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Taxonomic revision and phylogenetic hypothesis for the jumping spider subfamily Ballinae (Araneae, Salticidae)

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The subfamily Ballinae is revised. To test its monophyly, 41 morphological characters, including the first phylogenetic use of scale morphology in Salticidae, were scored for 16 taxa (1 outgroup and 15 ingroup). Parsimony analysis of these data supports monophyly based on five unambiguous synapomorphies. The paper provides new diagnoses, descriptions of new genera, species, and a key to the genera. At present, Ballinae comprises 13 nominal genera, three of them new: *Afromarengo*, *Ballus*, *Colaxes*, *Cynapes*, *Indomarengo*, *Leikung*, *Marengo*, *Philates* and *Sadies*. *Copocrossa*, *Mantisatta*, *Pachyballus* and *Padilla* are tentatively included in the subfamily. Nine new species are described and illustrated: *Colaxes horton*, *C. wanlessi*, *Philates szutsi*, *P. thaleri*, *P. zschokkei*, *Indomarengo chandra*, *I. sarawakensis*, *Leikung kinabaluensis* and *Marengo deelemanae*. *Colaxes nitidiventris* and *Ballus segmentatus* are redescribed. The Seychelles species *Baviola spatulata* is considered a junior synonym of *B. braueri*. The phylogenetic analysis suggests two independent origins of tentative Batesian mimicry of ants within Ballinae. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 142, 1–82.

ADDITIONAL KEYWORDS: Batesian mimicry – cladistics – exemplar approach – Indonesia – Malaysia – Seychelles – South-east Asia – spider scales – Sri Lanka.

INTRODUCTION

Jumping spiders are diverse in morphology, behaviour and predatory ecology (Foelix, 1996; Jackson & Pollard, 1996; Jackson & Carter, 2001), which makes them attractive model organisms for examining questions of evolutionary phenomena. Currently, very little is known about their phylogenetic relationships (Griswold, 1987; Hedin & Maddison, 2001; Szűts & Jocqué, 2001), hampering study of their intriguing natural history.

There is an increasing awareness of the need for sound systematics in the conservation of biodiversity (May, 1990; Vane-Wright *et al.*, 1991; Faith, 2002). Prior to the diffusion of Hennigian methods, most systematists based their classifications and evolutionary scenarios upon single character systems that were believed a priori to have greater importance than other characters (Hennig, 1966; Wiley, 1981; Brooks &

McLennan, 1991; Wenzel, 1992; Humphries & Parenti, 1999; Schuh, 2000; Benjamin, 2002). Despite early indications that a multiple character system approach provides better results (Peckham & Peckham, 1885), salticid systematics has been no exception. The classifications of both Simon (1901) and Proszynski (1976) are based on character systems believed to be of special importance at the time of study – for Simon, the dentition of the lower margin of the chelicerae; for Proszynski, the overall similarity of male genitalia. However, recent studies, which have included additional character systems, have been more successful in deducing phylogenetic relationships of some of the salticid subfamilies (Wanless, 1984b; Griswold, 1987; Rodrigo & Jackson, 1992; Maddison, 1996; Wijesinghe, 1997; Hedin & Maddison, 2001).

The salticids treated in this study form a small subfamily within the so-called salticine division (Salticoida in Maddison & Hedin, 2003). Ballinae, together with Dendryphantinae, Euophryinae and Synagelinae, are grouped by an embolus that is separated from the tegulum by a fully expandable embolic haem-

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atodocha (eh), that is freely movable in relation to the tegulum, and by an embolus (e) that is coiled counterclockwise (Maddison, 1988, 1996; Hedin & Maddison, 2001). Dendryphantinae is the only subfamily to have received considerable phylogenetic attention to date (Maddison, 1988, 1996; Hedin & Maddison, 2001).

Ballinae were tentatively defined by the following putative synapomorphies: a tegulum divided by a pale longitudinal furrow and a well-coiled embolus lying flat on the tegulum (Maddison, 1988, 1995, 1996). A group of basically similar composition, 'Marenginae', was proposed by Dippenaar-Schoeman & Jocqué (1997), based on the presence of a well-coiled embolus laying flat on the tegulum and the presence of a thin straight, retrolateral tibial apophysis (rta). However, they did not include *Ballus* C.L. Koch, 1850 and *Pachyballus* Simon, 1900 in 'Marenginae', in spite of the fact that these species featured these diagnostic characters.

Simon (1901) placed many of the Ballinae genera treated in this study in his groups Balleae and Ligonipedeae. *Cynapes* Simon, 1900 and *Padilla* Peckham & Peckham, 1894, here considered to be within Ballinae, were placed in Bavieae, together with *Baviola* Simon, 1898. Petrunkevitch (1928) grouped *Colaxes* Simon, 1900, *Marengo* Peckham & Peckham, 1892 and *Philates* Simon, 1900 in Myrmarachninae, while he included *Baviola*, *Cynapes* in Thiodininae, and *Ballus* and *Pachyballus* in Magoninae.

The last comprehensive treatment of Ballinae was by Wanless (1978, 1979, 1984a) as part of his series of revisions of salticid genera. Unfortunately, his generic concepts were loosely established. The monophyly of some, such as *Marengo*, *Sadies* Wanless, 1984 and *Cynapes* is not well established. Wanless (1978, 1984a) and Zabka (1999) provided little discussion of generic or species interrelationships. The few characters employed by them cannot be regarded as convincing synapomorphies. The confusion in salticid systematics may be due to studies mainly being restricted in scope to male genital morphology. Salticid genitalia are relatively simple and uniform, thus less informative within the context of a detailed classification. Here, I attempt to remedy this situation by appraising characters newly documented by electron microscopy in concert with those employed by previous workers, including Wanless.

Motivation for a phylogenetic revision of Ballinae was provided by incomplete knowledge of established species and generic relationships. Misplaced species and vaguely defined genera have led to this situation. A major obstacle was the difficulty in obtaining specimens for study. Despite this, I have managed to synthesize morphological data for 11 genera in a cladistic context. The primary objective was to revise and

define the genera of Ballinae, provide keys and diagnoses, and describe and illustrate newly discovered species; the second to propose a phylogeny for Ballinae, resolve relationships among genera and test its monophyly.

MATERIAL AND METHODS

This study focuses on the Ballinae fauna of Sri Lanka and South-east Asia. The specimens are from two recent collections, the first from Sri Lanka, collected by myself, and the second from South-east Asia, collected by Christa L. Deeleman-Reinhold (for more details see Benjamin, 1999 and Deeleman-Reinhold, 2001). The cladistic analysis highlights numerous characters that have not previously been used taxonomically, such as modified setae or scales. These are scattered over the entire body of the spider, or restricted to well-defined areas. With the exception of Galiano (1975), Hill (1979) and Townsend & Felgenhauer (1999), this diverse character system has been rarely used in systematics. Hill (1979) convincingly demonstrated that scale morphology could be used to assign species to genera and to determine relationships between them. This paper builds on these previous studies, hoping to encourage their use in future systematic studies.

Specimens used for habitus illustration were placed on washed sand in 70% ethanol and drawn using a dissecting microscope (Leica MZ8) with top illumination and a magnification of up to 50×. Most illustrations are based on observations of multiple specimens. Palpi and legs were dissected, positioned for illustration in temporary mounts, embedded in glycerine (Benjamin, 2000) and viewed with a compound microscope (Leica DMLB). Vulvae were cleared with trypsin (0.1% trypsin, 0.1% CaCl₂, in 0.05 M tris-buffer, pH 7.6) as described in Benjamin (2000) or treated with 'ReNu' (Enzymatic contact lens cleaner, Bausch & Lomb Inc.). After treatment they were examined, drawn and photographed in temporary mounts embedded in glycerine. The final illustrations were rendered using technical pens on drafting paper. Apart from a few instances (noted in the figure captions) left structures were drawn. Hairs and macrosetae are only illustrated in some drawings. All measurements are given in millimetres and were made with a compound microscope (Leica DMLB) equipped with a 10× ocular and an ocular micrometer scale.

A JEOL 8600 scanning electron microscope (SEM) was used to study and photograph morphological features. The structures examined were dehydrated with 100% ethanol (transferred from 70% ethanol to absolute ethanol and left overnight), then critical point-dried and mounted on SEM stubs for sputter coating. Additionally, some structures were examined with the

environmental scanning electron microscope (ESEM; PHILIPS XL30 FEG ESEM). They were hydrated gradually up to 100% with distilled water and left overnight, prior to examination. ESEM enables examination of nonconductive specimens without first having to sputter coat them. Such an examination is essential when viewing 'type' specimens. Original SEM images were saved as high-resolution TIFF files. They were edited using Adobe Photoshop; plates were assembled and labelled using Adobe Illustrator.

Known taxa are re-described only when deemed necessary or to document new information such as scale morphology. Character descriptions are included. When specimens could not be obtained for critical examination, information was obtained from Wanless (1978, 1979, 1984a). The intention was to base species descriptions on many individuals taken from as wide a geographical range as possible. However, this approach was only achieved in part, due to the lack of material. Each diagnostic section is based on available information. A complete synonymy of the genera and species is given in Platnick (2003).

Anatomical abbreviations

aeb	anterior epigynal border
ale	anterior lateral eye
ame	anterior median eye
ap	apical plates of epigynum
as	asymmetrical scales
b	bulbus
c	copulatory atrium
cag	gland of the copulatory atrium
cd	copulatory duct
co	copulatory opening
cy	cymbium
dm	dark markings
dp	dark patch on posterior opisthosoma
e	embolus
ec	embolic coil
eh	embolic haematodocha
ek	epigynal septum
f	femur
fd	fertilization duct
lp	lateral plates of epigynum
lps	leaf-like prosomal scales
lts	leaf-like tibial setae
os	ordinary setae
pbl	posterior bulbus lobe
pc	pseudo-conductor
peb	posterior epigynal border
ple	posterior lateral eye
pme	posterior median eye
ps	plumose scales
pp	prosomal protuberance
rta	retrolateral tibial apophysis
s	spermatheca

scp	sclerotized projection
sp	scattered papillae
ss	pits with sensory setae
st	shoulder of tegulum
sv	translucent septum
to	tooth
v	velum
wp	white patches on sides of opisthosoma

Institutional abbreviations

BMNH	British Museum, Natural History, London
BORN	Borneensis Collection, Institute for Tropical Biology and Conservation, Kota Kinabalu, Sabah, Malaysia
HMNH	Hungarian Museum of Natural History, Budapest
MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Koninklijk Museum voor Midden-Afrika, Tervuren
MZT	Zoological Museum, Department of Biology, University of Turku, Turku
NMB	Naturhistorisches Museum, Basel
NRS	Naturhistoriska Riksmuseet, Stockholm
RMNH	Naturalis, National Museum of Natural History, Leiden
UMO	University Museum, Hope Entomological Collections, Oxford
ZIZM	Zoologisches Institut und Zoologisches Museum, Hamburg
ZMUC	Zoological Museum University of Copenhagen, Copenhagen

CLADISTIC ANALYSIS

OUTGROUP CHOICE

I chose the putatively closely related genus *Baviola* as outgroup to root the tree. In previous studies, a number of taxa have been considered as related to Ballinae. In his revision of *Marengo* Wanless (1978) proposed *Mantisatta* Warburton, 1900 and *Cheliferooides* F.O.P.-Cambridge, 1901. He and Platnick (1984) suggested that the similarities in body form and genital structures indicate a phylogenetic relationship. Wanless changed his mind in 1984 by proposing *Sadies* as sister to *Marengo* and *Baviola* + *Cynapes* as sister to *Marengo* + *Sadies*, on the basis of similarities in the genitalia, especially the male palps. Moreover, he suggested that *S. trifasciata* should be considered 'midway' between the two generic groups (Wanless, 1984a).

I have included *Baviola*, *Cynapes* and *Sadies*. I was unable to include *S. trifasciata* due to the lack of material. Another possible outgroup consists of *Ballus*, *Pachyballus* and possibly *Attidops* Banks, 1905 (Mad-

dison, 1995, 1996; Edwards, 1999). *Ballus chalybeius* (Walckenaer, 1802) and *B. segmentatus* Simon (1900), from Sri Lanka have been included as exemplars for *Ballus* + *Pachyballus* in this study. Due to practical limitations I was unable to include *Attidops*, *Admestina*, *Cheliferooides*, although I doubt that they are correctly placed in Ballinae; see Discussion below. As no complete phylogeny for salticid genera exists, the

choice of an outgroup for Ballinae is questionable; only a cladistic analysis of all salticid genera would fully resolve this issue (but see Maddison & Hedin, 2003).

TAXA AND CHARACTERS SCORED

The aim of the cladistic analysis was to test the monophyly of Ballinae and resolve generic relation-

Table 1. Distribution of characters scored for 15 Ballinae exemplar taxa. Character states are scored 0–2, ‘?’ for unknown, ‘-’ for inapplicable. Outgroup taxon is denoted with an asterisk. Consistency index (CI), retention index (RI), and rescaled consistency index (RC) are from the preferred most parsimonious tree

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Baviola braueri</i> *	0	0	–	0	0	0	0	0	0	1	0	0	0
<i>Cynapes wrighti</i>	0	1	?	1	1	0	0	0	0	1	0	0	0
<i>C. conosus</i>	1	1	?	1	1	0	?	0	0	1	1	0	0
<i>Colaxes wanlessi</i>	1	1	0	1	1	0	0	0	0	1	1	0	0
<i>Ballus chalybeius</i>	1	1	1	1	1	0	0	0	0	1	1	0	0
<i>B. segmentatus</i>	1	1	0	1	1	0	1	0	0	1	1	0	0
<i>Philates chelififer</i>	1	1	1	1	1	0	1	0	0	1	1	0	0
<i>P. grammicus</i>	1	1	?	1	1	0	?	0	0	1	1	1	0
<i>P. zschokkei</i>	1	1	1	1	1	0	1	1	0	1	1	0	0
<i>Indomarengo sarawakensis</i>	1	1	1	1	1	1	0	1	0	1	1	0	0
<i>I. chandra</i>	1	1	1	1	1	1	0	1	1	?	?	?	?
<i>Sadies fulgida</i>	1	1	2	1	1	0	0	0	0	1	1	0	0
<i>Leikung porosa</i>	1	1	2	1	2	1	0	0	0	0	–	0	1
<i>Afromarengo coriacea</i>	1	1	1	1	2	1	0	0	0	0	–	0	1
<i>Marengo crassipes</i>	1	1	0	1	1	0	0	0	0	1	1	0	0
<i>M. deelemanae</i>	1	1	1	1	1	0	0	0	0	1	1	0	0
Tree steps	1	1	5	1	2	2	3	2	1	1	1	1	1
CI	1.00	1.00	0.40	1.00	1.00	0.50	0.33	0.50	1.00	1.00	1.00	1.00	1.00
RI	1.00	0	0	0	1.00	0.67	0	0.50	0	1.00	1.00	0	1.00
RC	1.00	0	0	0	1.00	0.33	0	0.25	0	1.00	1.00	0	1.00

	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Baviola braueri</i> *	0	0	0	–	0	–	0	0	0	0	0	0	0	0
<i>Cynapes wrighti</i>	0	0	0	–	0	–	0	0	0	0	0	1	0	1
<i>C. conosus</i>	0	0	0	–	1	0	0	0	0	0	0	0	0	1
<i>Colaxes wanlessi</i>	0	0	0	–	1	0	1	0	0	0	0	1	0	0
<i>Ballus chalybeius</i>	0	0	0	–	1	2	1	1	0	0	0	0	0/1	1
<i>B. segmentatus</i>	0	0	0	–	1	0	1	1	0	0	0	0	1	1
<i>Philates chelififer</i>	0	0	0	–	1	1	1	0	0	1	0	0	0	1
<i>P. grammicus</i>	0	0	1	1	1	0	1	0	1	0	0	0	0	1
<i>P. zschokkei</i>	0	0	1	1	1	0	1	0	1	0	1	0	0	1
<i>Indomarengo sarawakensis</i>	0	0	1	1	1	0	1	0	0	0	1	0	0	1
<i>I. chandra</i>	?	?	?	?	?	?	1	0	0	0	1	0	0	1
<i>Sadies fulgida</i>	0	1	1	0	0	–	1	0	1	0	1	0	0	1
<i>Leikung porosa</i>	1	1	1	1	0	–	1	0	0	0	1	0	0	1
<i>Afromarengo coriacea</i>	0	1	1	1	0	–	1	0	1	0	1	0	0	1
<i>Marengo crassipes</i>	0	0	0	–	1	0	1	0	1	1	0	0	0	1
<i>M. deelemanae</i>	0	0	0	–	1	0	1	0	1	1	0	0	0	1
Tree steps	1	1	1	1	2	2	1	1	5	2	1	2	1	2
CI	1.00	1.00	1.00	1.00	0.50	1.00	1.00	1.00	0.20	0.50	1.00	0.50	1.00	0.50
RI	0	1.00	1.00	0	0.75	0	1.00	1.00	0.20	0.50	1.00	0	0	0
RC	0	1.00	1.00	0	0.37	0	1.00	1.00	0.04	0.25	1.00	0	0	0

Table 1. Continued

	28	29	30	31	32	33	34	35	36	37	38	39	40	41
<i>Baviola braueri</i> *	0	0	0	0	0	0	–	1	1	0	0	0	0	0
<i>Cynapes wrighti</i>	0	0	1	0	0	0	–	1	0	1	0	0	0	0
<i>C. conosus</i>	0	0	1	0	0	0	–	1	?	?	0	0	1	0
<i>Colaxes wanlessi</i>	0	0	1	1	0	0	–	0	1	0	0	0	0	0
<i>Ballus chalybeius</i>	0	0	1	1	0	0	–	0	1	0	0	0	0	0
<i>B. segmentatus</i>	0	0	1	0	0	0	–	0	1	0	0	0	0	0
<i>Philates chelifera</i>	0	0	0	1	0	1	0	1	1	0	0	0	0	0
<i>P. grammicus</i>	0	0	1	1	0	1	?	1	?	?	0	0	0	0
<i>P. zschokkei</i>	0	0	1	1	0	1	0	1	?	?	0	0	0	0
<i>Indomarengo sarawakensis</i>	1	0	1	1	0	1	2	1	0	0	0	0	0	0
<i>I. chandra</i>	1	0	1	1	0	1	2	1	1	?	0	1	0	0
<i>Sadies fulgida</i>	1	0	1	0	0	0	–	1	0	1	0	0	0	0
<i>Leikung porosa</i>	1	1	1	1	0	1	2	2	0	0	1	1	0	0
<i>Afromarengo coriacea</i>	1	0	1	1	1	1	1	1	0	0	0	1	0	0
<i>Marengo crassipes</i>	0	0	1	1	0	1	1	1	0	0	0	0	0	1
<i>M. deelemanae</i>	0	0	1	1	0	1	0	1	?	?	0	0	0	1
Tree steps	1	1	2	3	1	2	3	2	3	2	1	2	1	1
CI	1.00	1.00	0.50	0.33	1.00	0.50	0.67	1.00	0.33	0.50	1.00	0.50	1.00	1.00
RI	1.00	0	0	0.50	0	0.83	0.67	1.00	0.60	0	0	0.50	0	1.00
RC	1.00	0	0	0.17	0	0.42	0.44	1.00	0.20	0	0	0.25	0	1.00

ships, using a sample representing ten genera (Table 1). Genera were represented by two species each and the type species included if material was available for study. Inclusion of all or most species when attempting to resolve relationships is desirable, but is often not practicable (Mishler, 1994; Rice *et al.*, 1997; Prendini, 2000, 2001). Species rather than groundplans were used as terminals, a method commonly referred to as the exemplar approach (Griswold, 1993; Mishler, 1994; Yeates, 1995; Griswold *et al.*, 1998; Prendini, 2001). I did not favour the use of groundplans for reasons that have been discussed elsewhere (e.g. Prendini, 2001). Moreover, higher-level phylogenetic studies that do not use an explicit exemplar approach quickly become redundant when additional taxa are discovered, or when it becomes necessary to extend the scope of an analysis (Bond & Opell, 2002).

Characters are hypothesized to be statements of homology (Griswold, 2001). In operational terms, homologies are features that define monophyletic groups. They need to be confirmed by congruence with other characters (Patterson, 1982; Brooks & McLennan, 1991; de Pinna, 1991; Wenzel, 1992). The consideration of characters as operationally equivalent to putative synapomorphies enables the discovery of common patterns among taxa (de Pinna, 1991; but see Wagner, 1989a, b and references therein, for a different opinion). Codings were checked against as many species as possible for each genus. Hence the phyloge-

netic analysis was based on observations from many more than the 16 taxa explicitly included. A list of characters is given below. Table 1 summarizes the character states scored for each of the taxa included in the study. I used the character trace option of MacClade 4.0 (Maddison & Maddison, 2000) to map characters.

