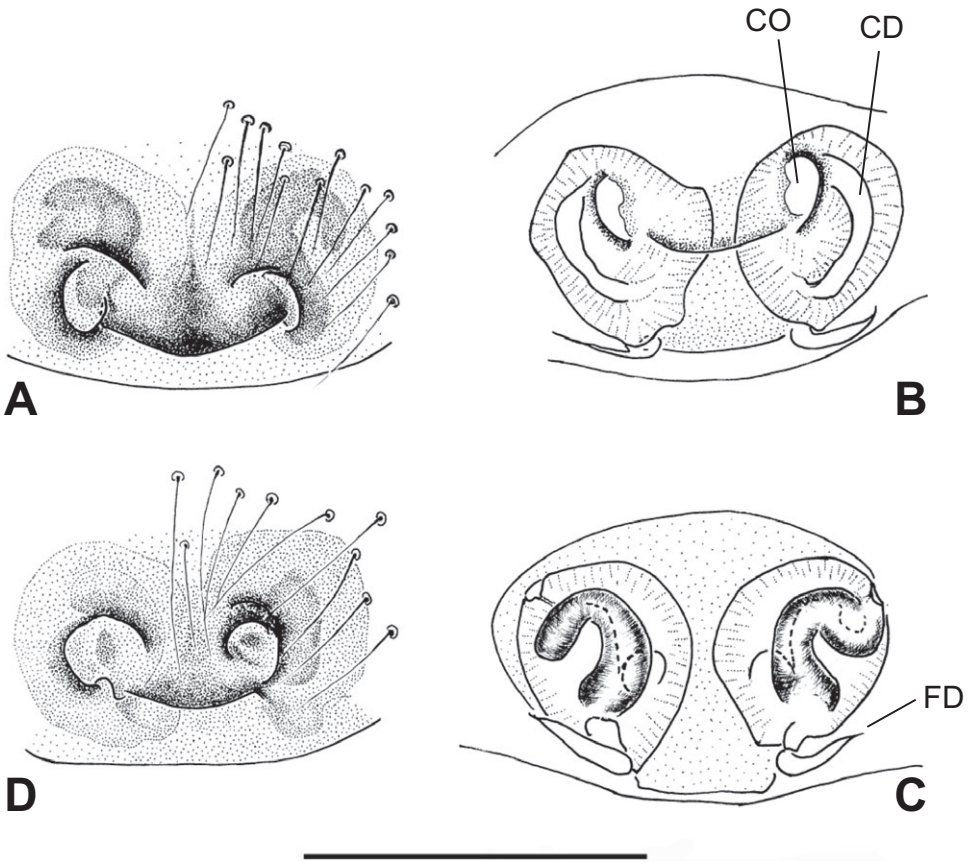

Figure 21. ***Onomastus pethiyagodai*** **sp. nov.** from Agrapathana, Sri Lanka. A, D, epigynum, ventral view. B, vulva, ventral view. C, ditto, dorsal view. Abbreviations: CD, copulatory duct; CO, copulatory opening; FD, fertilization duct. Scale bars = 0.2 mm.

ity, 18–21.ii.2007, 3♂ 2♀, leg. Suresh P. Benjamin and Ziyard Jaleel. Central Province, Nuwara Eliya District, Horton Plains National Park, *c*. 2000 m, 20–21.ii.2007, 15♂ 5♀, leg. Suresh P. Benjamin and Ziyard Jaleel. Deposited in MHNG.

ONOMASTUS QUINQUENOTATUS SIMON, 1900 (FIGS 23A–D, 24A–D, 25A–H)

Onomastus quinquenotatus Simon, 1900: 29. 2♀ from Sri Lanka in MNHN 20771, examined.

O. quinquenotatus Wanless, 1980: 183, fig. 2a–e. Designation of lectotype and paralectotype.

Diagnosis: Males are readily separated from *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. complexipalpis*, *O. kanoi*, *O. kaharian*, and *O. nigrimaculatus* by the filiform conductor. Separated from *O. pethiyagodai* and *O. nigricauda* by the shape of the MA (Fig. 23B). *Onomastus quinquenotatus* is most closely related to *O. pethiyagodai* and they may be separated from each other by the shape of the conductor and MA (Fig. 23A–D). Females are difficult to diagnose, but may be separated by details of the internal genitalia.