Male palp

1. *Shape of Subtegulum/tegulum*: (0) tegulum pear-shaped, subtegulum does not extend above the tibia (ventral view); (1) tegulum oval, bilobed, subtegulum extending above tibia (Maddison, 1995, 1996: 'tegulum divided by a pale longitudinal furrow'; Zabka, 1999: 'bulbus lobe'; Edwards, 1999: 'unequally bilobed'). State 0 is observed in *Baviola* (Figs 5A, C, E, 7A; Proszynski, 2003; Wanless, 1984a), *Cynapes wrighti* and *C. baptizatus* (Butler, 1876) (Fig. 8A, B; Wanless, 1979). All other species considered in this study have a bilobed tegulum which extends above the tibia (Figs 8C, D, 11C, 12B, 17A, B, 25A, 34B, 38D, E, 45A, 48A, B, 57A–C, 60B, C). Further, a bilobed tegulum has been described for *Attidops* & *Admestina* Peckham & Peckham, 1888 (Edwards, 1999: figs 14, 15, 18, 19, 22–25).
2. *Embolic coil (ec)*: (0) absent; (1) present. The basal section of Ballinae emboli contains a sclerotized outer edge (Alicata & Cantarella, 1987: 'sclerotized laminar coil') and a membranous

- middle core (velum). The sperm duct does not follow the course of the embolic coil; instead it is restricted to the velum (Figs 17B, 21B, 25A, 34B). It then enters the sclerotized embolus proper with the end of the sclerotized outer edge and termination of the membranous middle core or velum (Figs 24G, H, 28B, 40B). Euophryinae, Synagelinae and Dendryphantinae have a core through which the duct passes, although in Euophryinae the duct is associated with the spiral (Maddison, 1996: figs 28–31). Except for *Baviola* (Fig. 7A, B), all genera treated in this study possess an embolic coil. Illustrations in Wanless (1979: fig. 1c, h) suggest that ec is absent in *Cynapes baptizatus*.
3. *Shape of embolic coil*: (0) concave; (1) convex; (2) convex and wrinkled. In *Philates chelififer*, *Indomarengo chandra* and *I. sarawakensis* the ec is convex (Figs 28B, C, 40A, B, 43A, B, C). In *Sadies fulgida* and *Leikung porosa* it is convex and wrinkled (Figs 47C–E, 52B, D).
 4. *Orientation of the embolus*: (0) embolus stout, projecting outwards from its base (Figs 5A–F, 7A, B); (1) embolus spiralled. In most cases the embolus is dorsoventrally flattened (Figs 15B, 20A, B, 47C–E, 63A). The presence of a well-coiled embolus, laying flat on the tegulum, was proposed by Maddison (1995) as a synapomorphy delimiting Ballinae. Dippenaar-Schoeman & Jocqué (1997) used this character (state 0) to define the subfamily ‘Marenginae’. Their concept of ‘Marenginae’ included all African genera treated in this study, except for *Ballus* and the related genus *Pachyballus* (represented by *Ballus chalybeius* and *B. segmentatus* in my cladistic analysis). In this study I suggest that they should be included in Ballinae.
 5. *Length of the embolus*: (0) Short and stout, less than one spiral (Figs 5A–F, 7A, B); (1) one spiral but less than two (Figs 8A–D, 11B, C, 15A, B, 24A, 28B, 31A–D, 38D, E, 42A, B, 45A, B); (2) more than two spirals (Figs 48A, B, 49A, B, 52A, B, 55A, B, 57A–C, 58A, C, D; Wesolowska & Russell-Smith, 2000: figs 172–174).
 6. *Path of the sperm duct*: (0) C-shaped (Figs 5A–F, 11B, C, 17A, 21B, C, 25A, 31A–D, 45A, B, G, H, 60B, C, 65B, C, E, F, 68E, F); (1) S-shaped (Figs 38D, E, 41E, F, 42A, B, 48A, B, 49A, B, 55A, B, 57A, B; Wesolowska & Russell-Smith, 2000: figs 172–174).
 7. *Proximal end of embolus modified to a possible pseudo-conductor*: (0) absent; (1) present. This modification of the proximal part of the embolus, termed the pseudo-conductor (pc), is reported for the first time in this study. It is documented for *Ballus segmentatus* (Fig. 24G, H), *Philates chelififer* (Fig. 28B, C) and *P. zschokkei*. (Fig. 36C, D). It is absent in *B. chalybeius* (Fig. 20A, B).
 8. *Retrolateral tibial apophysis of the male palp*: (0) tilted forwards in the direction of the tegulum (Figs 5A–F, 8A–C, 11B, C, 20C, D, 21C, 45A, B, G, H, 48B) or pointed straight upwards (Figs 25A, B, 28A); (1) tilted backwards towards the cymbium. A backwards tilted rta is present in *Indomarengo sarawakensis*, *I. chandra* (Figs 38E, 40A, 41E, F, 42B, 43A, D) and *Philates zschokkei* (Figs 34A, B, 36A, B).
 9. *Retrolateral tibial apophysis of the male palp*: (0) no constriction just below the apex; (1) constriction present. Found only in *Indomarengo chandra* (Figs 42B, 43A, D).
- Female genitalia*
10. *Septum separating epigynal atria (ek) and the two copulatory openings (co)*: (0) absent; (1) present. Epigynal septum is absent in *Leikung porosa* (Figs 48E, 50A–C, 51A–F) and *Afromarengo coriacea* (Wanless, 1978: fig. 1f, g).
 11. *Shape of ek*: (0) broad (Figs 6, 9B); (1) narrow (Figs 9A, 14 A, 16B, 18 A, B, 22B, D).
 12. *Epigynal septum with a sclerotized projection (scp)*: (0) absent; (1) present. Found only in *Philates grammicus* (Fig. 32C).
 13. *Copulatory openings (co) connected to each other by a posterior epigynal border (peb)*: (0) absent; (1) present. Continued sclerotized margin between the two copulatory openings is present only in *Leikung porosa* (Figs 48E, 50A–C, 51A–F) and *Afromarengo coriacea* (Wanless, 1978: fig. 1f, g).
 14. *Anterior epigynal border (aeb) with a tooth (to)*: (0) absent; (1) present. Anterior sclerite on epigynum, only present in *Leikung* spp. (Figs 48E, 50A–C).
 15. *Shape of copulatory atrium (c)*: (0) lengthy and L-shaped at the posterior end (Figs 9A, 23A, B, 26A–C, 39B, 61B, 62A–D); (1) short and pouch-like in *Leikung porosa* (Fig. 50B, C), *Sadies fulgida* (Fig. 45C) and *Afromarengo coriacea* (Wanless, 1978: fig. 1f, g).
 16. *Gland of the copulatory atrium (cag)*: (0) absent; (1) present. A sclerotized ‘gland-like’ structure (Zabka, 1999: ‘accessory gland’) is present in *Philates* (Fig. 35B, C), *Sadies* (Figs 45C, 46A, B), *Indomarengo* (Fig. 39B), *Afromarengo coriacea* (Wanless, 1978: fig. 1f, g) and *Leikung porosa* (Figs 50A–C, 51A–F). It is absent in the rest. A similar structure has been described for *Philates* spp. from the island of New Guinea (Zabka, 1999: figs 4c, 9c).

17. *Position of cag*: (0) at the opening of copulatory atrium; (1) at the base of copulatory atrium. The cag is situated at the opening only in *S. fulgida* (Figs 45C, 46A, B).
18. *Vulva with a thin, translucent, septum (sv)*: (0) absent; (1) present. Absent in *Baviola* (Fig. 6), *Leikung* (Figs 50A–C, 51A–F), *Afromarengo* (Wanless, 1978: fig. 1f, g), *Sadies* (Figs 45C, 46A, B) and *Cynapes wrighti* (Fig. 9B). Present in the rest, including *C. canosus* (Fig. 9A).
19. *Size of sv*: (0) large; (1) small; (2) enlarged to a sac-like structure, partly sclerotized as in *Ballus chalybeius* (Fig. 18B, C). SV is reduced in *Philates chelifera* (Fig. 26A–C).
- Somatic morphology*
20. *Height of prosoma*: (0) convex, sharply elevated; (1) dorsoventrally flattened. Convex in *Baviola* (Wanless, 1984a: figs 9b, 10b, 11b, 12b), *Cynapes canosus* and *C. wrighti* (Wanless, 1979: fig. 2b; Wanless, 1984a: fig. 13b; Proszynski, 2003). *Marengo striatipes* also has a sharply elevated prosoma (Wanless, 1978: fig. 5b). All other Ballinae have a flattened prosoma. Edwards (1999: fig. 3) illustrates specimens of *Ballus chalybeius* that have an elevated prosoma, although this feature was not found in specimens examined by me.
21. *Length of prosoma*: (0) longer than wide; (1) as long as wide. All Ballinae except for *Ballus* spp. have a prosoma longer than wide (Figs 4A, 21A, 22A, C). In *Ballus* spp. the prosoma is as long as wide.
22. *Dark patch (dp) on posterior half of the opisthosoma*: (0) absent; (1) present. This is characteristic for most species formerly placed in *Marengo*, but absent in *Ballus* (Figs 4A, 21A, 22A, C), *Baviola* (Wanless, 1984a), *Cynapes* (Wanless, 1979, 1984a; Proszynski, 2003), *Indomarengo* (Figs 4B, 38A, 41C), *Leikung* (Figs 4D, 48C, D, 49C, D) and *Philates chelifera* (Fig. 25D). It is also absent in *Colaxes wanlessi* (Figs 12A, 13A, E) and *C. horton* (Fig. 16A). However, such a marking is present in *C. nitidiventris* (Fig. 11A).
23. *White patches on lateral sides of the opisthosoma*: (0) absent; (1) present (arrowed in Fig. 61A). Present in *Marengo* (Figs 60A, 61A, 68G) and *Philates chelifera* (Fig. 25D).
24. *Transverse white line on opisthosoma*: (0) absent; (1) present (arrowed in Fig. 48C). Present in *Sadies fulgida* (Fig. 45D, F), *Indomarengo* (Figs 38A, 41C), *Afromarengo* (Fig. 4C), *Philates* (Fig. 33A), and *Leikung* spp. (Figs 48C, 49C).
25. *Dark markings (dm) laterally on the opisthosoma*: (0) absent; (1) present. Present in *Colaxes wanlessi* (Figs 12A, 16A) and *Cynapes wrighti* (Wanless, 1984a: fig. 13a, e).
26. *Reticulate markings on the opisthosoma*: (0) absent; (1) present. Present in *Ballus* spp. (Figs 4A, 21A, 22A, C), although only discernible in some males of *B. chalybeius*.
27. *Dark band on both lateral sides of legs I–IV*: (0) absent; (1) present. Absent in *Baviola* spp. and *Colaxes* spp. Absent in some males of *Ballus chalybeius*, faintly discernible in most.
28. *Protuberance on the posterior part of the prosoma*: (0) absent; (1) present. Present in *Leikung* (Figs 4D, 48D, 49D), *Indomarengo* (Figs 38C, 42D) and *Afromarengo* (Wanless, 1978: 'thoracic hump', fig. 1d). Also present in *Sadies fulgida*, *S. gibbosa* (Fig. 45D; Wanless, 1984a: figs 2d, 4d) but may be absent in *S. seychellensis* and *S. trifasciata* (Wanless, 1984a: figs 5a, d, 6d). Wanless (1978: figs 7f, 8f; pls. 2e, 3c) first illustrated the prosomal protuberance (pp) for *Indomarengo thomsoni* and *Leikung porosa*. The protuberance possibly serves to add a false body segment, imparting an ant-like appearance to the spider; such an appearance might deceive visually hunting predators (Oliveira, 1988).
29. *Posterior lateral eyes (ple)*: (0) not raised; (1) raised. Posterior lateral eyes in *Leikung* are positioned on a protuberance (Figs 48D, 49D, 52G, 53A; Wanless, 1978: fig. 7f; pls. 2e, 3a).
30. *Femur I*: (0) not enlarged; (1) enlarged. Except for *Baviola* (Wanless, 1984a), *Philates chelifera* (Fig. 25C, G) and *Marengo striatipes* (Fig. 67A; Wanless, 1978: fig. 5c), all other species treated in this study have an enlarged femur I.
31. *Tibia I*: (0) not enlarged; (1) enlarged. Tibia I is not enlarged in *Baviola* (Wanless, 1984a: figs 9g, h, 10f, 11g, h, 12h), *Ballus segmentatus* and *Cynapes* (Wanless, 1979: figs 1b, 2c, j; Wanless, 1984a: fig. 13g; Proszynski, 2003). *Sadies gibbosa* (Wanless, 1984a: fig. 4h) is the only species in the genus with an enlarged tibia I; coded absent for *S. fulgida* (Fig. 45E).
32. *Single-shafted, asymmetrical scales (as), on the lateral sides of the tibia*: (0) absent; (1) present. Only observed in *Afromarengo coriacea* (Fig. 59C, E). Tibiae of all other Ballinae appear not to possess these scales.
33. *Leaf-like tibial setae (lts)*: (0) absent; (1) present (Figs 27A–C, 37A–C, 40D, E, 59A–C, 63E, F). Absent in *Ballus* (Figs 4A, 19D, E, 24D–F), *Baviola* (Fig. 7D, E), *Colaxes* (Fig. 15G, H), *Cynapes* (Fig. 10D–G) and *Sadies* (Fig. 45E). Absent in *Leikung kinabaluensis* (Fig. 55C). However, more specimens need to be examined.
34. *Surface of leaf-like tibial setae (lts)*: (0) ribbed, spines inconspicuous, fewer in number (Figs 27A–

- C, 69F, G); (1) ribbed with prominent spines, numerous in number; (2) smooth with thin long spines. Leaf-like tibial setae are ribbed with prominent spines in *Afromarengo coriacea*, *Marengo crassipes*, smooth and with thin and long spines in *Indomarengo* (Figs 40E, 44C) and *Leikung* (Fig. 53C–F). Coded nonapplicable for *Baviola*, *Cynapes*, *Sadies* and *Colaxes*.
35. *Number of spines on tibia I*: (0) 2/0/0/2; (1) 2/2/0/2; (2) 2/2/2/2. The number of tibial spines (ts) found in Ballinae varies from four to eight. They are found promarginally at the dorsal and ventral side. A tibia I with four spines (one proximal, one distal, on the dorsal and ventral promargins) is found in *Ballus* (either two or four in *Ballus chalybeius*; Alicata & Cantarella, 1987) and *Colaxes*. Six spines (one proximal, one median and one distal, on the dorsal and ventral promargins) are found in *Baviola* (Wanless, 1984a: figs 9g, h, 10f, 11g, h, 12h), *Cynapes wrighti* (Wanless, 1984a: fig. 13g), *C. canosus* (Wanless, 1979: fig. 2c, j) and all other Ballinae except for *Leikung*, which has eight spines (one proximal, two median and one distal, on the dorsal and ventral promargins; Figs 49D, 53E, 55C).
36. *Prosomal scales: plumose scales (ps)*: (0) absent; (1) present. Plumose setae consist of a relatively broad central shaft and a regular series of broad marginal spines with blunt apices (Fig. 15F). They are found behind the anterior lateral eyes and ple of *Philates chelifer* (Figs 27E, H), behind the eyes and on the central parts of the prosoma of *Colaxes wanlessi* (Fig. 15F), behind the ame, anterior lateral eyes of *Ballus chalybeius* and *B. segmentatus* (Figs 19B, 24C) and *Baviola braueri* (Fig. 7D, E). Absent in *Cynapes wrighti*, *Sadies fulgida*, *Indomarengo chandra*, *Leikung* spp. and *Marengo crassipes*.
37. *Prosomal scales: leaf-like prosomal scales (lps)*: (0) absent; (1) present. Oval, central shifted scales, only present in *Sadies fulgida* (Fig. 47A, B) and *Cynapes wrighti* (Fig. 10A–C).
38. *Sides of prosoma – pits with sensory setae (ss)*: (0) absent; (1) present; (2) bases of pits with a single sensory seta each. Pits on the cuticula of the lateral sides of the prosoma (Wanless, 1978: ‘perforations’) are present in *Indomarengo* and *Leikung* spp. Those of *Leikung* spp. possess a putative sensory seta originating from the base of the pit (Fig. 53B).
39. *Surface of anterior part of prosoma with scattered papillae (sp.)*: (0) absent; (1) present. This character was first described, termed ‘scattered papillae’ by Wanless (1978). Present in *Leikung* (Fig. 52G; Wanless, 1978: fig. 3a, b), *Indomarengo* (Fig. 44D) and *Afromarengo coriacea* (Wanless, 1978: fig. 1a–c).
40. *Chelicerae enlarged*: (0) absent; (1) present. Present in *Cynapes baptizatus* (Wanless, 1979: fig. 1d, e) and *C. canosus* (Wanless, 1979: fig. 2a), absent in *C. wrighti* (Wanless, 1984a).
41. *Sexual dimorphism*: (0) absent; (1) present. Marked sexual dimorphism is present in *Marengo crassipes* (Figs 60A, 61A, 65D) and *M. deelemanae* (Fig. 68A, G). Also found in some populations of *Ballus* spp. Some females of *Ballus chalybeius* are much larger and have reticulate markings whereas males are much smaller and uniformly dark with few markings (Locket & Millidge, 1951; Heimer & Nentwig, 1991; Roberts, 1995; Proszynski, 2003).

RESULTS

PHYLOGENETIC ANALYSIS

PAUP* version 4.0b10 (Swofford, 2002) was used to perform a cladistic analysis of generic relationships. Character polarity was assessed by outgroup comparison. All multistate characters (5 out of a total of 41; Table 1) were treated as nonadditive or unordered (Fitch minimum mutation model; Fitch, 1971). Unordered characters were preferred, because ordered characters exclude all other possible hypotheses regarding the evolutionary relationships among character states (Hauser & Presch, 1991; Hormiga, 1994; Griswold *et al.*, 1998; but see Lipscomb, 1992, and Prendini, 2000, for a different opinion). Missing characters are coded ‘?’ and inapplicable characters ‘–’. Below, characters and states are abbreviated and boldened, e.g. character 2 becomes **2**, character 2, state 1, becomes **2-1**.

I performed a heuristic search with 100 replicates of random taxon addition subjected to tree bisection-reconnection (TBR) branch swapping, with equally weighted characters and ‘MulTrees’ set to 100 000. 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. They were also discarded if they could not be completely justified with the data available (Coddington & Scharff, 1995). Character optimization – minimizing the number of character-state changes or ad hoc hypotheses on a cladogram – is central to the implementation of quantitative cladistics (Schuh, 2000). I used the ACCTRAN option (Farris optimization), which favours secondary loss over convergence to explain homoplasy and therefore maximizes homology (Hormiga, 1994; Griswold *et al.*, 1998; Schuh, 2000), although not of losses or reductions. It also minimizes homology of presence of a primitively present character. Tree sta-

tistics were only calculated from phylogenetically informative characters. Hypotheses of character evolution were investigated with the aid of MacClade version 4.0 (Maddison & Maddison, 2000).

BALLINAE RELATIONSHIPS

Initial cladistic analysis of 29 equally weighted, informative characters produced three most parsimonious trees, with a consistency index (CI) of 0.66, a retention index (RI) of 0.68, and a length of 69 steps. The analysis was then repeated twice after successive character weighting (Farris, 1969; Carpenter, 1988), using the maximum value of the rescaled consistency index. This analysis produced a single tree (length = 34 steps, CI = 0.90, RI = 0.90, rescaled CI = 0.81), identical in topology to one of the trees produced in the unweighted analysis. This tree is presented as the preferred hypothesis of Ballinae generic relationships (Fig. 1).

The subfamily Ballinae is resolved at node 1, supported by the presence of ec (2-1), ec that coils at least once over 360° (4-1, 5-1, 5-2), dark band on both lateral sides of legs I–IV (27-1) and enlarged femur (30-1). Within Ballinae, the presence of an oval, bilobed tegulum (1-1), narrow epigynal septum (11-1) and the presence of a translucent septum (18-1) support node 2. Species that were formerly placed in *Marengo* (except for *Cynapes canosus* and *Sadies*) are united at node 4 as sister to *Colaxes* + *Ballus* (node 6). Node 4 is supported by the presence of a convex embolic coil (3-1), white patches on sides of opisthosoma (23-1) and lts (33-1); node 6 by the presence of 2/0/0/2 spines on tibia I (35-0). Nodes 4 and 6 are united at node 3, supported by the presence of a dorsoventrally flattened prosoma (20-1) and an enlarged tibia I (31-1).

Copocrossa Simon, 1901, *Mantisatta* and *Padilla* are included in Ballinae, although only *C. tenuilineata*

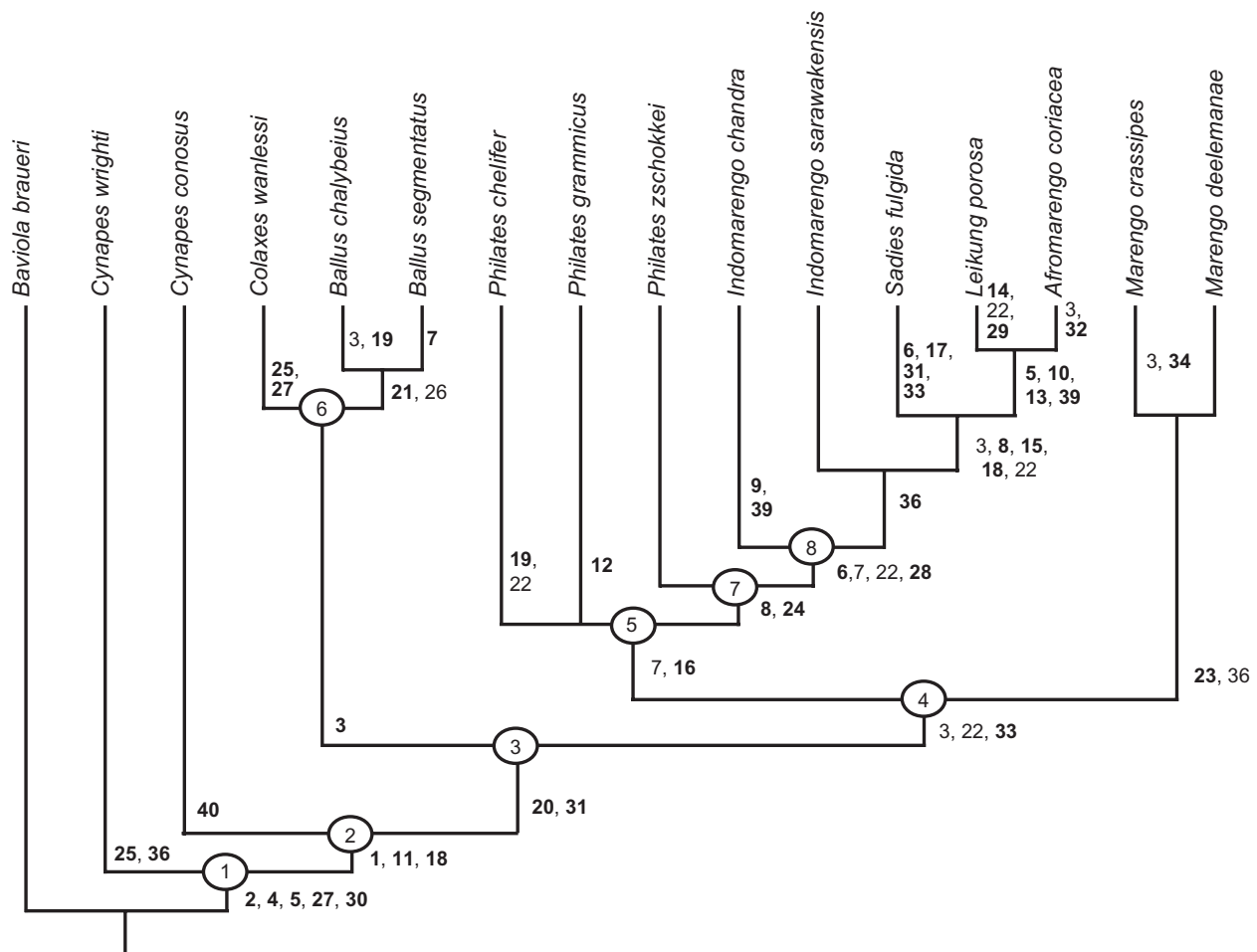


Figure 1. Preferred most parsimonious tree of Ballinae genera based on successive character weighting (length = 34 steps, CI = 0.84, RI = 0.90). Character state changes are mapped using Farris optimization. Bold numbers indicate unambiguous character changes.

(Simon, 1900) has been studied. The male genitalia of *C. tenuilineata* are similar to those of other Ballinae. The same can be said for *Padilla*, a genus of seven species, all from Madagascar. Judging from illustrations in Proszynski (2003) they may be included in Ballinae, as male genitalia show Ballinae synapomorphies: presence of ec (2-1) and spiralling embolus (4-1). Unfortunately, drawings are only available for *P. armata* Peckham & Peckham, 1894, and *P. cornuta* (Peckham & Peckham, 1885).

Mantisatta consists of two known species: *M. longicauda* Cutler & Wanless, 1973 from the Philippines and *M. trucidans* Warburton, 1900 from Borneo. *M. longicauda* is the only species known from both sexes. Judging from illustrations of male genitalia in Proszynski (2003) and Cutler & Wanless (1973: figs 5–7) they are probably correctly placed in Ballinae. Their genitalia show Ballinae synapomorphies: presence of ec and a terminally coiled embolus. However, they possess enlarged femur I and tibia I, but lack lts.

Admestina, *Attidops* and *Cheliferoidea* have been tentatively included in Ballinae by various authors. Maddison (1995, 1996) included *Admestina* in Ballinae, based on male genital structure. Edwards (1999) tentatively included *Attidops* in Ballinae, based mainly on male genital characters: presence of a pale longitudinal furrow, well-coiled embolus lying flat on the tegulum, unequally bilobed tegulum and presence of a flattened carapace. Platnick (1984) observed that *Cheliferoidea* possess a palp similar to that of *Marengo*. However, I do not consider any of these genera to be correctly placed in Ballinae due to the absence of ec (2-1), a spiralled embolus that coils at least once (4-1, 5-1, 5-2).

Maddison (1995, 1996) used the following two characters to place *Admestina* and *Cheliferoidea* in Ballinae: (1) a well-coiled embolus lying flat on the tegulum, and (2) a tegulum which is divided by a pale longitudinal furrow. Emboli of *Admestina* and *Cheliferoidea* coil less than once around the tegulum, they are broad-based, stout and project outwards; *Attidops* has a longer embolus (Edwards, 1999). While the presence of an oval, bilobed tegulum in *Admestina* and *Attidops* suggests placement within Ballinae, the lack of an embolic coil means that their affinity to the subfamily remains unclear. These genera might form a taxon that is sister to Ballinae. The presence of an unequally bilobed tegulum (1-1) and flattened carapace (20-1) might turn out to be plesiomorphic for Ballinae. Thus, the phylogeny of Ballinae needs to be reassessed in future studies.

Salticidae is the largest spider family, with 4834 described species and 531 genera (Platnick, 2003). Many have been inadequately described and estab-

lishing their evolutionary relationships is an enormous task. It is my hope that the present study will go some way towards achieving this goal and encourage other workers to examine scales and other morphological characters, together with cheliceral dentition and genitalia.

NATURAL HISTORY

DISTRIBUTION AND HABITAT

Members of Ballinae are found in Africa, Asia and Europe. Almost all species occur in tropical rain forest, at various elevations. They have been mostly collected by beating vegetation. *Marengo*, *Colaxes* and *Ballus segmentatus* from Sri Lanka were collected by beating shrubs and plants up to a height of c.1 m. The type localities are remnant patches of primary tropical montane cloud forests (Benjamin, 1999). The only species reported to be collected from forest litter was *Marengo deelemanae* (per label of female specimen) which was found in secondary forest bordering a limestone outcrop and young mangroves (habitat described in Deeleman-Reinhold, 2001). The natural history of *Marengo inornata* and *M. striatipes* is unclear, as the original labels give no details of the collecting method or the exact locality. *Ballus chalybeius* is known to occur only on broad-leaved bushes and trees, particularly oaks (Roberts, 1995).

SALTICID SCALES

Salticid scales are composed of cuticular filaments. Unlike other setae, however, each pedicel or stalk of the scale is bent at an angle where it emerges from its integumental socket (Figs 7G, 15G; Hill, 1979: fig. 1). This results in the axis of the scale being parallel with the surface of the integument. Another characteristic of salticid scales is the presence of inferior spines orientated distally (Figs 7G, 15G, 40E, 44C, 69G; Hill, 1979: fig. 6b). The results of this study suggest that salticid scales are an informative character system.

ANT MIMICRY

As spiders are small, soft-bodied, and without defensive chemicals, they are often preyed upon by wasps and birds. These predators exert a selective pressure which favours the evolution of protective devices. A great diversity of passive antipredator devices has evolved among spiders, as wasps and birds use visual cues to detect their prey (Pekár & Král, 2002). Batesian mimicry, which is an imitation of noxious, armed or distasteful animals, provides such a protective device. Due to restrictions on

size and morphology, most spider mimetic models are insects, particularly ants (Oliveira & Sazima, 1984; Oliveira, 1988; Pekár & Král, 2002). Experimental evidence of reduced predation on most ant-like spiders is lacking (however, see Engelhardt, 1971; Palmgren *et al.*, 1937; Cutler, 1991). Wanless (1978) suggested Batesian mimicry in spider species formerly placed in *Marengo*, pointing out their resemblance to ants or pseudoscorpions. Recently, Zabka (1999) implied that they mimic flies instead: 'Marengo specimens may mimic flies in reverse, with first legs held in the manner of flies' wings'. It has been postulated that *Ballus* spp. mimic weevils (Dahl, 1926: 34). However, Murphy & Murphy (2000) disagreed, remarking: 'some authors suggest they mimic ants or even pseudoscorpions, but we remain unconvinced'.

The confusion appears to originate with the original description of the genus by George W. and Elizabeth G. Peckham (Peckham & Peckham, 1892). Their paper, titled 'Ant-like Spiders of the Family Attidae', describes a range of genera with either prosomal or opisthosomal modifications or both. In the introduction they mention the reason for grouping the genera: 'the likeness to ants is rendered striking by a constriction of the cephalothorax or of the abdomen, by which the body seems to be made up of three segments instead of two'. They further give convincing behavioural observations for many species described in the paper.

Unfortunately, they included a few species, such as *Marengo crassipes*, without listing body modifications. No behavioural observations have been published either by the Peckhams or any author since for *M. crassipes*. Instead, subsequent authors have simply adopted the term 'ant-like' or its equivalent from their title whenever referring to *Marengo*. Based simply on their overall similarity, Peckham & Peckham (1892) grouped jumping spiders which were not closely related to each other. Obviously, these taxa did not share a common evolutionary history. Further, in the absence of a phylogenetic hypothesis, no proper analysis of character evolution and life history variation could be undertaken.

I investigated two characters describing morphological modifications that might be considered to give an appearance of three segments as found in ants (Figs 2, 3). The first character, the presence of white patches on lateral sides of the opisthosoma (**23-1**) is found in *Marengo* (Figs 60A, 61A, 68G) and *Philates chelififer* (Fig. 25D). However, whether these patches can be considered as evidence of the presence of mimicry is unclear. The second character is the presence of a protuberance (pp) on the posterior part of the prosoma (**28-1**). It originates once at node 8 and includes the genera *Afromarengo* (Wanless,

1978: fig. 1d), *Indomarengo* (Figs 38C, 41A, 42D), *Leikung* (Figs 4D, 48D, 49D) and *Sadies* (Fig. 45D). However, this character is present in *Sadies fulgida*, *S. gibbosa* (Fig. 45D; Wanless, 1984a: figs 2d, 4d), but is absent in *S. seychellensis* and *S. trifasciata* (Wanless, 1984a: figs 5d, 6d). Thus, only a small proportion of the species formerly placed in *Marengo* could be even considered as possible ant mimics. However, as this is only a tentative hypothesis, caution should be used when drawing conclusions about ant-mimicking behaviour in such a morphologically diverse group as Ballinae. In the absence of behavioural observations, all such hypotheses remain arbitrary.

DISCUSSION

SYSTEMATICS

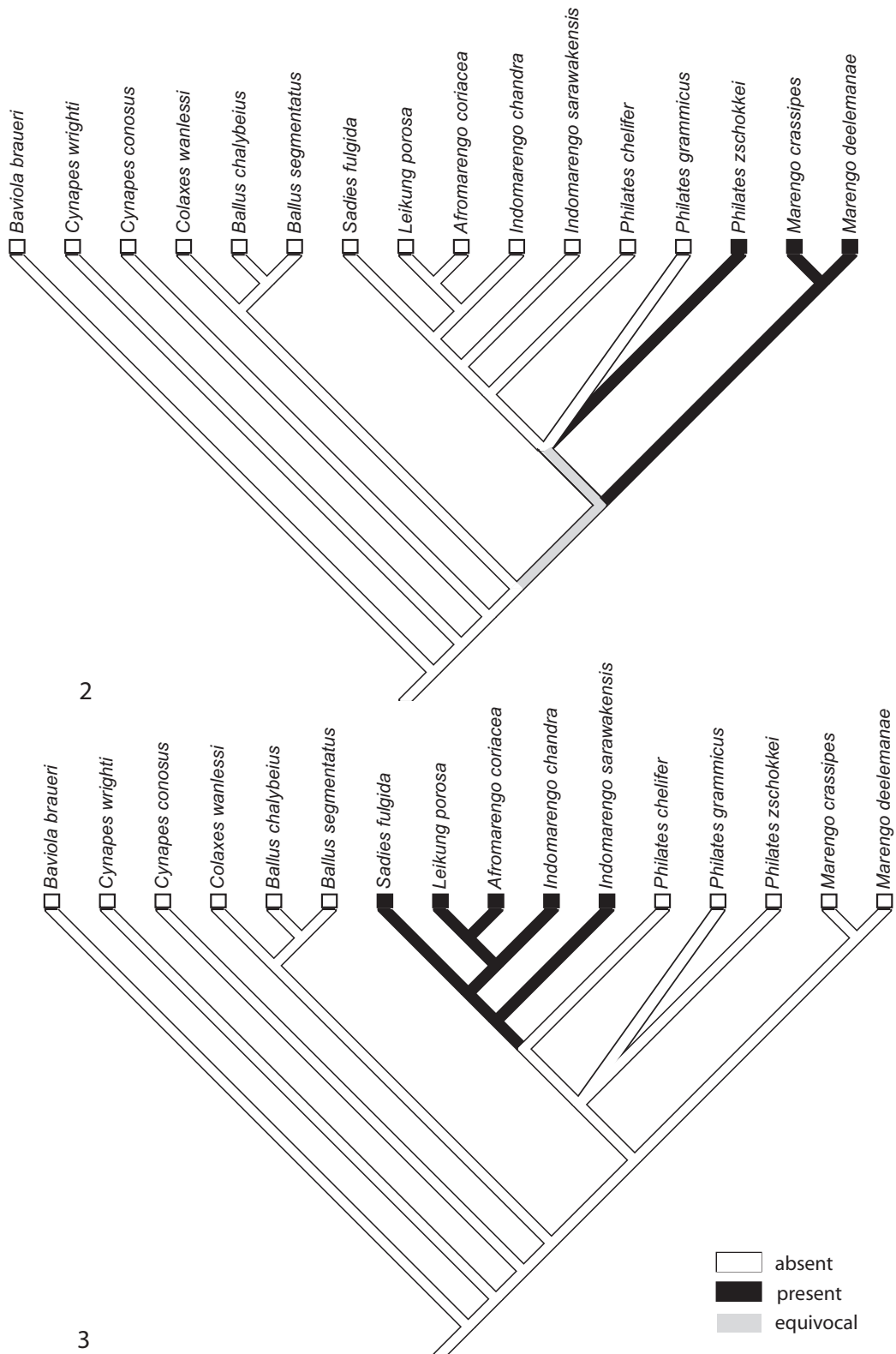
Ballinae Simon, 1897

Diagnosis: Ballinae differ from other jumping spiders by the following combination of characters:

- (1) The presence of an embolic coil (ec in Figs 15A, B, 28B, D), a thin long embolus that lies flat on the apical part of the tegulum (Figs 15B, 20A, B, 47C–E, 63A) and coils at least 360° (e in Figs 8A–D, 11B, C, 15A, B, 57A–C, 58A, C, D); pars pendulum, conductor and palpal apophysis are lacking.
- (2) Presence of a subtegulum that extends above the tibia (except for *Cynapes wrighti*; Figs 8C, D, 11C, 17A, B, 48A, B, 57A–C, 60B, C).
- (3) Epigynum with a narrow septum (except for *C. wrighti*, *Leikung*, *Afromarengo*; ek in Figs 9A, 13B–D, 14A–C, 16B–D, 18A–C, 22B, D, 61B, 62A–D, 66B–D, 67B, C, 68B–D).
- (4) Copulatory opening leading to long tangled ducts that end in spermathecae with internal spicules.
- (5) Enlarged femur I (f in Figs 16A, 22A, 33A, B, 68A, G) and dark band on both lateral sides of legs I–IV.
- (6) Small to medium size, enlarged tibia I (except for *Ballus segmentatus* from Sri Lanka, *Cynapes* (Wanless, 1979, 1984a; Proszynski, 2003) and *Sadies* spp. (except for *S. gibbosa*, Wanless, 1984a: fig. 4h).

Distribution: Ballinae is known from Africa, Europe and Asia.

Composition: Thirteen genera, of which nine are included in this revision. *Copocrossa*, *Mantisatta*, *Padilla* and *Pachyballus* are tentatively included. *Goleta* is not included for the time being, due to the lack of characters discussed earlier. Its position needs to be assessed in future studies.



Figures 2, 3. Parsimony reconstruction of morphological modifications that confirm structural resemblance to ants. The most parsimonious tree, as shown in Fig. 1, is presented. Fig. 2, reconstruction of the evolution of white patches on sides of opisthosoma. Fig. 3, reconstruction of the evolution of the prosomal protuberance, see text for details.

KEY TO GENERA

(1)	Tibia I without leaf-like tibial setae (Figs 7D, 10D, 15H, 19D, 24D, E).....	2
-	Tibia I with leaf-like tibial setae.....	4
2(1)	Prosoma as long as wide (Figs 21A, 22A, C).....	<i>Ballus</i>
-	Prosoma longer than wide.....	3
3(2)	Four (two pairs) spines on tibia I, prosoma dorsoventrally flattened, vulva with a thin, translucent, septum (sv in Figs 13C, D, 14A-C, 16D), without a dark band on both lateral sides of legs I-IV; Sri Lanka, India.....	<i>Colaxes</i>
-	Six spines on tibia I, prosoma sharply elevated, vulva without a thin, translucent, septum (sv in Fig. 9B; except for <i>Cynapes canosus</i>), with a dark band on both lateral sides of legs I-IV.....	<i>Cynapes</i>
4(1)	Protuberance on the posterior part of the prosoma, present (pp in Figs 48D, 49D, 38C, 42).....	5
-	Protuberance on the posterior part of the prosoma, absent.....	8
5(4)	Embolus long: more than two spirals (Figs 48A, 49A, 52A, B, 57A-C), copulatory openings connected to each other by a posterior epigynal border (peb in Figs 48E, 50A).....	6
-	Embolus short: less than two spirals.....	7
6(5)	Eight spines on tibia I (Figs 49D, 53E, 55C), posterior lateral eyes raised (ple in Figs 49D, 53A; (Wanless, 1978: fig. 7f; pls. 2e, 3a), anterior epigynal border with a tooth (T in Figs 48E, 50A-C); Indonesia, Malaysia.....	<i>Leikung</i>
-	Six spines on tibia I, posterior lateral eyes not raised, anterior epigynal border without a tooth; Africa.....	<i>Afromarengo</i>
7(5)	Path of the sperm duct C-shaped (Figs 45C, 46A, B), vulva without a thin, translucent, septum; Seychelles.....	<i>Sadies</i>
-	Path of the sperm duct S-shaped (Figs 38E, 41E, 42A), vulva with a thin, translucent, septum (sv in Fig. 39A-B); Indonesia, Malaysia.....	<i>Indomarengo</i>
8(4)	Femur I (fl in Fig. 25C, G) not enlarged (except for <i>Marengo striatipes</i>), translucent septum small (Fig. 26A-C), opisthosoma relatively elongated (Figs 25D, 29A), plumose scales present (ps in Fig. 27E, H); Indonesia, Malaysia.....	<i>Philates</i>
-	Femur I enlarged (except for <i>Marengo striatipes</i>), translucent septum large.....	9
9(8)	Copulatory atrium with a gland (cag in Figs 32A-D, 35B, C), septum separating epigynal atria with a sclerotized projection (scp in Fig. 32C; except for <i>Philates zschokkei</i>), no white patches on lateral sides of opisthosoma (wp in Figs 25D, 61A), proximal end of embolus modified to a pseudo-conductor (Fig. 36A-D; except for <i>Philates grammicus</i>); Papua New Guinea, Philippines and Indonesia.....	<i>Philates</i>
-	Copulatory atrium without a gland, septum separating epigynal atria without a sclerotized projection, a dark patch on posterior half of the opisthosoma is present (dp in Figs 61A, 65A, D), no transverse white line on opisthosoma (Figs 33A, 45F), sexual dimorphism present; Sri Lanka, India, Thailand.....	<i>Marengo</i>

BAVIOLA SIMON, 1898

Type species: Baviola braueri by original description.