Male from Kandaela: Total length: 3.1; prosoma length: 1.6, width: 1.3. Legs I: femur 1.6, patella 0.5, tibia 1.5, metatarsus 1.3, tarsus 0.6. Prosoma round to oval, longer than wide, pale amber to light yellow. Eyes with black surrounds except for AME. Opisthosoma oval, longer than wide, lighter in colour, no markings. Living specimens green in colour. Leg 1 posterior laterally black along its length, all other legs uniformly yellow. Chelicerae light yellow, with seven retromarginal and three promarginal teeth. Spider ventrally light yellow. Leg formula 4132. Leg spination: metatarsus V 4-2-2; tibia D 2-0-0, V 2-4-4; patella D 1-0-0; femur D 0-2-2. Palp as in Figures 23A–D, 25A–H.

Female from Kandaela: Total length: 2.2; prosoma length: 1.8, width: 1.3. Leg 1: femur 1.4, patella 0.5,

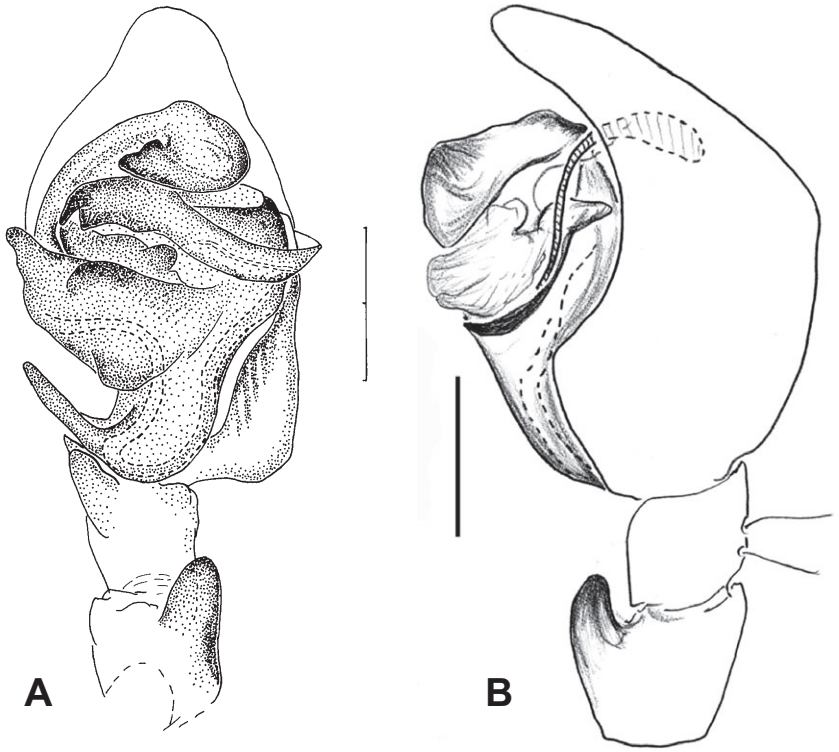

Figure 22. ***Onomastus pethiyagodai*** **sp. nov.** from Agrapathana, Sri Lanka (MHNG). A, left male palp, ventral view. B, ditto, retrolateral view. Scale bar = 0.2 mm.