Diagnosis: Baviola can be distinguished from Ballinae by the following characters: absence of ec (2) (Fig. 7A, B), embolus stout, projecting outwards from its base (4, 5) (Figs 5A-F, 7A, B), absences of a dark band on lateral sides of legs I-IV (27) and enlarged femur I (30) (Wanless, 1984a: figs 9g, h, 10f, 11g, h, 12h).

Monophyly and phylogenetic placement: Baviola is most probably monophyletic, although this remains to be tested in future studies.

Description: See Wanless (1984a).

Composition: Three species: *Baviola braueri* Simon, 1898, *B. luteosignata* Wanless, 1984 and *B. vanmoli*, Wanless, 1984. All three are known only from the Seychelles. *B. tenuimana* (Simon, 1893), also from the

Seychelles, was regarded as a *nomen dubium* by Wanless (1984a).

Distribution: Endemic to the Seychelles.

BAVIOLA BRAUERI SIMON, 1898

(FIGS 5A, B, 6, 7A-G)

B. braueri Simon, 1898: 386, 1♂ lectotype in ZIZM, Hamburg, not examined.

B. braueri Simon, 1901: 471, fig. 537.

B. braueri Wanless, 1984, 29, fig. 9a-k.

B. spatulata Wanless, 1984: 31-33, fig. 10a-g. 1♂ holotype, Silhouette, Mare aux Cochons, 500 m, 3-4.7.1972, PLG Benoit & JJ Van Mol (MRAC 150.957) and 1♀ paratype, from the same locality (MRAC 143.138), examined. **syn. nov.**

Diagnosis: Baviola braueri can be distinguished from other species in the genus by details of the palpal tibia

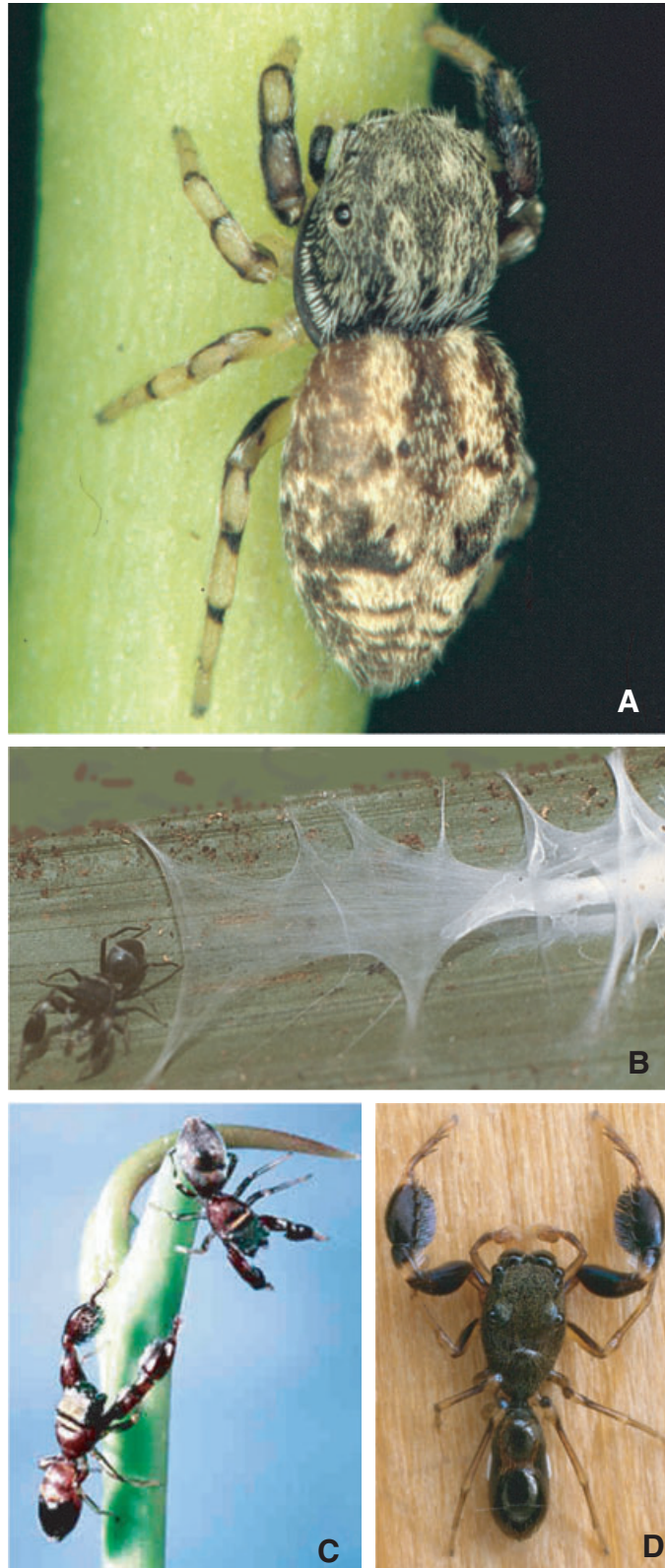


Figure 4. Photographs of live Ballinae species. A, *Ballus chalybeius* (Barbara Knoflach). B, *Indomarengo sarawakensis* sp. nov. (Christa L. Deeleman-Reinhold). C, *Afromarengo coriacea* (John Murphy). D, *Leikung porosa* from Malaysia, Gunung Trus Madi (Peter Koomen).

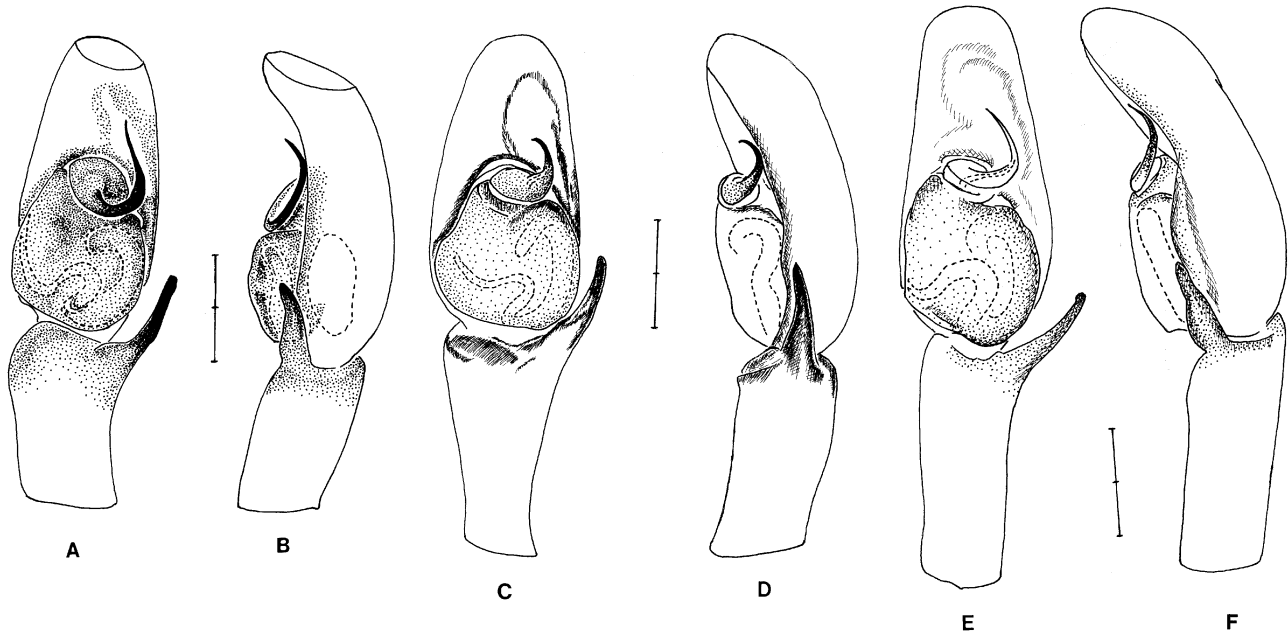


Figure 5. Male palp. A, B, *Baviola braueri* (MZT). A, ventral view. B, retrolateral view. C, D, *B. luteosignata* (MRAC 150.962). C, ventral view. D, retrolateral view. E, F, *B. vanmoli* (MRAC 150.964). E, ventral view. F, retrolateral view. Scale bars = 0.2 mm.

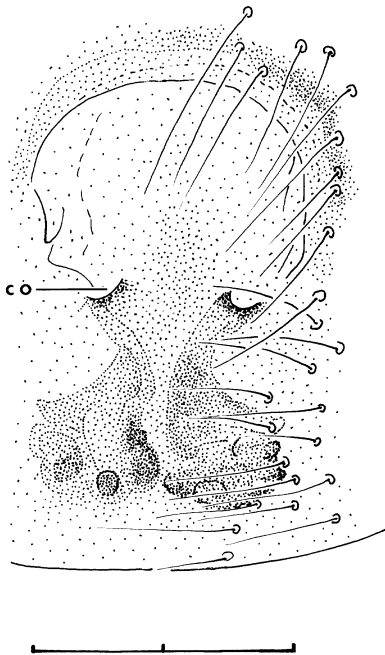


Figure 6. *Baviola braueri* (MRAC 143.138). Epigynum, ventral view. Scale bar = 0.2 mm.

and rta (Fig. 5A, B); *B. braueri* has the shortest tibia; the rta is broad-based with a constriction at the apical half, which is confirmed by ESEM observation (Fig. 7D) and is shorter than in the other two species.

Remarks: *Baviola spatulata* Wanless, 1984 is considered a junior synonym of *B. braueri*, as I am unable to distinguish the type material using the diagnosis provided by Wanless (1984a).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

Other material examined: SEYCHELLES, Silhouette, La Passe, among palm leaves; 1♂, 13.1.1999, leg & det Michael Saaristo, MZT; Praslin, Fond Ferdinand, forêt, pure *Delodoicea maldivica*; 1♂, 24.7.1972, leg. PLG Benoit & JJ Van Mol, det Wanless (1978), MRAC 143.399.

BAVIOLA LUTEOSIGNATA WANLESS, 1984
(FIG. 5C, D)

B. luteosignata Wanless, 1984: 34–36, fig. 11a–h. 1♂ holotype, Seychelles, Mahé, Centre, Morne Séchellos, 750–800 m forêt endémique, 13–17.7.1972, PLG Benoit & JJ Van Mol (MRAC 150.962), 1♂ (MRAC 143.284) and 2♀ paratypes, data as above (MRAC 150.968), all at MRAC, examined.

Diagnosis: *Baviola luteosignata* can be distinguished from other species in the genus by the length of the palpal tibia and details of the rta (Fig. 5C, D); *B. luteosignata* has an rta that is broad-based, which tapers to a pointed end. The palpal tibia is midway in

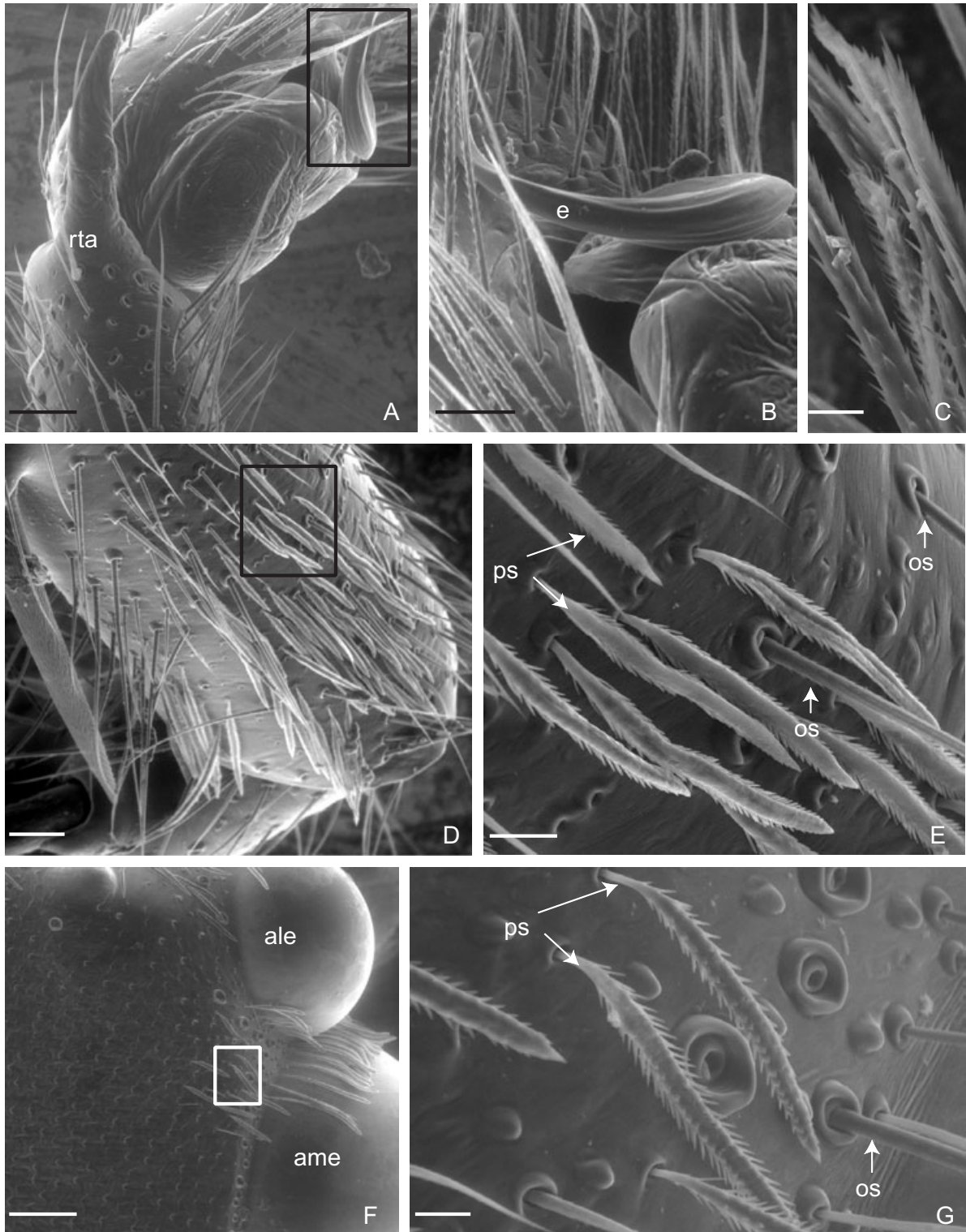


Figure 7. ESEM, *Baviola braueri* (MZT). A, B, right male palp, retrolateral view. C, setae of the cymbium apex. D, E, tibia of left leg I, lateral view. F, G, prosoma, frontal section, dorsal view. Scale bars = 5 μm (C); 10 μm (E, G); 30 μm (B); 50 μm (A, D); 100 μm (F).

length in *B. luteosignata*, shortest in *B. braueri* and longest in *B. vanmoli* (Fig. 5A–F).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

Other material examined: None.

BAVIOLA VANMOLI WANLESS, 1984
(FIG. 5E, F)

B. vanmoli Wanless, 1984: 36–38, fig. 12a–h. 1♂ holotype, Seychelles, Mahé sud, Anse à la Mouche 16–31.7.1972, PLG Benoit & JJ Van Mol, MRAC 150.964 and 1♀ paratype, Seychelles, Silhouette, Mare aux Cochons, 500 m, 3–4.7.1972, PLG Benoit & JJ Van Mol, MRAC 143.443, examined.

Diagnosis: *Baviola vanmoli* can be distinguished from other species in the genus by details of the length of the palpal tibia and rta (Fig. 5E, F): *B. vanmoli* has the longest palpal tibia; the rta is broad-based with a constriction at the apical half as in *B. braueri*, but is longer than in the other two species in the genus. The female of *B. vanmoli* may be distinguished from those of *B. braueri* and *B. luteosignata* by the longer and parallel copulatory ducts (Wanless, 1984a: fig. 12f, g).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

Other material examined: SEYCHELLES, Mahé, Mare aux Cochons; 1♂, pitfall traps. Jan. 1999, leg: Michael Saaristo, Pat Matyot and Maureen Kirkpatrick, det: Michael Saaristo, MZT.

CYNAPES SIMON, 1900

Type species: *Cynapes wrighti*, by original description.

Monophyly and phylogenetic placement: Probably polyphyletic. Based on my cladistic analysis of Ballinae generic relationships, *C. canosus* should be placed in a new monotypic genus. However, I prefer not to describe a new genus at this stage. The status of *Cynapes* remains to be tested with rigorous sampling and phylogenetic methods.

Remarks: Prior to the study of Wanless (1979) *Cynapes* included three species: the type *C. wrighti*, *C. baptizatus* and *C. canosus*. Wanless tentatively transferred *C. canosus* to *Marengo*, but gave no reasons for doing so, except for saying that the genitalia were in broad agreement with those of *Marengo*. However, he mentioned the lack of enlarged tibia I (31).

Further, he mentioned characters apomorphic for *C. canosus* (40-1) and suggested that its generic placement should be reconsidered when more is known of tropical salticids. Details of the genitalia, such as the shape of the subtegulum (1), presence of ec (2), embolus length (5) and lack of enlarged tibia I are all plesiomorphic and thus cannot be used to characterize a genus including *C. canosus* and *Marengo*. Moreover, such a transfer of *C. canosus* to *Marengo* would add four additional steps to the preferred tree. Wanless (1979, 1984a) suggested that *Cynapes* might be synonymous with *Baviola*. However, his hypothesis is not supported in this study.

Diagnosis: *Cynapes* can be distinguished from other Ballinae genera, except for *Sadies*, by the presence of a sharply elevated prosoma (20) (Wanless, 1979: fig. 2b; 1984a: fig. 13b) and the absence of an enlarged tibia I (Wanless, 1979: figs 1b, 2c, j; 1984a: fig. 13g). It is separated from *Baviola* by the presence of ec (Fig. 8A–D), embolus laying flat on ec (4; Fig. 8A–D) and an enlarged femur I (30) (Wanless, 1979: figs 1b, 2c, j; 1984a: fig. 13g), and from *Sadies* by the presence of cag in *Sadies* (16; Figs 45C, 46A, B).

Description: See Wanless (1979, 1984a).

Composition. Three species: *Cynapes baptizatus* (Butler, 1876) from Rodriguez, *C. canosus* from Mauritius and *C. wrighti* (Blackwall, 1877) from the Seychelles.

Distribution: Mauritius, Rodriguez and the Seychelles. Wanless (1984a) mentions its occurrence in Madagascar.

CYNAPES WRIGHTI (BLACKWALL, 1877)
(FIGS 8A, B, 9B, 10A–G)

Salticus wrightii Blackwall, 1877: 2, pl. 1, fig. 1. 1♂ lectotype (designated by Wanless, 1984a) from the Seychelles, UMO, vial 1778/1 not examined.

Bavia wrighti Simon, 1893: 209.

Cynapes wrighti Simon, 1901: 471, figs 533–534 (lapsus calami).

C. wrightii Wanless, 1984: 39, fig. 13a–g.

Diagnosis: The male of *C. wrighti* can be distinguished from that of *C. canosus* by a pear-shaped subtegulum that does not extend above the tibia (Fig. 8A, B), and from that of *C. baptizatus* by the stout rta (Fig. 8B; Wanless, 1979: fig. 1c, h). The female can be distinguished from that of *C. canosus* by the presence of a narrow epigynal septum in the latter (Fig. 9A). Wanless (1979) proposed that the position of tracheal slits can be used to distinguish *C. wrighti* from *C. baptizatus*: a short distance away from the anterior spinnerets in *C. wrighti* and just in front of the anterior spinnerets in *C. baptizatus*.

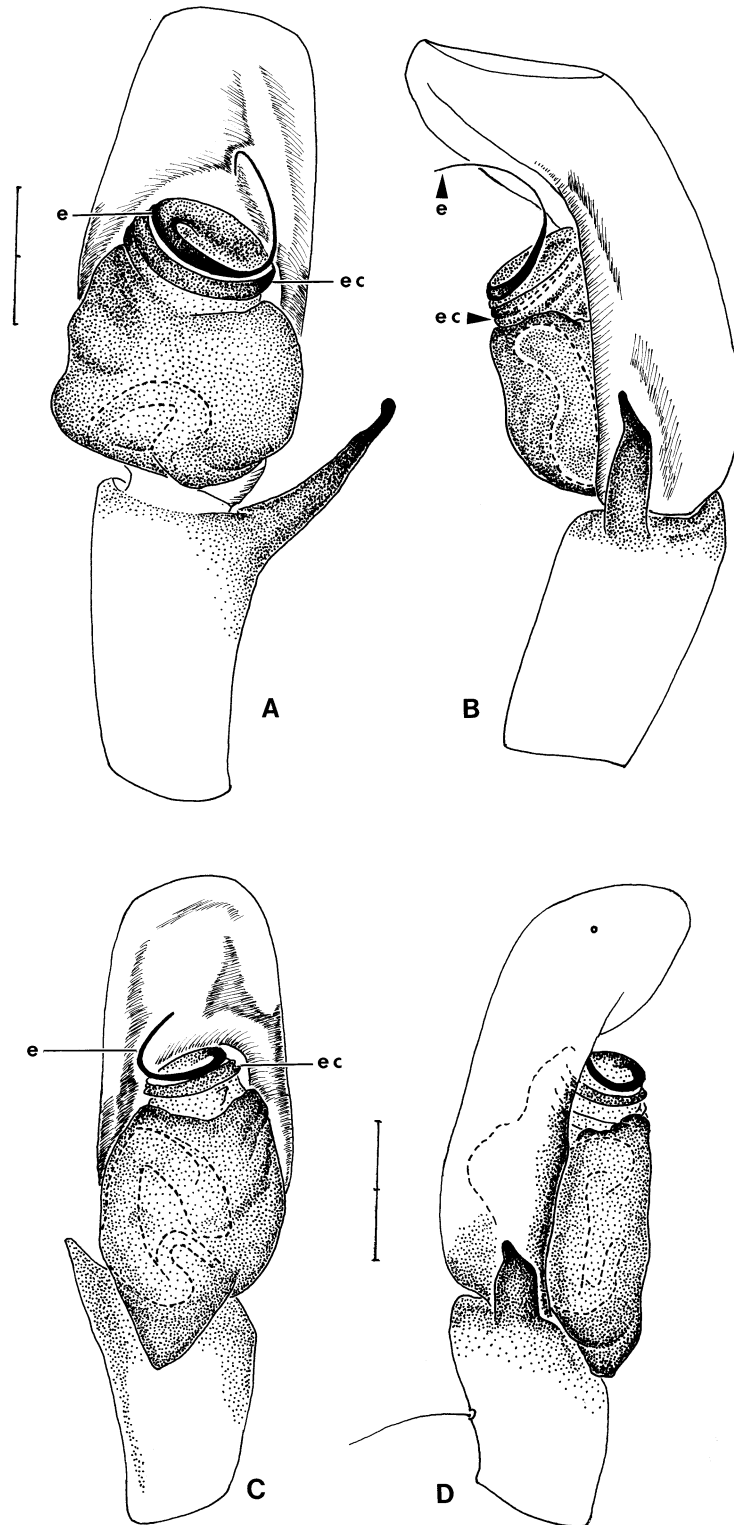


Figure 8. Male palp. A, B, *Cynapes wrighti* (MRAC 143.455). A, ventral view and B, retrolateral view of male palp. C, D, *C. canosus* (MHNH 20353). C, ventral view and D, retrolateral view of right male palp. Scale bars = 0.2 mm.

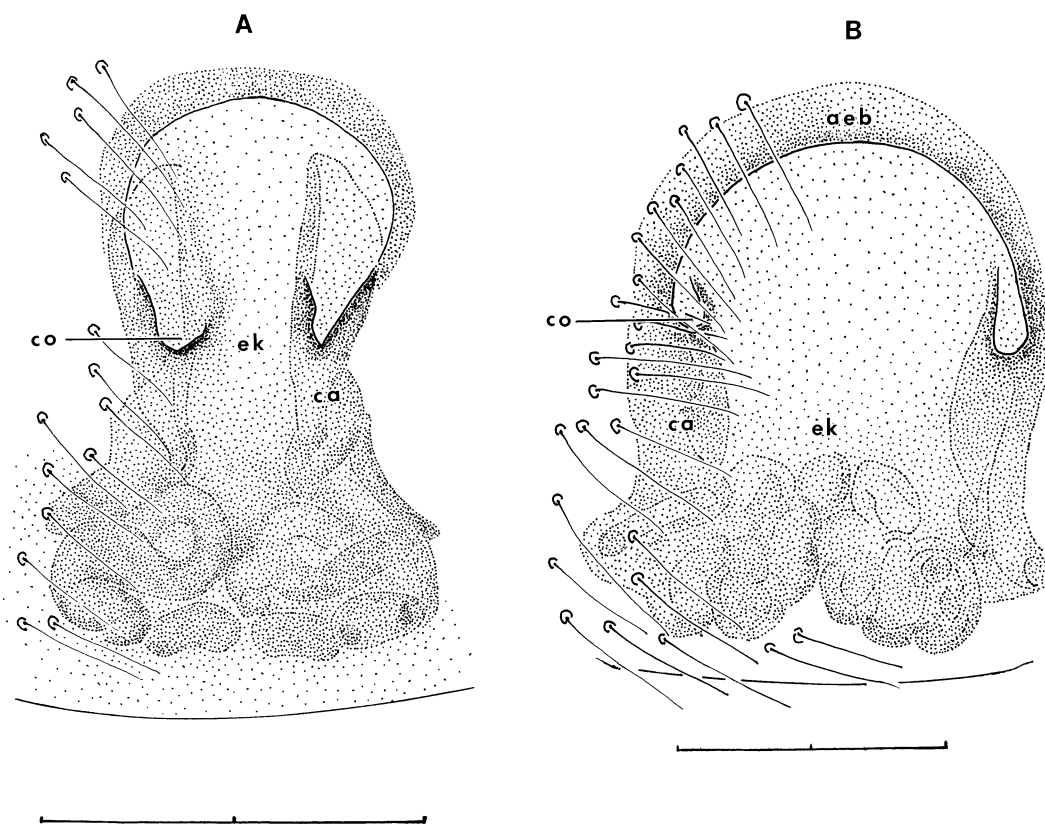


Figure 9. Female genitalia of *Cynapes* spp. Epigynum, ventral view A, *C. canosus* (MHNH 20353). B, *C. wrighti* (MRAC 143.455). Scale bars = 0.2 mm.

Description: See Wanless (1984a).

Distribution: The Seychelles.

Other material examined: SEYCHELLES: Mahé Nord, Beau Vallon: 1♂, 12.6.1972, MRAC, MT 143 174; Mahé Sud, Anse á la Mouche: 1♂ 1♀, 30.6.1972, MRAC, MT 143.455.

CYNAPES CANOSUS SIMON, 1900
(FIGS 8C, D, 9A)

Cynapes canosus Simon, 1900: 393. 1♂ 1♀, lectotype (MNH 2353), examined.

Marengo canosus Wanless, 1979: 70, fig. 2a–k. Designation of lectotypes.

Diagnosis: The male of *C. canosus* can be distinguished from that of all the other species of the genus by the presence of a subtegulum that extends above the tibia (Fig. 8C, D), the female by the presence of a narrow epigynal septum (Fig. 9A).

Description: See Wanless (1979).

Distribution: Mauritius.

Other material examined: None.

COLAXES SIMON, 1900

Colaxes Simon, 1900: 402. Simon, 1901: 492–493.

Type species: *Colaxes nitidiventris*, from Trichinopoly, India, by original designation (Simon, 1900).

Monophyly and phylogenetic placement: Apomorphic for this genus are dark markings on the laterals of the opisthosoma (**25-1**) and loss of the dark band on both lateral sides of legs I–IV (**27-0**). The presence of only four spines on tibia I unites *Ballus* and *Colaxes*.

Remarks: A single member of this genus has received taxonomic attention. Simon (1900, 1901) recognized that *C. nitidiventris* was not congeneric with *Philates* or *Marengo* and discussed how these taxa differ from each other. Despite its relative abundance, nothing further has since been published.

Diagnosis: *Colaxes* can be distinguished from all other Ballinae by: (1) the presence of dark markings on the laterals of the opisthosoma (Figs 12A, 16A) and absence of markings on the lateral sides of legs I–IV; (2) the presence of only four

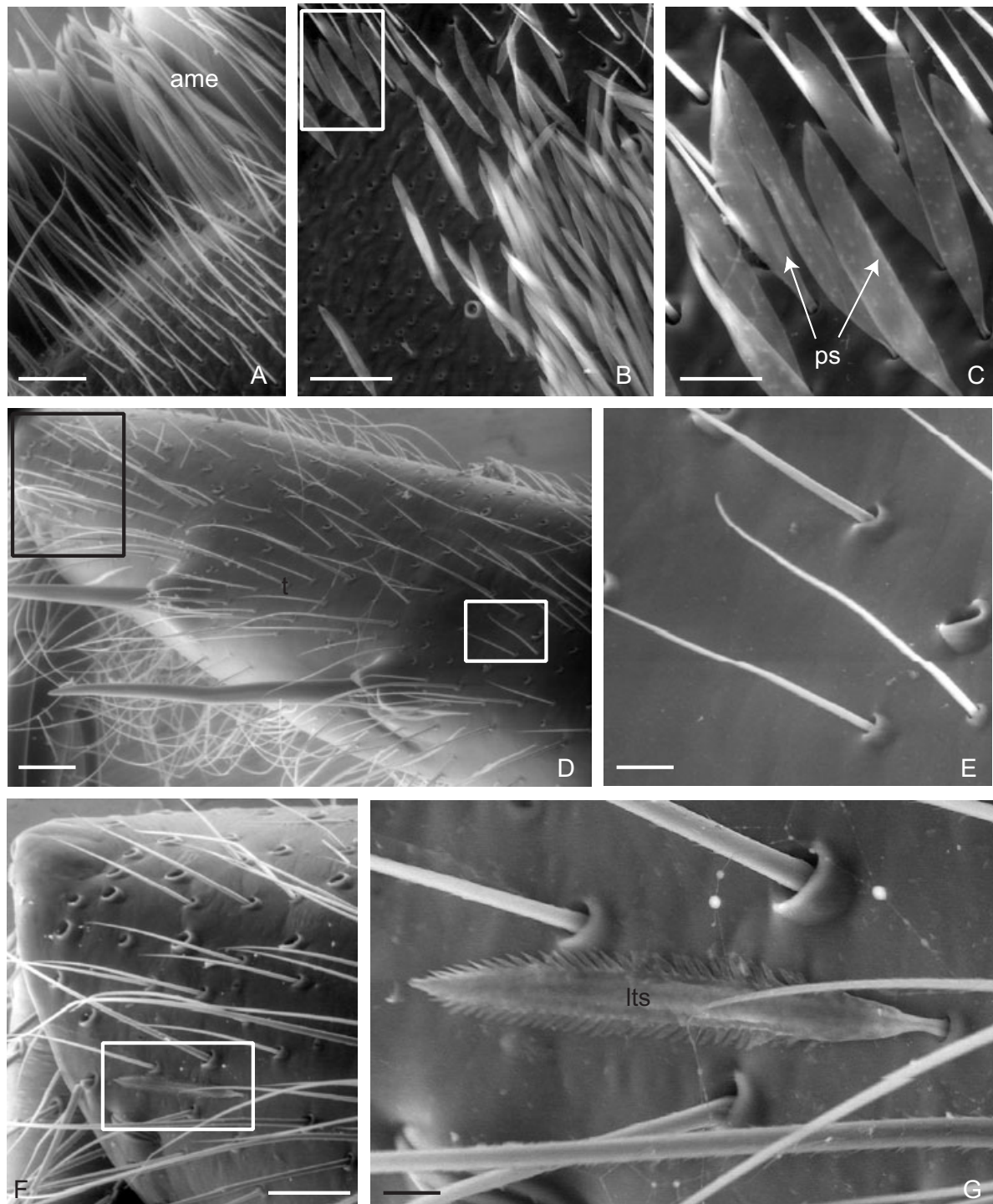


Figure 10. ESEM, *Cynapes wrighti* (MRAC 143.455). A–C, prosoma, dorsal view. D–G, tibia of right leg I, lateral view. Scale bars = 5 μm (G); 10 μm (A, C, E); 30 μm (B, F); 50 μm (D).

spines on tibia I (except for *Ballus*) and absence of lts (except for *Cynapes* and *Ballus*) (33; Fig. 15G, H).

Description: See description of type species.

Composition: Three species: *C. horton* sp. nov., *Colaxes nitidiventris* Simon, 1900, and *C. wanlessi* sp. nov.

Distribution: Currently, only known from South India and the central highlands of Sri Lanka.

COLAXES NITIDIVENTRIS SIMON, 1900
(FIG. 11A–C)

Colaxes nitidiventris Simon, 1900: 402. Single ♂ from Trichinopoly, India, MNHN 18919, examined. Designated here as lectotype to define the genus and species. The female is unknown. Many more new species and related new genera can be expected from the region.

Diagnosis: Distinguished from *C. wanlessi* by the tapering opisthosoma (Fig. 11A) and rta with a pointed end (Fig. 11B, C). The male of *C. horton* is unknown.

Male: Lectotype (MNHN 18919), total length 4.4; prosoma length 2.3, width 1.3. Leg I: femur 1.0, patella 0.5, tibia 0.8, metatarsus 0.6, tarsus 0.2. Markings as in Figure 11A. Prosoma oval, dorsoventrally flattened, tapering backwards, light brown, without prominent markings except for two black spots on the anterior end. Opisthosoma long, tapering, with dark markings, within a yellow background. Transverse white line at the centre, laterally darker, dorsally light

yellow. Legs laterally without dark markings. Eyes surrounded by dark rings. Chelicerae light brown, four retromarginal teeth. Labium triangular, light brown. Leg formula 1423. Tibia I with 2/0/0/3 spines, metatarsus I with 2/2 spines. Palp: cymbium corn shaped; apical end broader (Fig. 11B, C), rta long and thin, tapering to a pointed end. Tegulum bilobed, embolus coils 1.5 times (Fig. 11B, C).

Female: Unknown.

Natural history: Unknown.

Distribution: Trichinopoly, India, where the only known specimen was collected.

Other material examined: None.

***COLAXES WANLESSI* SP. NOV.**
(FIGS 12A–C, 13A–E, 14A–C, 15A–H)

Holotype: ♂ from Sri Lanka. Central Province, Hakgala, Hakgala forest, 1600 m, leg. Suresh P. Benjamin, 27.7.1996, deposited in MHNG.

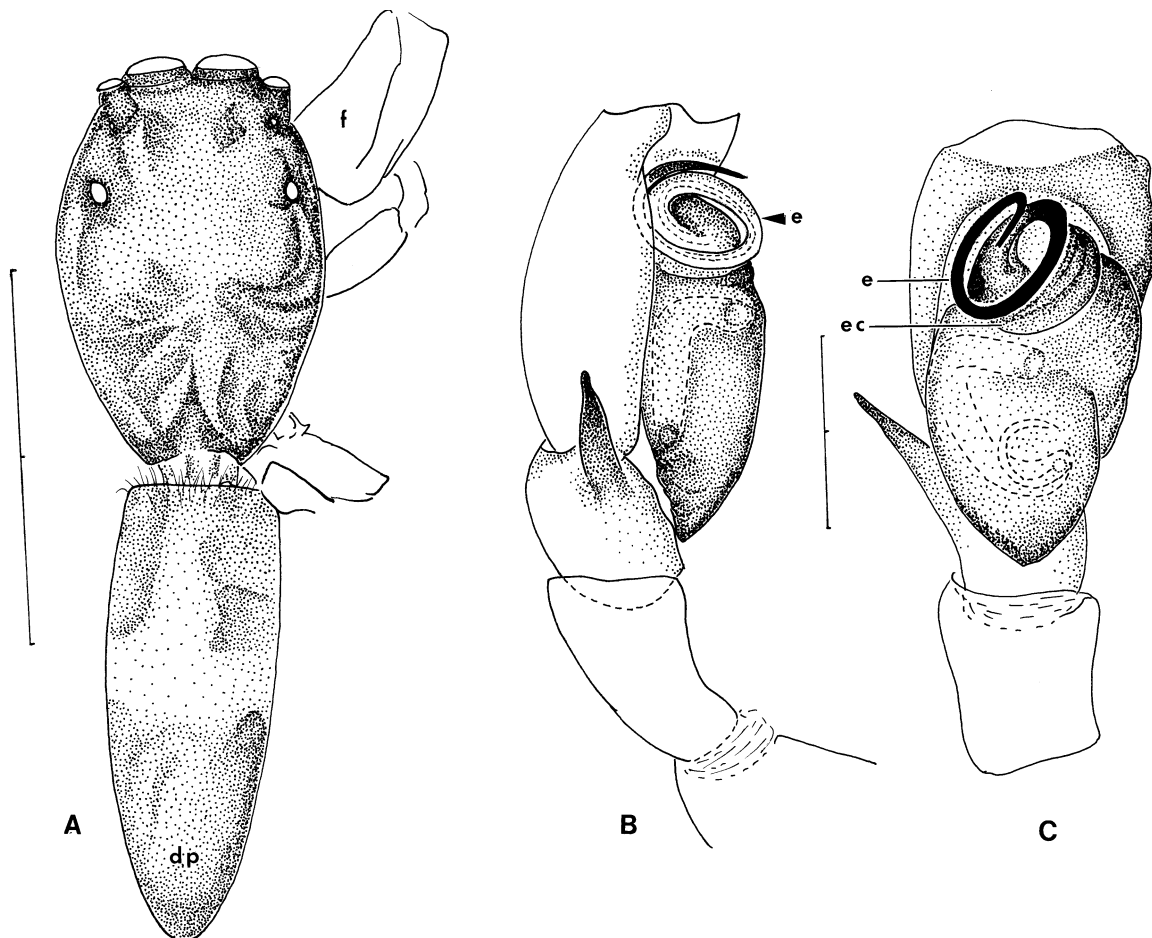


Figure 11. *Colaxes nitidiventris* (MNHN 18919). A, habitus, dorsal view. B, right male palp, retrolateral view. C, same, ventral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

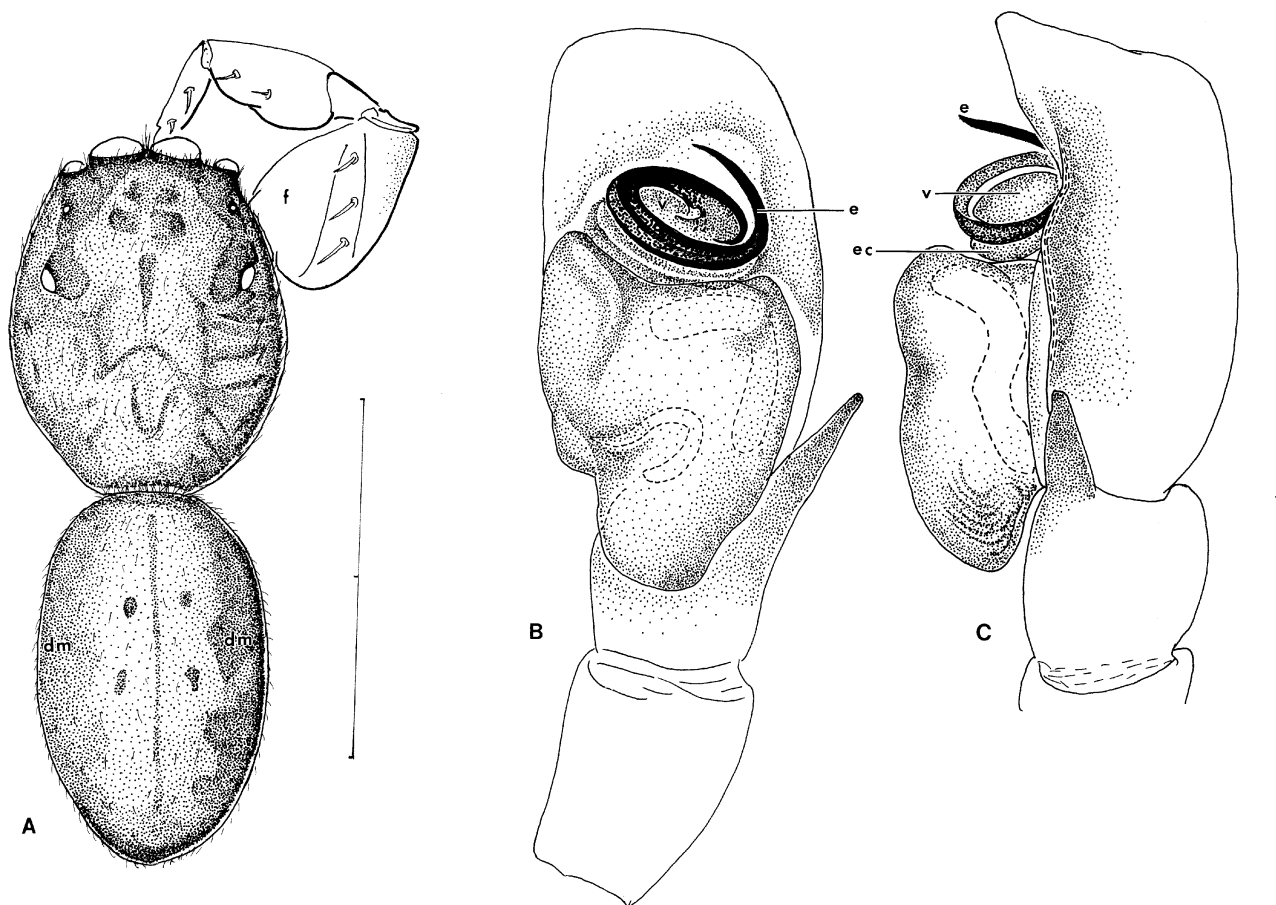


Figure 12. *Colaxes wanlessi* sp. nov. (MHNG). Male from Hakgala, Sri Lanka. A, habitus, dorsal view. B, male palp, ventral view. C, same, retrolateral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

Paratype: One ♀ from Sri Lanka: Central Province, Hakgala, Hakgala forest, 1600 m, leg. Suresh P. Benjamin, 27.7.1996; 1♀, Central Province, Agrapatana, Agra-bopath forest, 1100 m, leg. Suresh P. Benjamin and Sudath V. Nanayakkara, 8.3.2000. All deposited in MHNG.