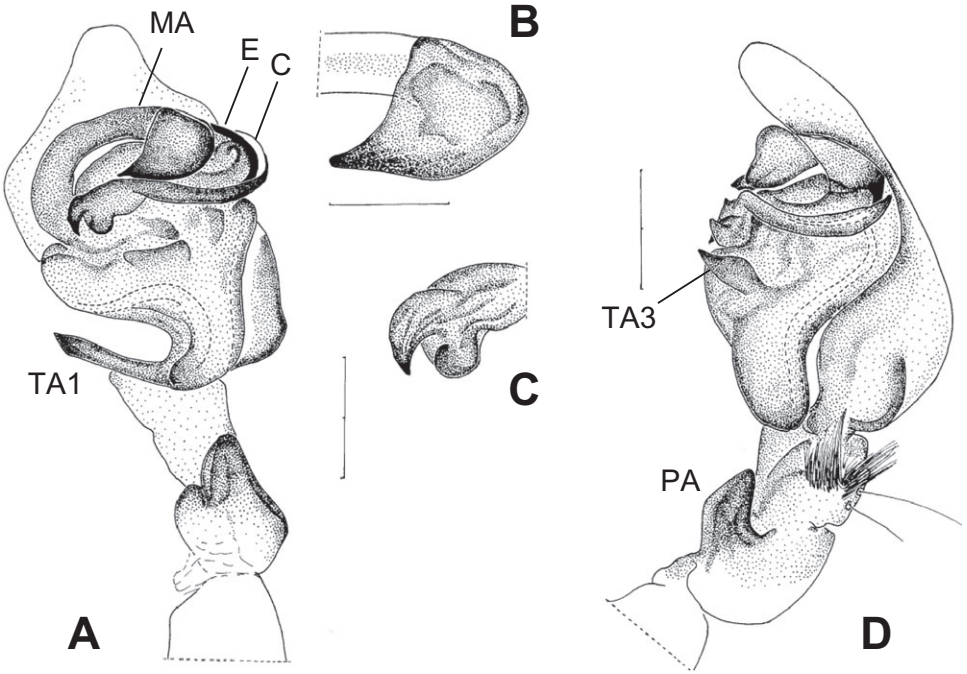

Figure 23. *Onomastus quinquenotatus*, male from Hakgala, Sri Lanka (MHNG). A, left male palp, ventral view. B, profile of MA. C, profile of C. D, left male palp, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PA, patella apophysis; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 0.1 mm (B, C), 0.2 mm (A, D).

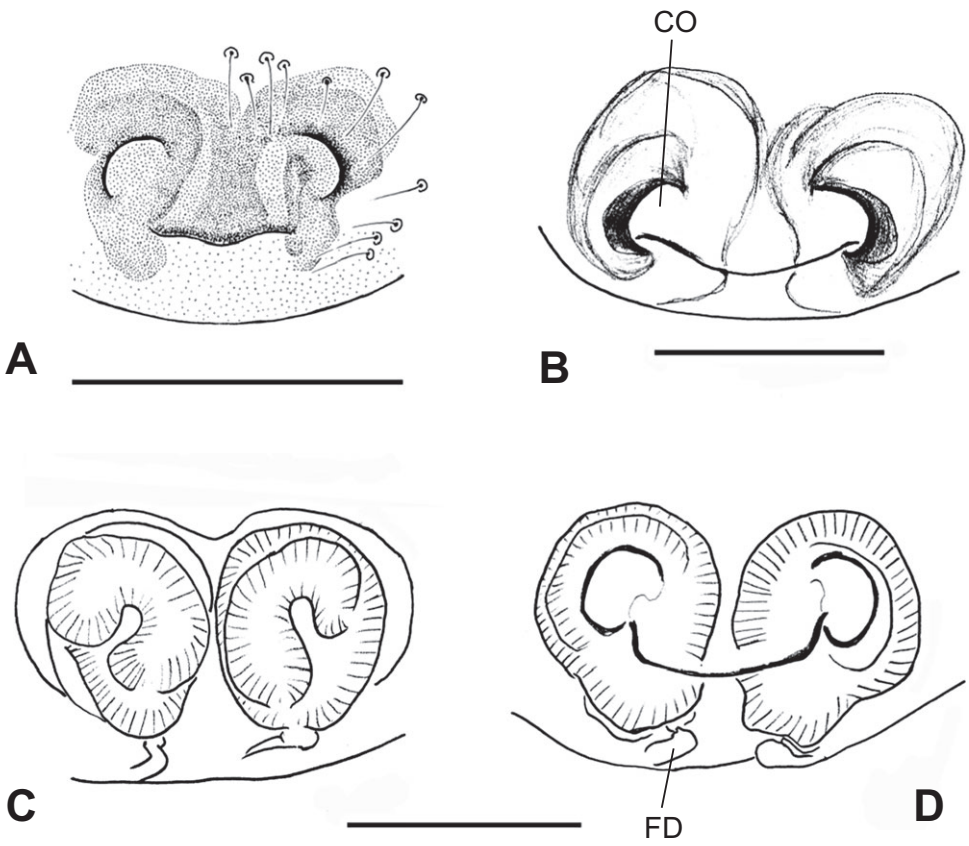

Figure 24. *Onomastus quinquenotatus*. A, female lectotype (MNHN 20771), epigynum, ventral view. B, female from Kandaela, Sri Lanka (USNM), epigynum, ventral view. C, vulva, ventral view. D, ditto, ventral view. Abbreviations: CO, copulatory opening; FD, fertilization duct. Scale bars = 0.2 mm.

tibia 1.6, metatarsus 1.3, tarsus 0.5. Morphology similar to the male except for the following: prosoma and opisthosoma lighter in colour; legs with lateral black blobs. Leg spination: metatarsus V 4-2-2; tibia V 2-2-2; femur D 0-1-2. Epigynum and vulva as in Figure 24A–D.

Distribution: Known from two localities, Kandaela and Hakgala, in the central highlands of Sri Lanka. The type locality in the labels is given as Sri Lanka (Simon, 1900). The exact locality of the lectotypes in Sri Lanka is unclear. *Onomastus quinquenotatus* is endemic to Sri Lanka.

Other material examined: SRI LANKA: Central province, north-east district, Kandaela reservoir, 5.6 miles south-west of Nuwara Eliya, 2000 m 10–21.ii.1970, 1♂ 1♀, leg. Davis and Rowe, deposited in USNM; Hakgala, Hakgala forest, 27.vii.1996, 1600 m, ♂, leg. Suresh P. Benjamin. Deposited in MHNG.

ONOMASTUS RATTOTENSIS SP. NOV.

(FIGS 26A–D, 27A–E, 28A–G)

Holotype: ♂ from Sri Lanka. Central Province, Knuckles range, along Rattota-Ilukkumbura Road, 900 m, 03–04.ix.2003, leg. Suresh P. Benjamin. Deposited in MHNG.

Paratype: ♀ from Sri Lanka. Data as above. Deposited in MHNG.

Etymology: Adjective, 'from Rattota', after the type locality.

Diagnosis: Males of *O. rattotensis* are readily separated from those of *O. patellaris* and *O. indra* by the absence of TA2. Separated from *O. complexipalpis*, *O. kanoi*, *O. kaharian*, and *O. nigrimaculatus* by the filiform conductor. Separated from *O. pethiyagodai* and *O. quinquenotatus* by the shape of the MA. Separated from *O. nigricauda* by the presence of a