Etymology: Named after Fred Wanless in recognition of his pioneering contribution to salticid systematics.

Diagnosis: This species can be distinguished from its sister species by the oval prosoma, opisthosoma, and the shorter, broad-based *rta* (Fig. 12A–C). *C. nitidiventris* has an opisthosoma which tapers backwards and a longer, sharply pointed *rta*, while *C. hortoni* has a central dark band on the opisthosoma (Fig. 16A).

Male holotype: Total length 4.0; prosoma length 2.0, width 1.5. Leg I: femur 1.2, patella 0.4, tibia 0.8, metatarsus 0.5, tarsus 0.3. Markings as in Figure 12A. Prosoma oval, almost as wide as long, dark brown, laterals darker, thin black median line. Opisthosoma oval, longer than wide, lighter in colour, four dark

markings (red in living specimens), black lateral patches. Leg I dark brown, legs II–IV light yellow; all legs laterally without dark markings. Eyes surrounded by dark rings. Chelicera dark brown, with three retromarginal, small teeth, labium triangular, dark brown. Leg formula 1423. Tibia I with 2/0/0/3 spines, metatarsus I with 2/2 spines. Palp: cymbium oval. Retrolateral tibial apophysis stout, tapering blunt end (Fig. 12B, C). Tegulum bilobed, projecting outwards, path of sperm duct as in Figure 12B, embolus stout, coils 1.5 times (Figs 12B, 15A, B).

Female paratype: Total length 3.8; prosoma length 1.7, width 1.1. Leg I: femur 0.7, patella 0.3, tibia 0.5, metatarsus 0.3, tarsus 0.2. Markings of specimens in alcohol as in Figure 13A, E. Prosoma oval, almost as long as wide, dark brown, with a central dark band. Opisthosoma long as wide, lighter in colour, two parallel dark bands set in a yellow background, dorsally uniformly yellow. Leg I dark brown, legs II–IV light yellow, all legs laterally without dark markings. Eyes surrounded by dark rings. Chelicera dark brown, with three small, retromarginal teeth, labium triangular,

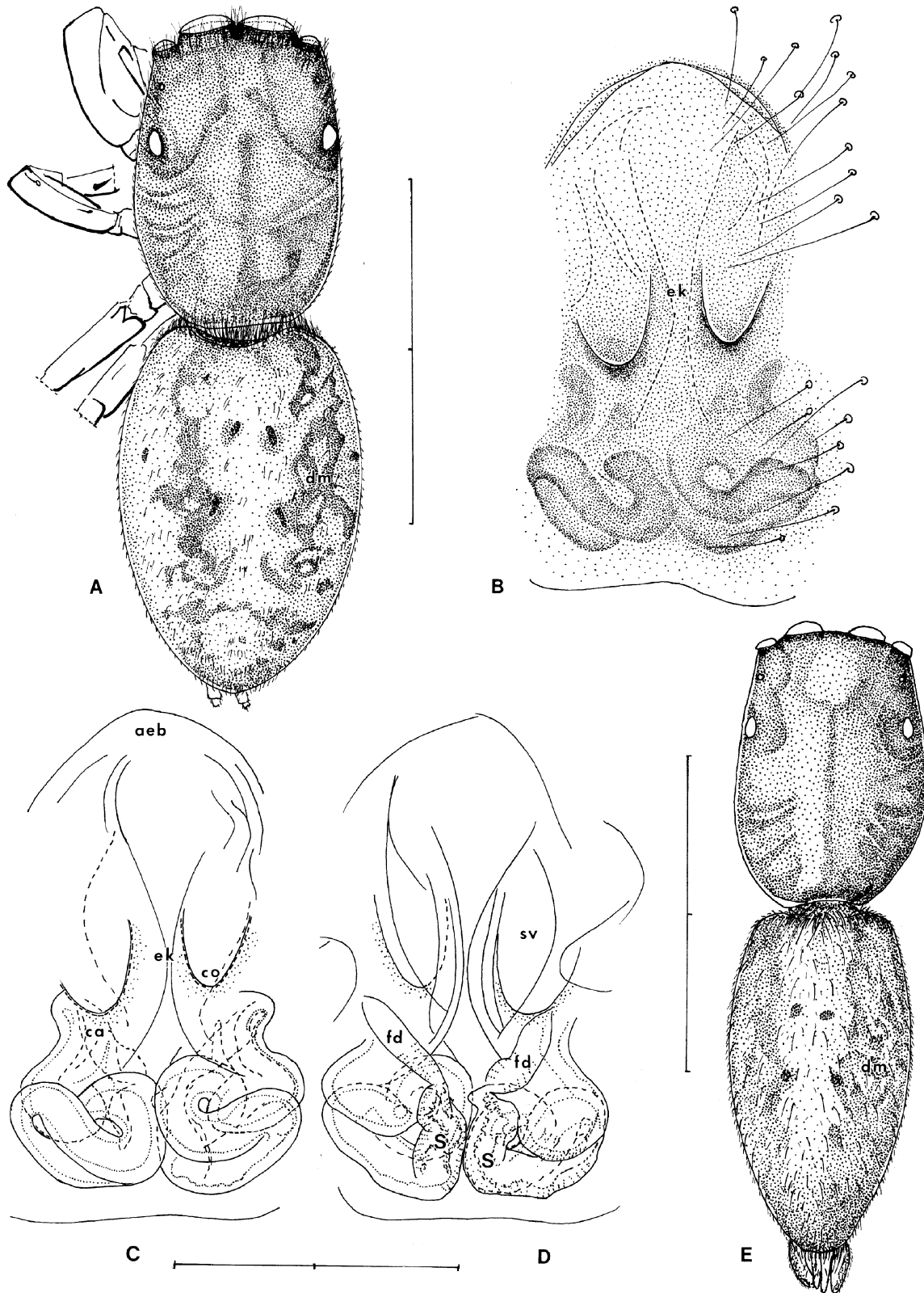


Figure 13. *Colaxes wanlessi* sp. nov. (MHNG). Females from Agrapatana (A–D) and Hakgala (E), Sri Lanka. A, habitus, dorsal view. B, epigynum, ventral view. C, vulva, ventral view. D, same, dorsal view. E, habitus, dorsal view. Scale bars = 0.2 mm (B–D); 2.0 mm (A, E).

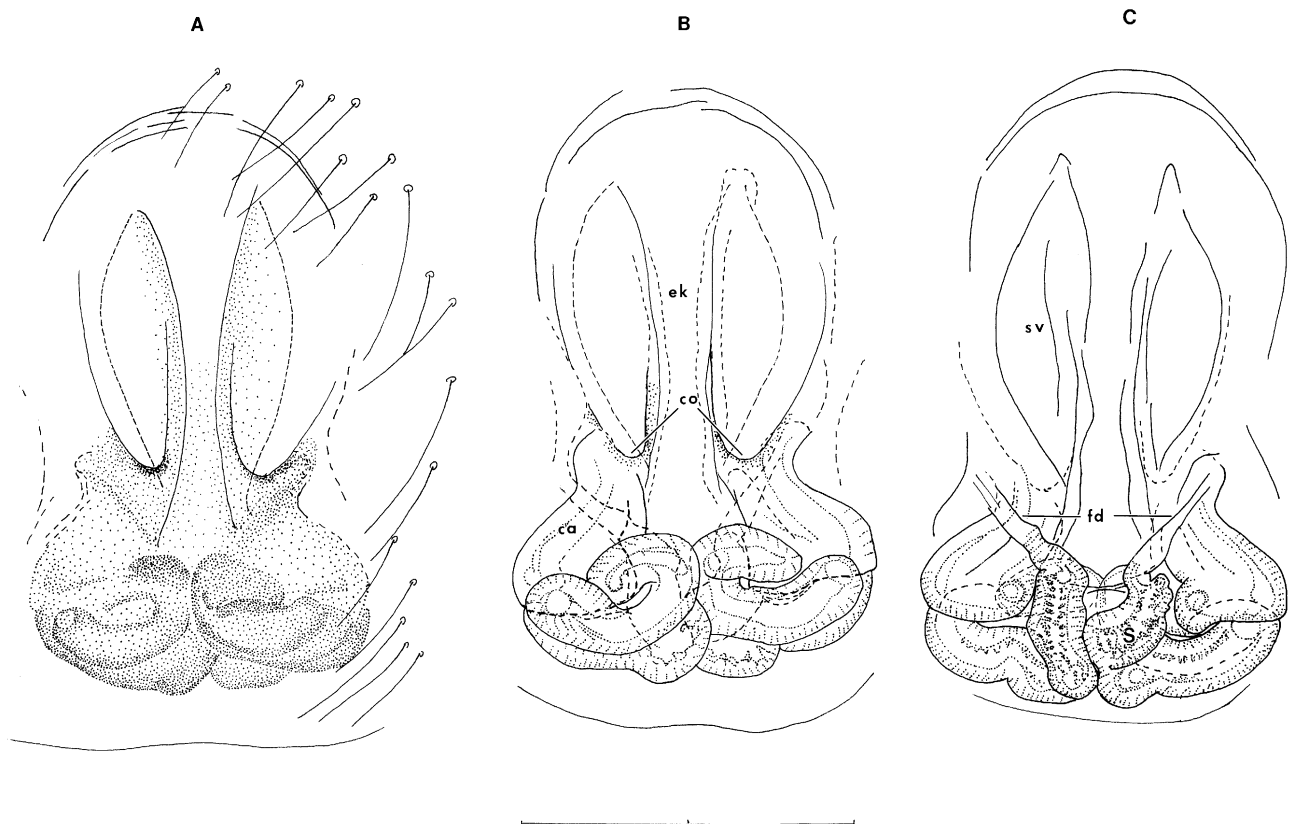


Figure 14. *Colaxes wanlessi* sp. nov. (MHNG). Female from Hakgala, Sri Lanka. A, epigynum, ventral view. B, vulva, ventral view. C, same, dorsal view. Scale bar = 0.2 mm.

dark brown. Leg formula 4132. Tibia I with 2/0/0/3 spines, metatarsus I with 2/2 spines. Epigynum and vulva as in Figure 13B–D.

Distribution: Sri Lanka, Central Province, Agrapattana/Hakgala Knuckles Range.

Other material examined: SRI LANKA: Central Province, Hakgala, Hakgala forest, 1600 m, 1♂, leg. Suresh P. Benjamin, 27.7.1996, deposited in MHNG (sputter coated SEM stub); Central Province, Knuckles Range, along the Rattota–Ilukkumbura road, 900 m; 1♀, leg. Suresh P. Benjamin, 1–30.6.2003, MHNG.

COLAXES HORTON SP. NOV.

(FIG. 16A–D)

Holotype: ♀, Sri Lanka. Central Province, Horton Plains National Park, 2100 m, 9.3.2000, leg. Suresh P. Benjamin, deposited in MHNG.

Paratype: ♀, same data as holotype.

Etymology: Named after the type locality.

Diagnosis: Distinguished from *C. wanlessi* sp. nov. by the central dark band on the opisthosoma (Fig. 16A).

C. horton is generally smaller and darker than the two previous species.

Female holotype: Total length 2.8; prosoma length 1.5, width 1.0. Leg I: femur 0.7, patella 0.3, tibia 0.4, metatarsus 0.3, tarsus 0.2. Prosoma longer than wide, lateral sides almost parallel, dark brown, sides lighter, anterior half darker, no white markings, central line hardly visible. Opisthosoma oval, with a dark, broad central band dorsally, followed by two yellow bands on both sides. Lateral flanks of the opisthosoma are darker, venter uniformly light yellow. Legs I–IV laterally without dark markings. Eyes surrounded by dark rings (Fig. 16A). Chelicera, labium and dorsal parts lighter in colour. Leg formula 4132. Tibia I with 2/0/0/3 spines, metatarsus I with 2/2 spines. Epigynum and vulva as in Figure 16B–D.

Male: Male unknown.

Distribution: Known only from the type locality.

Other material examined: None.

BALLUS C.L. KOCH, 1850

Type species: *Ballus chalybeius* (Walckenaer, 1802).

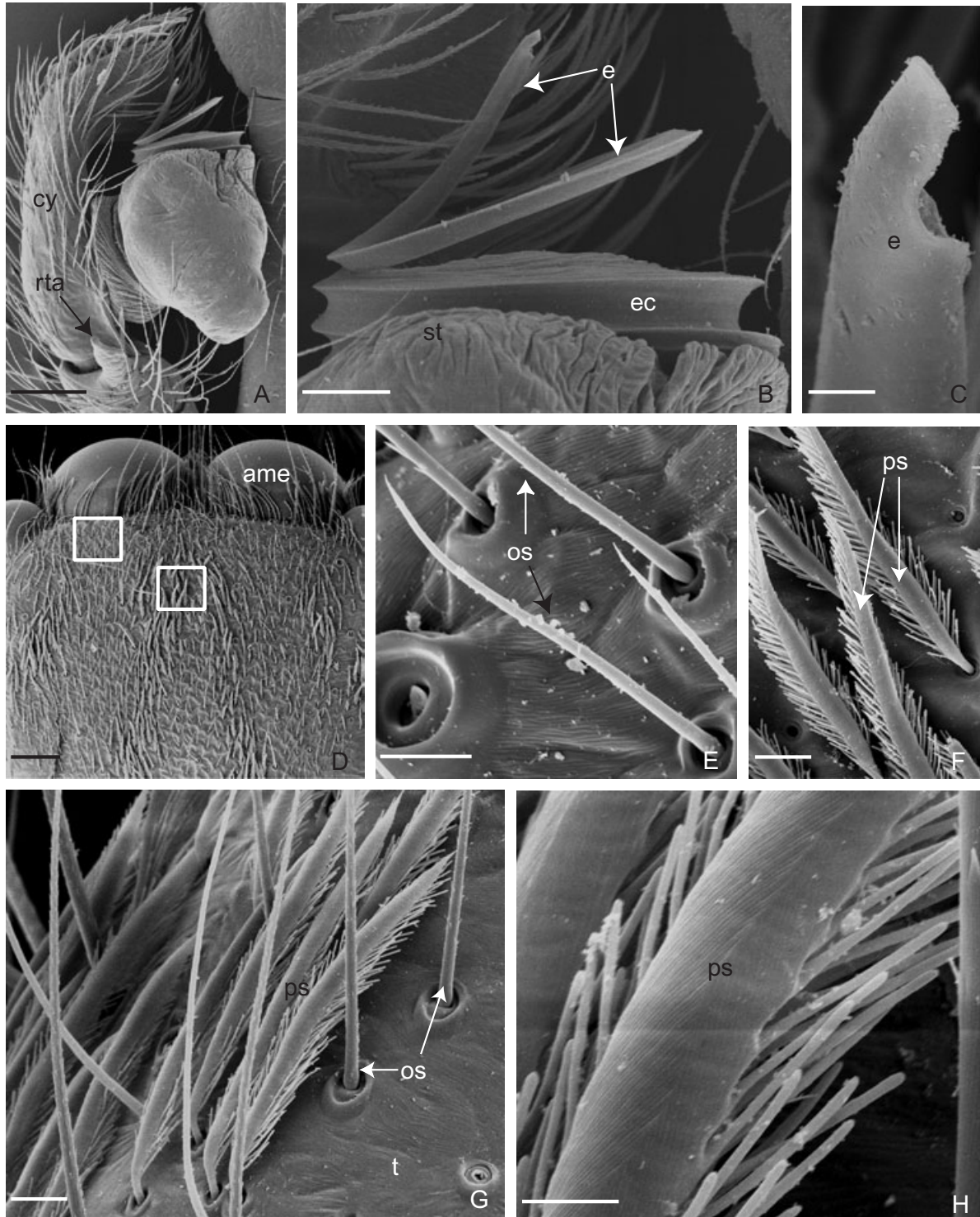


Figure 15. SEM, *Colaxes wanlessi* sp. nov. (MHNG). A–C, male palp. A, retrolateral view. B, st, ec and embolus. C, tip of embolus. D–F, prosoma, dorsal view. G, H, right leg. I, lateral view. Scale bars = 3 μ m (C, H); 10 μ m (E, F, G); 30 μ m (B); 100 μ m (A, D).

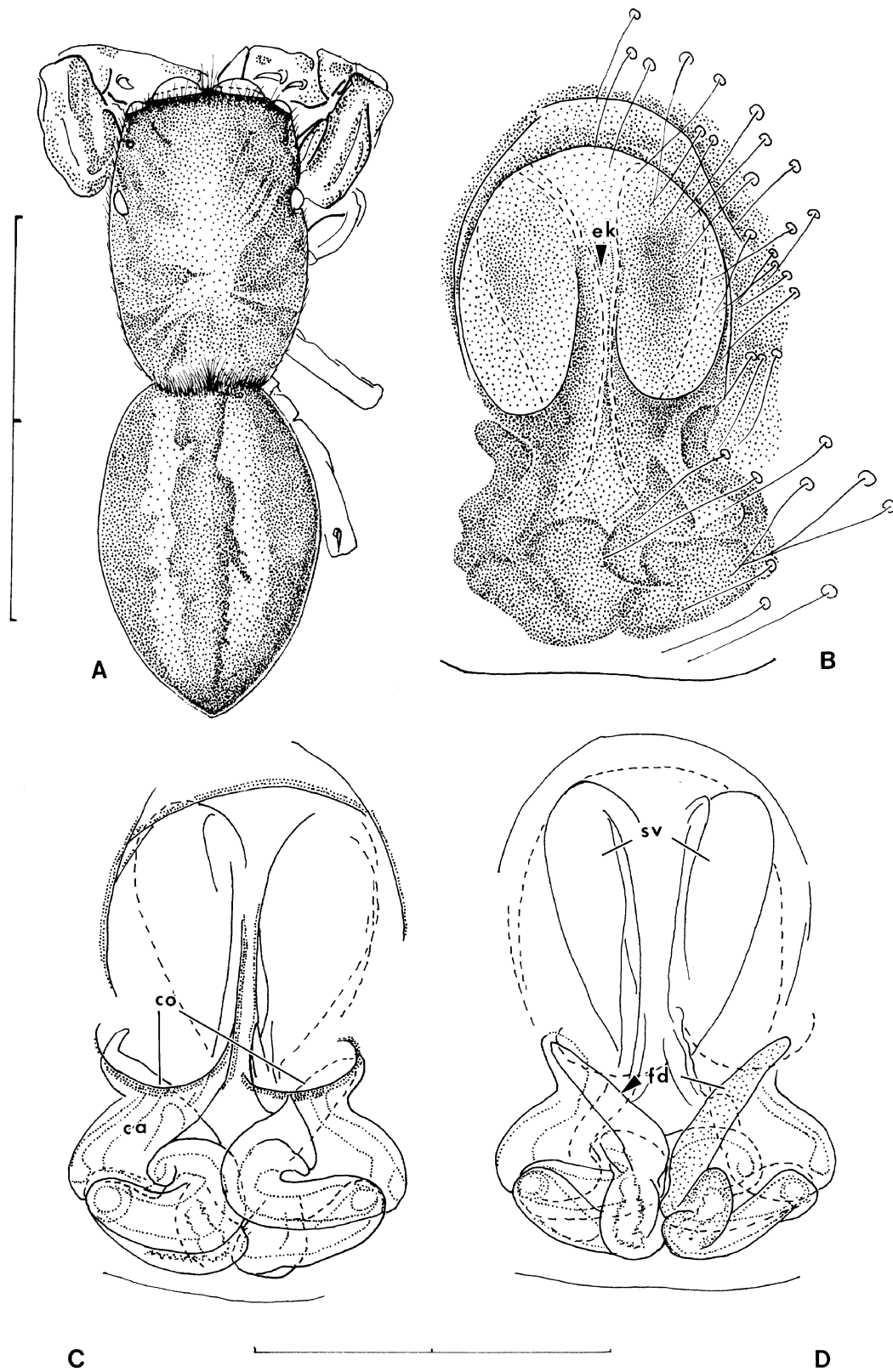


Figure 16. *Colaxes horton* sp. nov. (MHNG). Female from Horton Plains, Sri Lanka. A, habitus, dorsal view. B, epigynum, ventral view. C, vulva, ventral view. D, same, dorsal view. Scale bars = 0.2 mm (B–D); 2.0 mm (A).

Monophyly and phylogenetic placement: Monophyly of the genus is supported by the presence of a prosoma as long as wide (21-1) and of reticulate markings on the opisthosoma (26-1).

Diagnosis: *Ballus* can be separated from all other Ballinae genera by the presence of a prosoma as long as it is wide (Figs 21A, 22A, C).

Description: See Alicata & Cantarella (1987) and below.

Composition: Ten recognized species; see Platnick (2003) for a listing.

Remarks: Platnick (2003) provides a full list of synonyms. *Ballus* was revised by Alicata & Cantarella (1987), and is therefore not dealt with in detail here. Alicata & Cantarella (1987) recognized that the European members of *Ballus* constitute a homogeneous group.

Distribution: Africa, Asia and Europe.

BALLUS CHALYBEIUS (WALCKENAER, 1802)
(FIGS 4A, 17A–D, 18A–C, 19A–E, 20A–D)

Platnick (2003) provides a full list of synonyms.

Diagnosis: The stout rta and absence of reticulate markings on the opisthosoma (Figs 17A, C, D, 20C, D;

Alicata & Cantarella, 1987: 19–36), separate the male of *B. chalybeius* and those of other European species from that of *B. segmentatus*. Females can be distinguished by the presence of an enlarged, sac-like translucent septum (Fig. 18B, C; Alicata & Cantarella, 1987: 3–18).

Description: For a detailed description see Alicata & Cantarella (1987), Roberts (1995), Proszynski (2003), and Locket & Millidge (1951). European species of *Ballus* have been revised by Alicata & Cantarella (1987). Illustrations for most species can be found in Proszynski (2003).

Distribution: Europe, North Africa to Central Asia (Platnick, 2003).

Material examined: SWITZERLAND, Umgebung Basel, 9♂ 11♀, 5.1888–6.1891, leg. F. Müller, Schenkel, Menth., Knecht, G. Müller, NMB 76a; Umgebung Basel, 36♂ 8♀, 1949, leg. E. Schenkel, NMB 76d; Tessin, Losone, Piano d'Arbigo, 700.780/114.360, Hochmoor, angrenz. Wälder. CV, 275 m; 1♀, 24.7.1991, leg. F Rampazzi, NMB 76 h; Jura, Lisière xérotherm.struct. (a.our.), Chevenez, Trou du Creugenat. Koord: 568900/249800 470 m; 1♂, 4.6.1988, leg. UVP Transjurane, NMB 76i; Jura, Lisière à préman. de Rubus, Bressaucourt, Dos Chalembert. Koord:

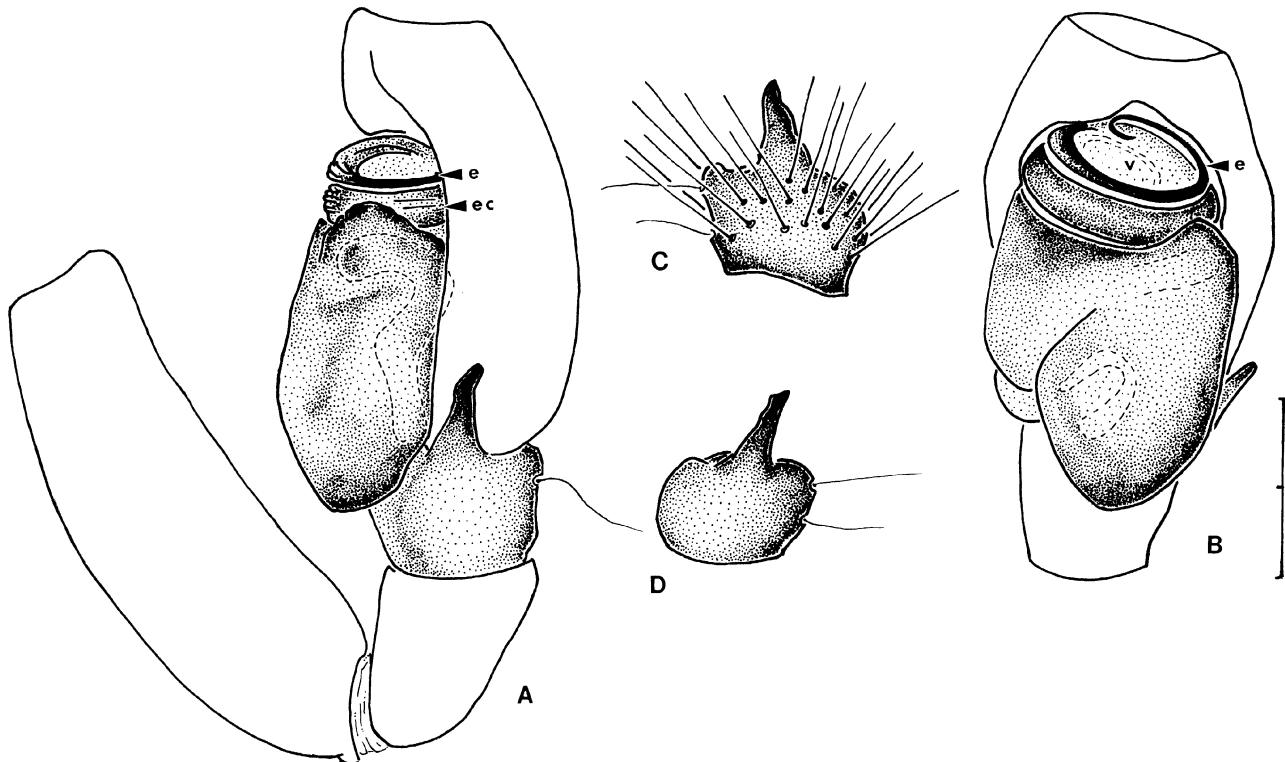


Figure 17. Male palp of *Ballus chalybeius*. A, B, Basel, Switzerland (NMB 76d). C, Chevenez, Switzerland (NMB 76i). D, Stara Tura, Slovakia (NMB 76 g). A, retrolateral and B, ventral view. C and D, rta. Scale bar = 0.2 mm.

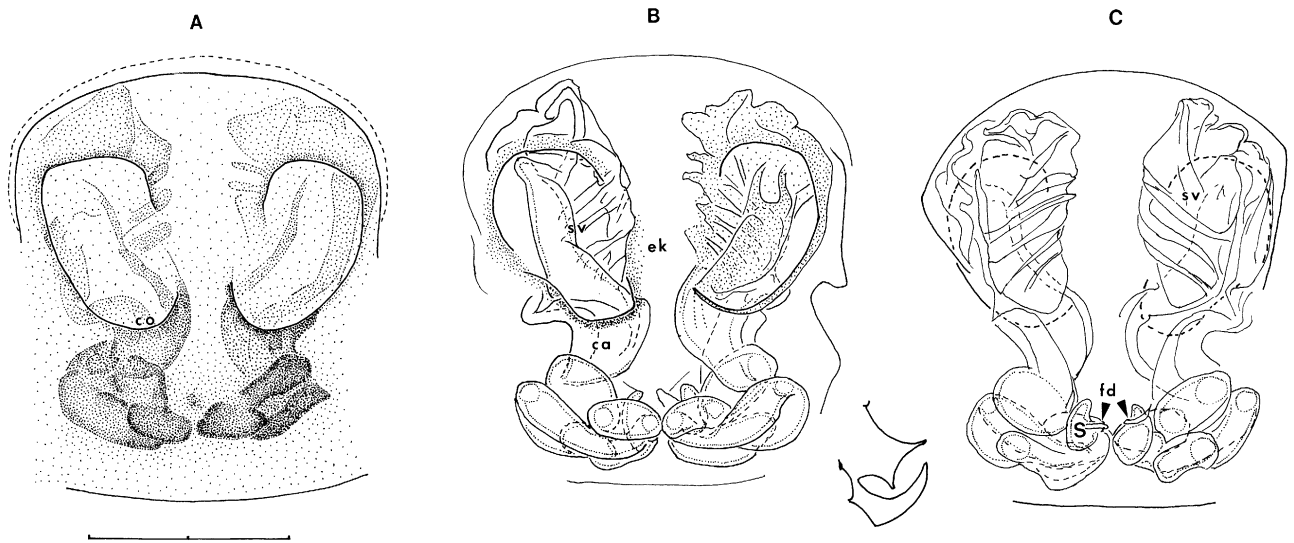


Figure 18. Female genitalia of *Ballus chalybeius* (NMB 76d). A, epigynum, ventral view. B, vulva, ventral view. C, same, dorsal view. Scale bar = 0.2 mm.

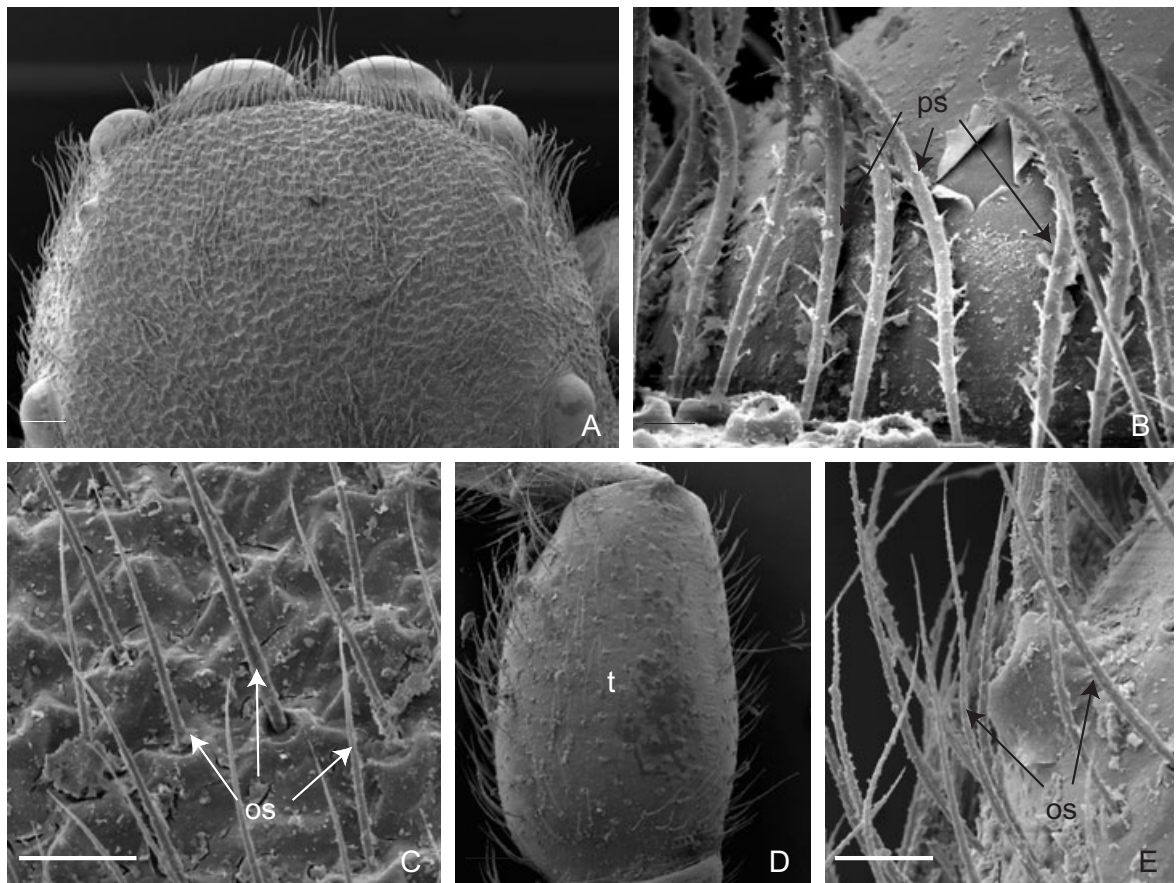


Figure 19. SEM, *Ballus chalybeius* (NMB 76d). A–C, prosoma, dorsal view. D, E, tibia of left leg I, lateral view. Scale bars = 10 μ m (B); 30 μ m (C, E); 100 μ m (A, D).

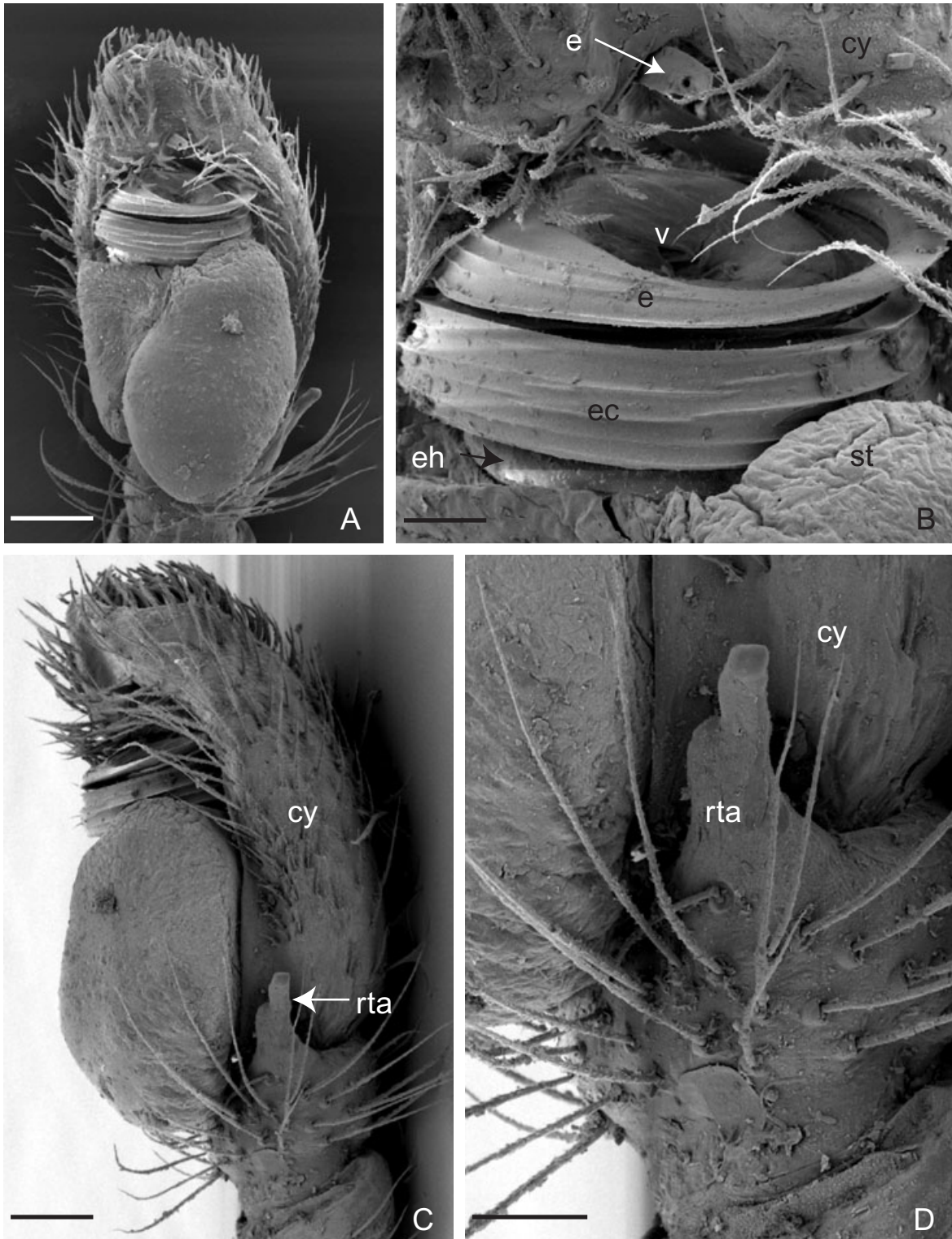


Figure 20. SEM, *Ballus chalybeius* (NMB 76d). A, male palp, ventral view. B, ec and embolus. D, male palp, retrolateral view. C, rta. Scale bars = 30 µm (B); 50 µm (D); 100 µm (A, C).

570400/249800 510 m; 1♀, leg. UVP Transjurane, NMB 76j; Choulex, 14♂ 22♀, coll. De Lessert, MHNG; Airelville 6E; 1♀, coll. S. Pozzi, m. 5.1996, det. S. Pozzi, MHNG. GERMANY, Baden-Wuerttemberg, Ober-Baden, 6♀, 9.1888, leg. F. Müller, NMB 76b; Baden-Wuerttemberg, Müllheim, 1♀, 12.10.1889, leg. F. Müller, NMB 76c; 3♂ 3♀ (probably from East Germany), coll. S. Heimer, MHNG; NSG Leutratal, 1♀, 8.1974, coll. S. Heimer, MHNG; Kreis Dresden, Borsbargbiet, 3♀, 28.6.1980 coll. S. Heimer, MHNG; Kreis Dresden, Borsbargbiet; 1♀, 24.5.1980 coll. S. Heimer, MHNG; Kreis Dresden, Borsbargbiet, Ober. Pillnitz, 3♀, 9.5.1981, coll. S. Heimer, MHNG; Kreis Dresden, Borsbargbiet, kahlschlag a.d. Rüsselkappe; 1♀, 11.7.1980, coll. S. Heimer, MHNG; Sächs. Schweiz, umg. Wehlen, Hanke bruch; 1♀, 28.5.1980, coll. S. Heimer, MHNG. SLOVAKIA, Weisse Karpaten (Stara Tura), Waldsteppe, Sträucher; 1♀, 17.8.1991, leg. J. Svaton, NMB 76f; Buchenwaldrand, Sträucher, 1♂ 1♀, leg. J. Svaton, NMB 76g; Bratislava, Donau-niederung, Extensivweide, 2♀, 6.1979, coll. S. Heimer, MHNG.

BALLUS SEGMENTATUS SIMON, 1900
(FIGS 21A–C, 22A–D, 23A, B, 24A–I)

Ballus segmentatus Simon, 1900: 389

Remarks: Types probably in MNHN, but not found (Tamas Szűts, pers. comm.). Simon (1900) described *B. segmentatus* and *B. sellatus* Simon, 1900, from Sri Lanka. The type of *B. segmentatus* is a male specimen whereas that of *B. sellatus* is a female. The presence of

two species in Sri Lanka has been doubted (Alicata & Cantarella, 1987). Judging from Simon's (1900) description and my material it is in fact likely that a second species exists. Taking into consideration the information available, my specimens are identified as *B. segmentatus* with some reluctance.

Diagnosis: The male is separated from European *Ballus* spp. by the presence of a pseudo-conductor, reticulate markings on the opisthosoma, and tapering rta (Figs 21A, C, 22A, C, 24G, H). The female can be distinguished by the absence of an enlarged, sac-like translucent septum (Fig. 23A, B).

Male: Total length 2.8; prosoma length 1.2, width 1.2. Leg I: femur 1.0 patella 0.3, tibia 0.5, metatarsus 0.3, tarsus 0.2. Markings as in Figure 21A. Prosoma rounded, wide as long, dark brown, laterals and eye region darker, anteriorly two black spots. Opisthosoma rounded, wide as long, lighter in colour, with reticulate markings. All legs light yellow and laterally without dark markings. Eyes surrounded by dark rings. Chelicerae dark brown, with three retromarginal, small teeth, labium triangular, light brown. Leg formula 1423. Tibia I with 2/0/0/2 spines, metatarsus I with 2/2 spines. Palp: cymbium oval. Retrolateral tibial apophysis stout, tapering to a pointed end. Tegulum bilobed, projecting outwards, path of sperm duct as in Figure 21B, C; embolus stout, coils once (Figs 21B, C, 24G, H).