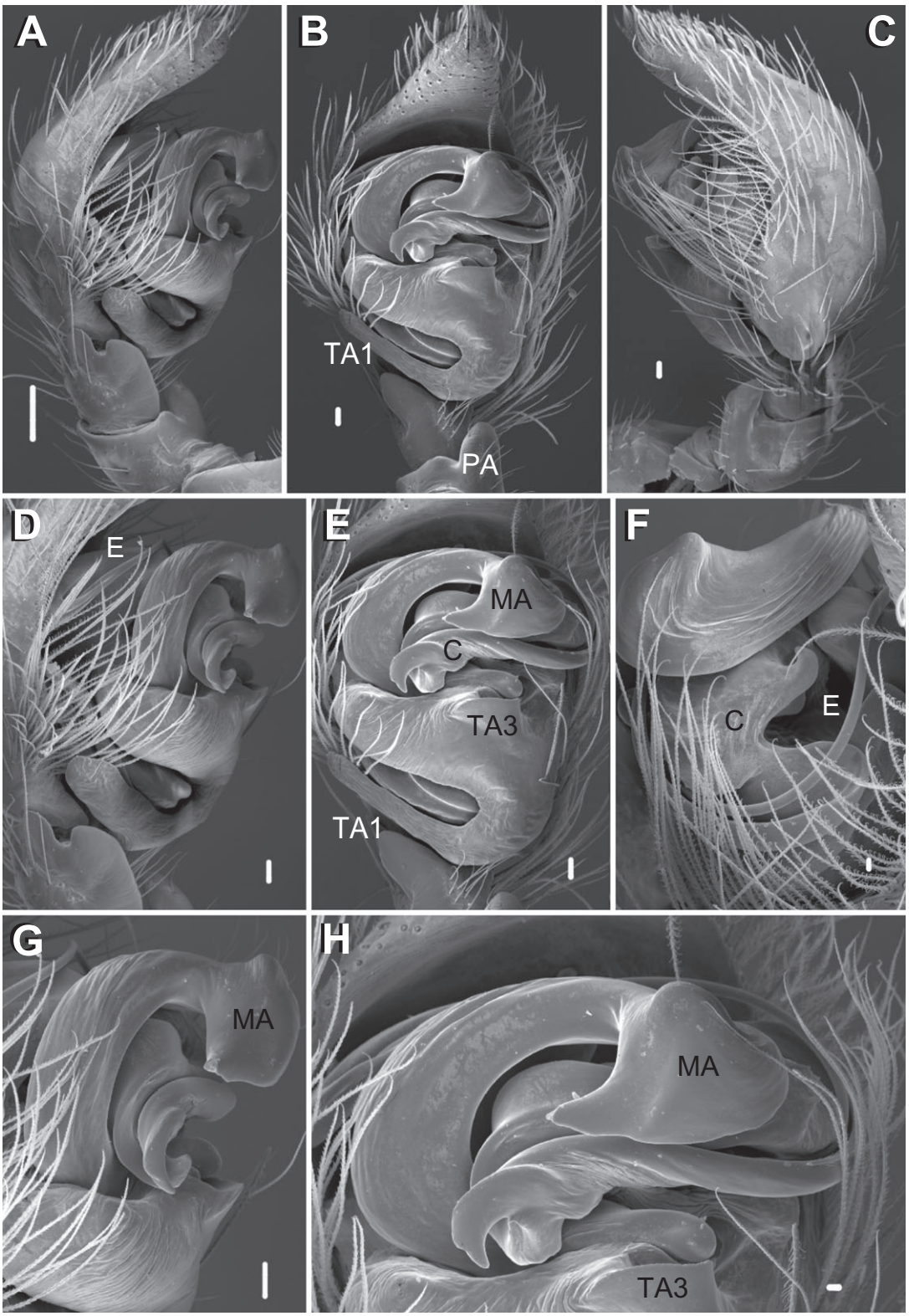

Figure 25. Scanning electron micrographs of *Onomastus quinquenotatus* male from Hakgala, Sri Lanka (MHNG). A, D, G, prolateral view. B, E, H, ventral view. C, F, retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PA, patella apophysis; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 10 μm (F, H), 30 μm (B–E, G), 100 μm (A).

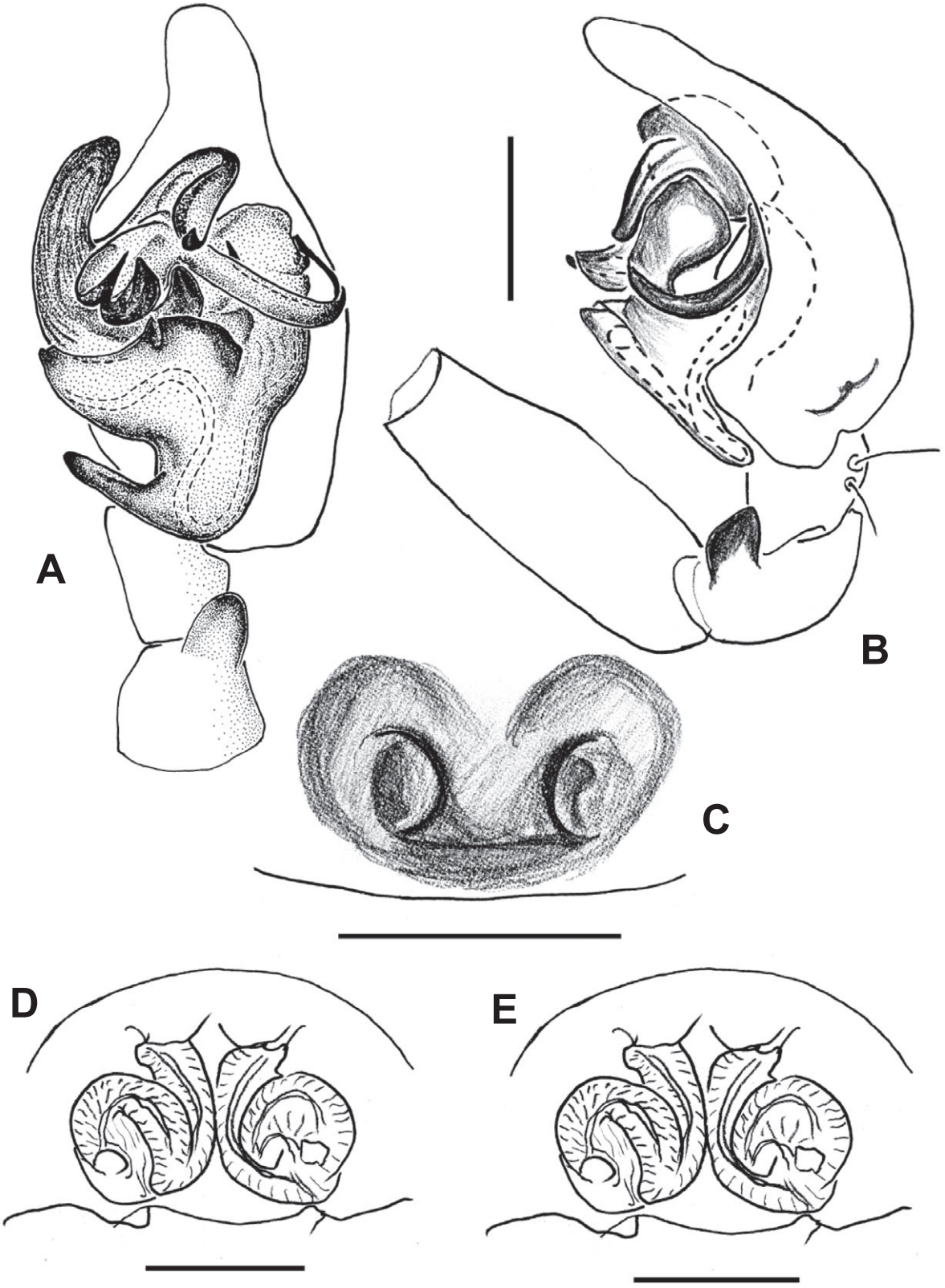

Figure 26. ***Onomastus rattotensis*** **sp. nov.** from Rattota, Sri Lanka (MHNG). A, left male palp, ventral view. B, ditto, retrolateral view. C, epigynum, ventral view. D, vulva, ventral view. E, ditto, dorsal view. Scale bars = 0.1 mm (D, E), 0.2 mm (A–C).

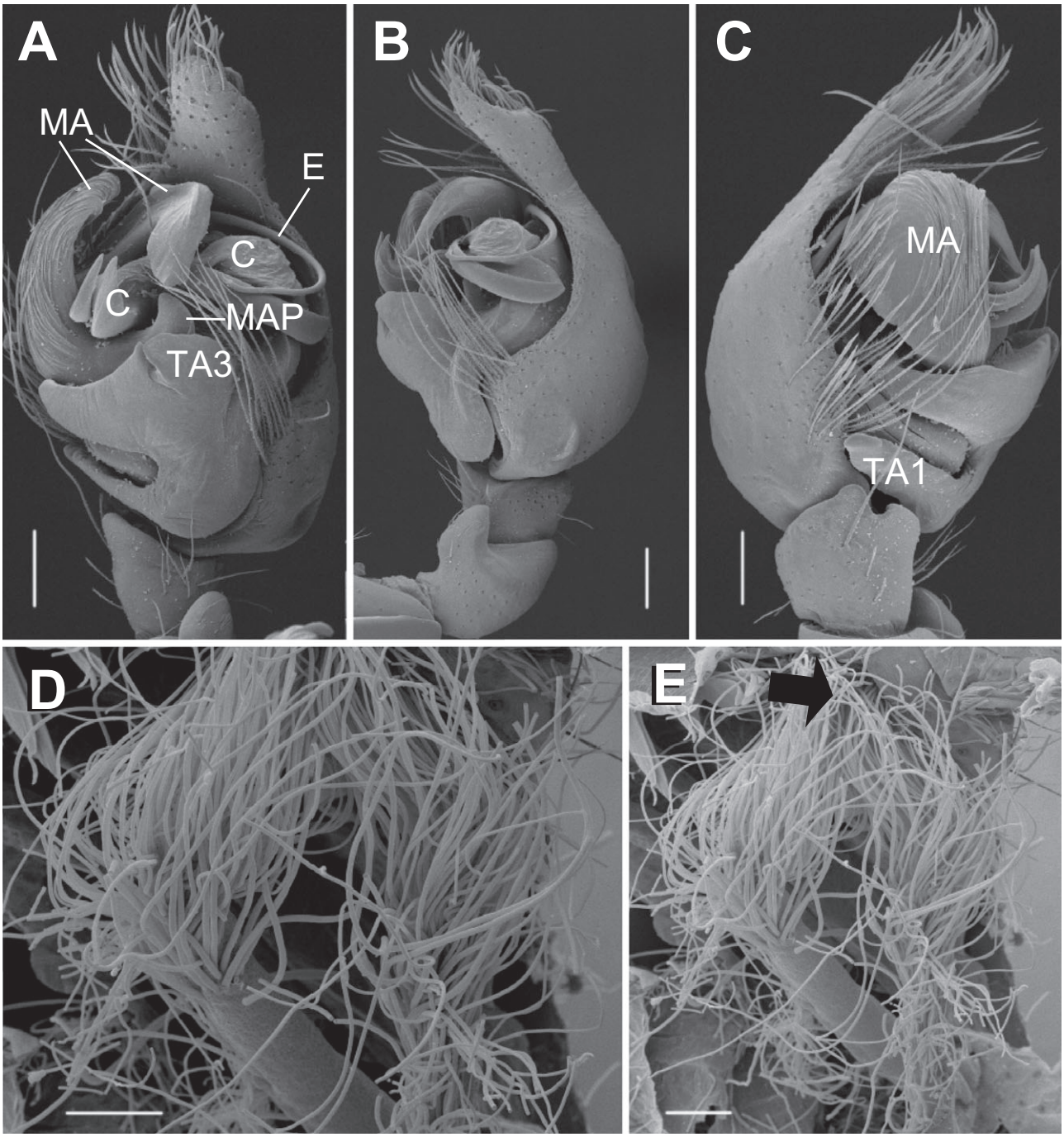

Figure 27. Scanning electron micrographs of ***Onomastus rattotensis* sp. nov.** from Rattota, Sri Lanka (MHNG). A, left male palp, retrolateral view. B, ditto, retrolateral view. C, ditto, prolateral view. D, female tracheal system, dorsal view. E, ditto, detail. Abbreviations: C, conductor; E, embolus; MA, median apophysis; MAP, mesal branch of MA; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 100 μm. The arrow points to the tracheae, which enter the prosoma.

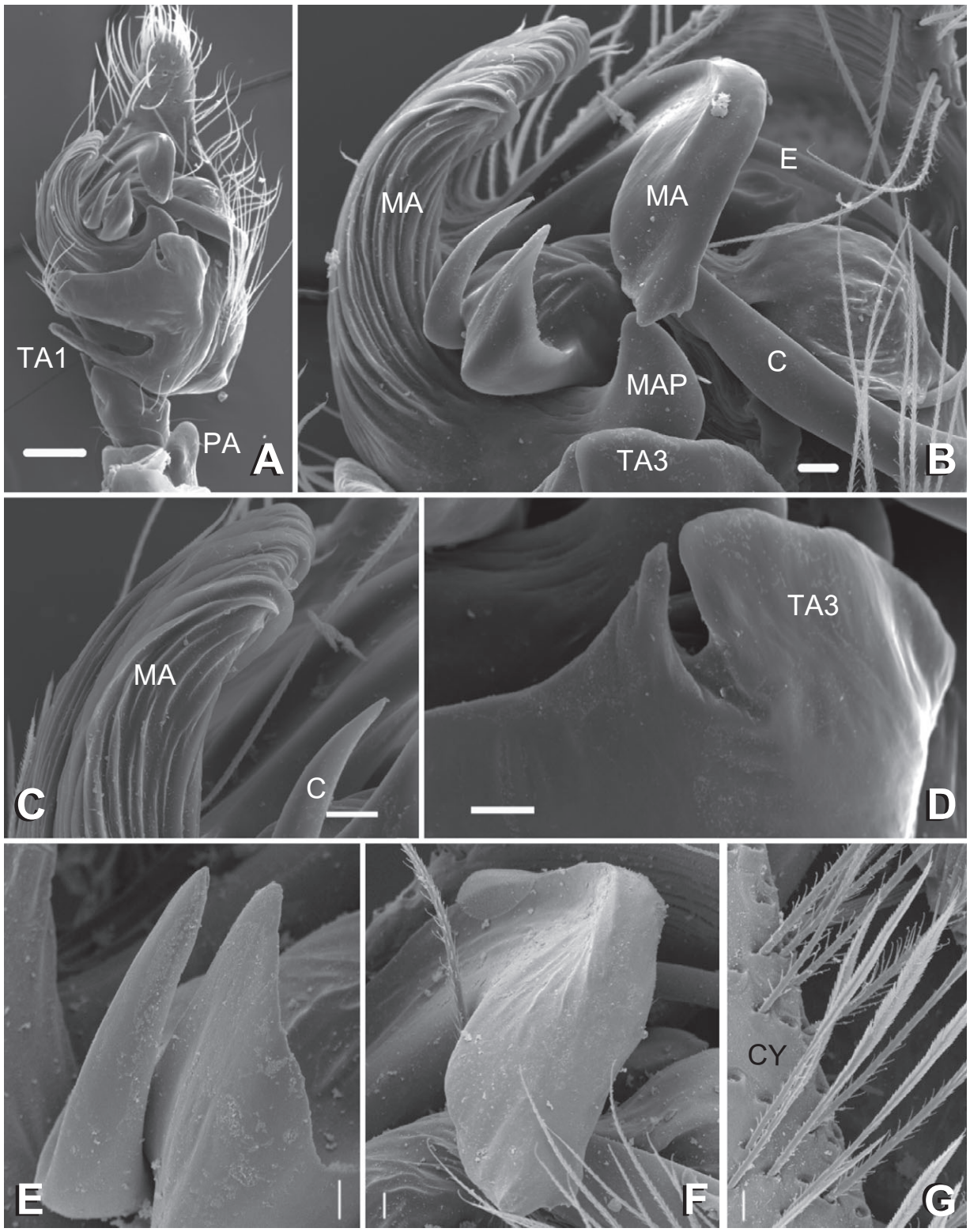

Figure 28. Scanning electron micrographs of ***Onomastus rattotensis* sp. nov.** from Rattota, Sri Lanka (MHNG). A, left male palp, ventral view. B, MA and C, ventral view. C, F, MA tip, ventral view. D, profile of TA3, ventral view. E, profile of C tip, ventral view. G, serrated setae of the cymbium. Abbreviations: C, conductor; CY, cymbium; E, embolus; MA, median apophysis; MAP, mesal branch of MA; PA, patella apophysis; TA1, tegular apophysis 1; TA3, tegular apophysis 3. Scale bars = 10 μm (B, E, F, G), 20 μm (C, D), 100 μm (A).

well-developed, pleated MA. Females are difficult to diagnose, but may be separated by details of the internal genitalia.

Male holotype: Total length: 2.8; prosoma length: 1.4, width: 1.1. Legs I: femur 1.1, patella 0.5, tibia 3.2, metatarsus 2.3, tarsus 1.3. The spiders are green in nature. They turn whitish to pale yellow in alcohol. Prosoma oval, longer than wide. Opisthosoma longer than wide, lighter in colour. Leg I yellowish brown, leg II–IV light yellow. Legs are laterally without dark markings. Eyes surrounded by dark rings. Chelicerae yellow, with seven retromarginal and three promarginal teeth. Leg formula 1432. Leg spination: metatarsus V 4-2-2; tibia D 1-0-0, V 4-2-4; patella D 1-0-0; femur D 0-2-2. Palp: cymbium oval. Retrolateral tibial apophysis stout, tapering blunt end (Figs 26A, 27B).

Female paratype: Total length: 3.2; prosoma length: 1.4, width: 1.2. Legs 1: femur 1.3, patella 0.8, tibia 1.8, metatarsus 1.0, tarsus 0.4. Morphology similar to the male except for the following. Leg spination: metatarsus V 2-2-2; tibia V 2-2-2; femur D 0-1-0, P 2-3-1, R 2-3-1. Epigynum and vulva as in Figure 26C–E.

Distribution: Sri Lanka, central province, known only from the type locality. Probably endemic to Sri Lanka.

Other material examined: SRI LANKA: Central Province, Knuckles range, along Rattota-Ilukkumbura Road, 900 m, 03–04.ix.2003, 9♂, leg. Suresh P. Benjamin. Deposited in MHNG.

ACKNOWLEDGEMENTS

This study was supported by a Smithsonian Institution postdoctoral fellowship and my personal funds. I am indebted to Christa L. Deeleman-Reinhold and E. J. van Nieukerken (RMNH) for kindly providing a substantial part of the specimens examined in this study. Thanks to Christine Rollard and Elise-Anne Leguin (MNHN) for providing E. Simon's types, to Jonathan Coddington and Dana De Roche (USNM) for providing access to additional material, to Dr Akio Tanikawa for providing specimens of *O. kanoi*, to Janet Beccaloni (BMNH) for providing the type of *O. complexipalpis*, to Charles Grisworld (CAS) for providing me with an undescribed species of *Onomastus* from India, and to Mr A. H. Sumanasena (Department of Wild Life Conservation, Colombo) for providing a research permit to collect in Sri Lanka. I want to express my gratitude to my brother Donald Benjamin and my student Ziyard Jaleel (Open University of Sri Lanka) and Sudath V. Nanayakkara for accompanying me during fieldwork in Sri Lanka.

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