Female: Total length 3.4; prosoma length 1.5, width: 1.3. Leg I: femur 0.7, patella 0.3, tibia 0.5, metatarsus 0.3, tarsus 0.2. Prosoma rounded, wide as long, dark

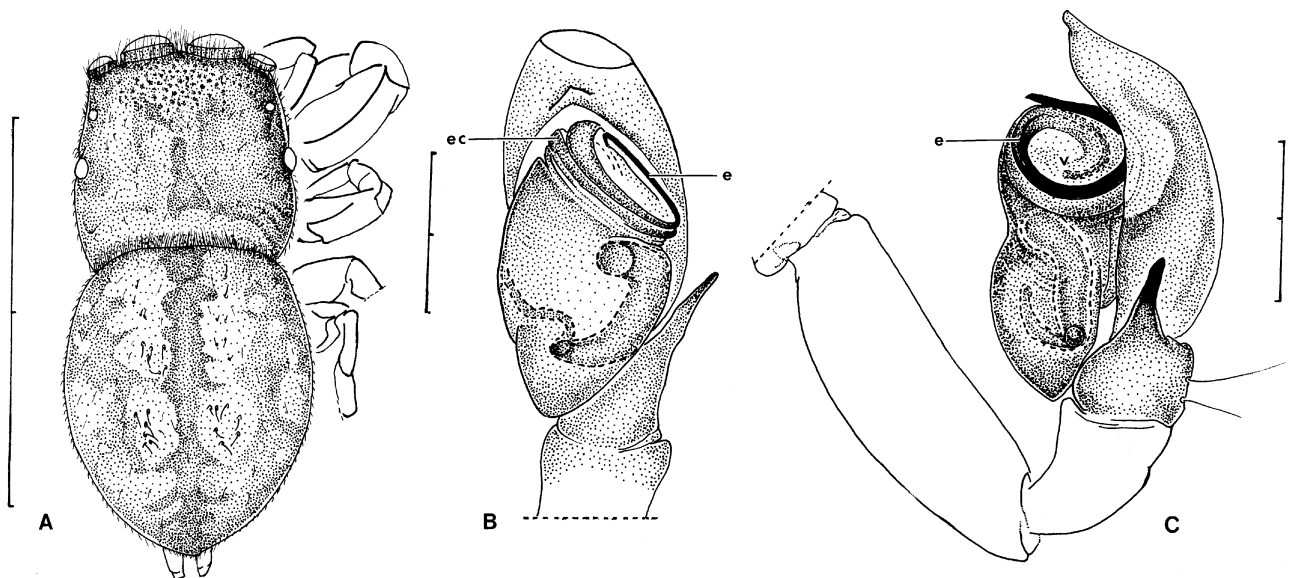


Figure 21. *Ballus segmentatus*. Male from Agrapatana, Sri Lanka (MHNG). A, habitus, dorsal view. B, male palp, ventral view. C, same, retrolateral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

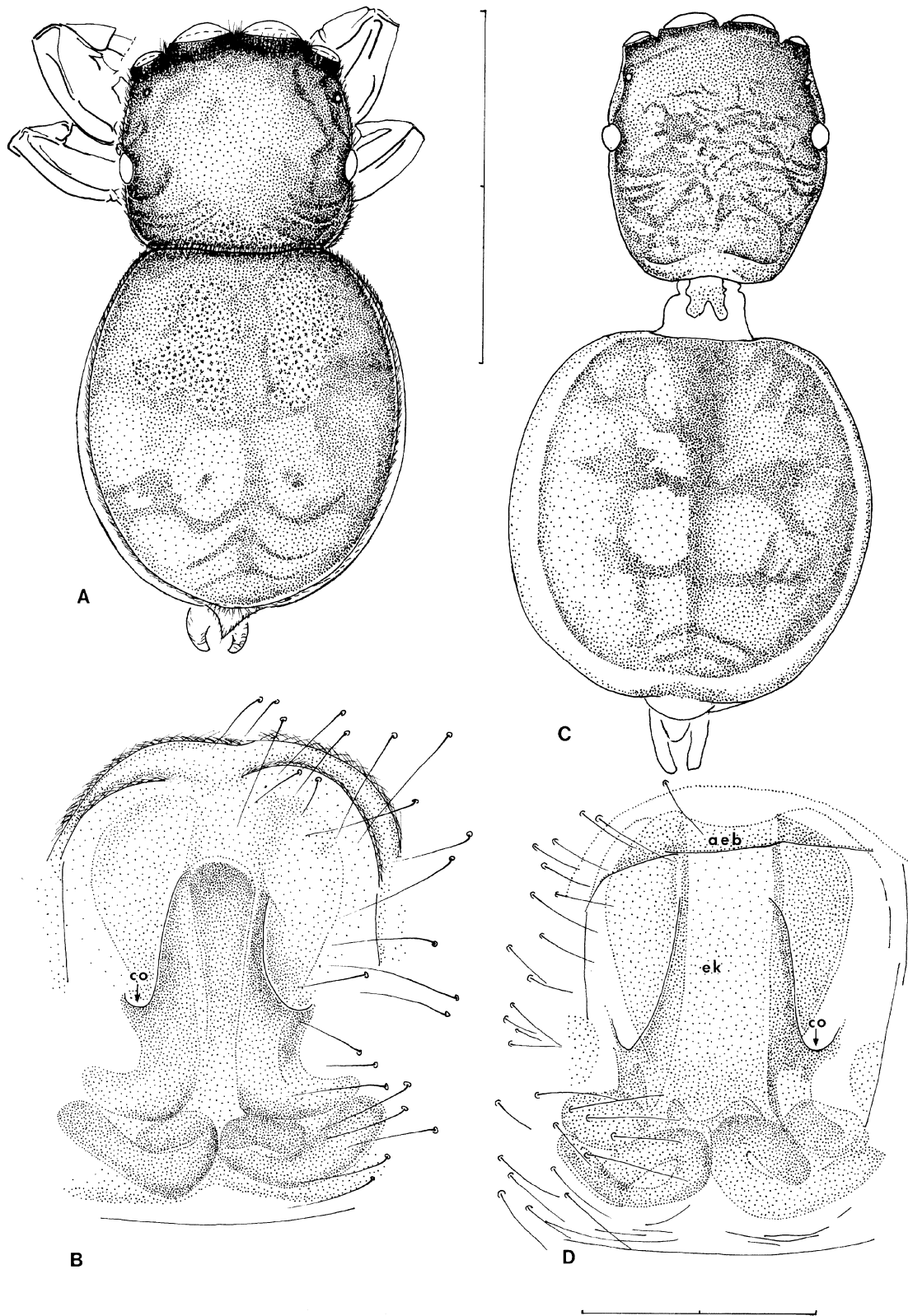
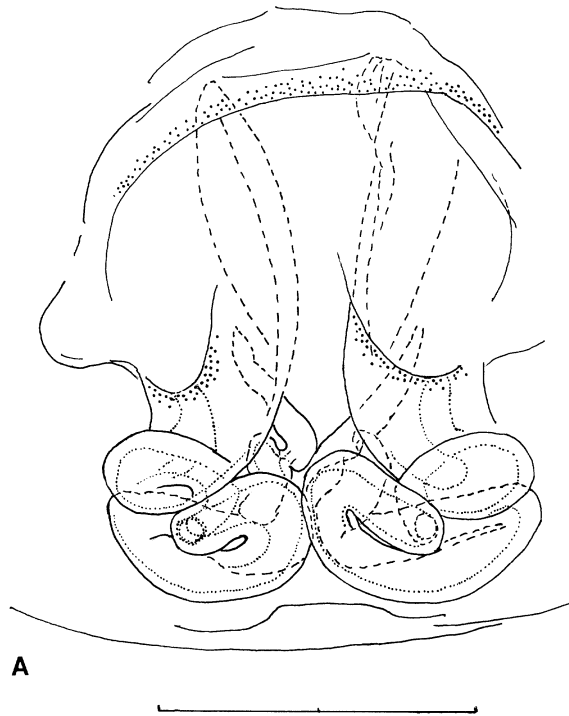
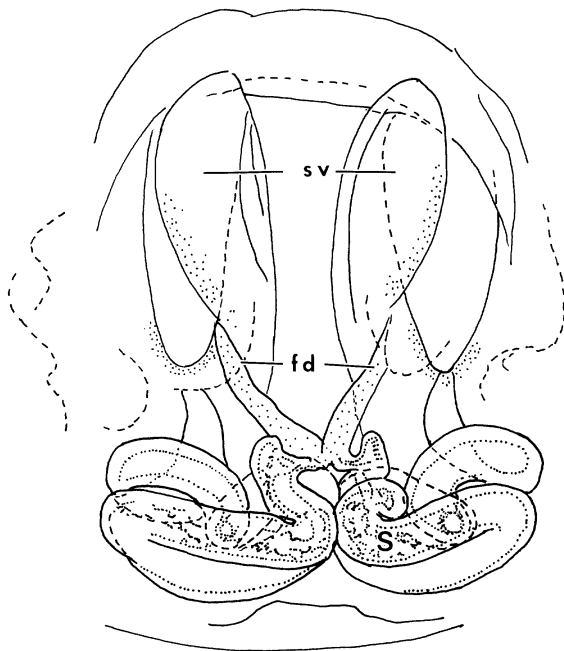


Figure 22. *Ballus segmentatus* (MHNG). A, female from Agrapatana, Sri Lanka; habitus, dorsal view. B, epigynum, ventral view. C, female from Hakgala, Sri Lanka; habitus, dorsal view. D, epigynum, ventral view. Scale bars = 0.2 mm (B, D); 2.0 mm (A, C).



A



B

Figure 23. *Ballus segmentatus* (MHNG). Female from Hakgala, Sri Lanka. A, vulva, ventral view. B, same, dorsal view. Scale bar = 0.2 mm.

brown, laterals and eye region darker, anteriorly with black spots. Opisthosoma rounded, wide as long, lighter in colour, with reticulate markings (Fig. 22A, C). All legs light yellow and laterally without dark markings. Eyes surrounded by dark rings. Chelicera dark brown, with three small, retromarginal teeth, labium triangular, light brown. Leg formula 1423. Tibia I with 2/0/0/2 spines, metatarsus I with 2/2 spines. Epigynum and vulva as in Figures 22B, C, 23A, B.

Distribution: Sri Lanka: Agrapatana, Hakgala and Horton Plains.

Material examined: SRI LANKA: Central Province, Hakgala, Hakgala forest, 1700 m; 1♀, leg. Suresh P. Benjamin, 27.7.1996, MHNG; Agrapatana, Agrapatana forest, 1100 m, 1♂ 1♀, leg. Suresh P. Benjamin, 8.3.2000, MHNG; Horton Plains, Horton Plains National Park, 1 (on a sputter coated SEM stab) 2 juveniles, leg. Suresh P. Benjamin, 7.3.2000, MHNG.

PHILATES SIMON, 1900

Philates Simon 1900: 402.

Marengo Wanless, 1978: 259.

Type species: *Philates grammicus* Simon, 1900, by original designation; lectotype designation by Wanless (1978).

Monophyly and phylogenetic placement: Probably polyphyletic; monophyly remains to be tested with rigorous sampling and phylogenetic methods.

Diagnosis: Distinguished from *Leikung*, *Indomarengo* and *Afromarengo* by the presence of pp (28) in these genera (Figs 4D, 48D, 49D, 38C, 42D; Wanless (1978: fig. 1d). Distinguished from *Ballus*, *Baviola*, *Colaxes*, *Cynapes* and *Sadies* by the presence of lts (33; Fig. 37A–C) and from *Sadies* by the presence of pp (Fig. 45D; Wanless, 1984a: figs 2d, 4d) and cag (17) situated at the opening of the copulatory atrium in *Sadies* (Figs 45C, 46A, B). *P. grammicus* can be separated from all other Ballinae by the presence of a sclerotized projection on the epigynal septum (12; Fig. 32A–C). *P. zschokkei* can be separated from all other Ballinae (except for *Ballus segmentatus*) by the presence of a pseudo-conductor (7; Fig. 36C, D).

Description: See description of type species below, Simon (1900) and Wanless (1978).

Composition: Ten species: *P. chelifera* (Simon, 1900) comb. nov., *P. courti* comb. nov., *P. grammicus*, Simon, 1900, *P. platnicki* comb. nov., *P. proszynskii* comb. nov., *P. rafalskii* comb. nov., *P. szutsi* sp. nov., *P. thaleri* sp. nov., *P. varirata* comb. nov., and *P. zschokkei* sp. nov. (all new combinations are from *Marengo*).

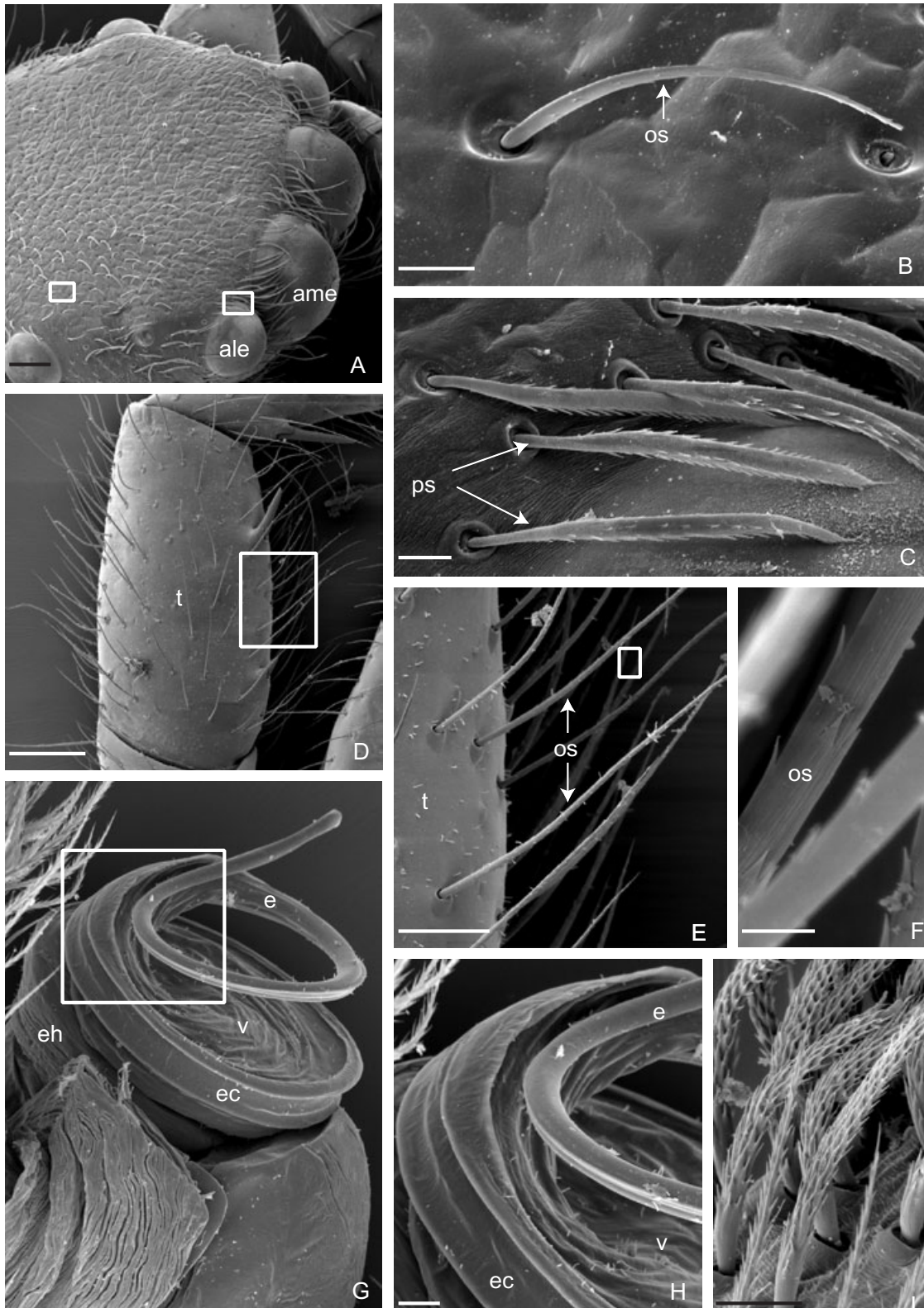


Figure 24. SEM, *Ballus segmentatus* (MHNG). A–F, female from Horton Plains, Sri Lanka. A, prosoma. B, ordinary setae. C, ps. D–F, tibia I. G–I, male from Agrapatana, Sri Lanka. Retrolateral views of: G, right male palp. H, ec and embolus. I, setae on apex of cy. Scale bars = 3 μ m (F); 10 μ m (B, C, H, I); 30 μ m (E, G); 100 μ m (A, D).

Remarks: The Papuan *Philates* have been well described by Zabka (1999) and are not treated further here. The characters shared by *P. zschokkei* and the Papuan species are the transverse white band, massive leg I of the male (much larger than that of, for example, *M. crassipes*) and the presence of cag. The preferred hypothesis of relationships among the Ballinae suggests that the Papuan species are best placed between nodes 5 and 8 (Fig. 1). Therefore, based on the current state of knowledge, they are placed in *Philates*. Alternatively, one could define a genus exclusively for the Papuan species + *P. zschokkei*. However, there are no unambiguous character state changes that would support such a genus.

Distribution: Indonesia, Malaysia, Papua New Guinea and Philippines.

PHILATES GRAMMICUS SIMON, 1900
(FIGS 31A, B, 32A–D)

Philates grammicus Simon, 1900: 402, fig. 580 (♂ lectotype and ♀ paralectotype from Philippines, Manila, Quingua, Antipolo in MNHN 20563/1: 3 and 2: 3, examined).

Philates grammicus Simon, 1901: 493, figs 580–581.

Marengo grammica Wanless, 1978: 272–275, fig. 10a–h.

Diagnosis: Distinguished from *P. zschokkei* by the presence of a sclerotized projection on the female epigynum (Fig. 32C). The male may be distinguished by the relatively rounded subtegulum (Fig. 31A, B).

Lectotype: ♂ from Philippines, Manila, Antipolo (MNHN 20563/1: 3), total length 3.8; prosoma length 1.8, width 1.4. Leg I: femur 1.0 patella 0.4, tibia 0.7, metatarsus 0.5, tarsus 0.3. Prosoma dark brown, sides darker, with dark patches; venter, uniformly yellow. Opisthosoma longer than wide, light yellow to light brown, dorsally with inconspicuous dark spots; venter, uniformly light yellow. Legs I–IV laterally with dark markings. Eyes surrounded by dark rings. Chelicera, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with three spines. Palp: tibia short, rta broad-based, thin, pointed upward (Fig. 31A, B; Wanless, 1978: fig. 10c, j). Apex of cymbium with chemo-sensitive hairs. embolus short, coils 1.5 times (Fig. 31A).

Paralectotype: One ♀ from the type locality. Description as in male. Epigynum and vulva as in Figure 32A–D and Wanless (1978: fig. 10d, g, h).

Distribution: Philippines and Indonesia.

Other material examined: None.

PHILATES CHELIFER (SIMON, 1900) **COMB. NOV.**

(FIGS 25A–G, 26A–C, 27A–I, 28A–D, 31C, D)

Marengo chelifer Simon, 1900: 400 (1♂ lectotype from Java, Buitenzorg, in MNHN B 2305); examined.

Marengo chelifer Simon, 1901: 488, fig. 577.

Marengo chelifer Wanless, 1978: 272, fig. 9a–f.

Etymology: The specific epithet might be substantive (hence invariable) or an adjective, meaning either ‘chela-carrier’ or ‘chela-carrying’. If Simon (1900) had used it as an adjective, he would have named the species *M. chelifera* instead of *M. chelifer*.

Diagnosis: *Philates chelifer* is distinguished from all Ballinae, except *M. striatipes*, by the absence of an enlarged femur (30; Fig. 25C, G). *M. striatipes* is known only from India and Sri Lanka (see later). The female of *P. chelifer* can be distinguished by the reduced translucent septum (19; Fig. 26A–C). Except for *Ballus* sp. (Fig. 24G, H), males of *P. chelifer* and *P. zschokkei* (Fig. 36C, D) may be distinguished from those of other Ballinae by the presence of a pseudo-conductor. *P. chelifer* can be distinguished from *P. szutsi* and *P. thaleri* by the shape of the rta and the presence of white patches on the sides of the opisthosoma. The females of *P. szutsi* and *P. thaleri* are unknown.

Lectotype: ♂ from Java, Buitenzorg. Total length 3.2; prosoma length 1.4, width 0.8. Leg I: femur 1.0 patella 0.4, tibia 1.0 metatarsus 0.6, tarsus 0.2. Markings as in Figure 25D, F. Prosoma dark brown, anterior parts much darker with two black patches. Opisthosoma oval, yellow-brown, shining, with two white patches (wp in Fig. 25D). Venter uniformly yellow, some specimens brighter than the others. Femur I not enlarged (Fig. 25C, G). Legs I–IV laterally with dark markings. Eyes surrounded by dark rings. Chelicera, labium dark brown, without marking. Leg formula 1432. Tibia I with 2/2/0/2 long thin spines, metatarsus I with 2/2 spines. Palp: cymbium oval (Figs 25A, B, 28A, 31C, D). Retrolateral tibial apophysis thin and long, projecting upwards. Tegulum bilobed, path of sperm duct as in Figures 25A, 31C, D; embolus broad-based, tapering, thin, short, coils once (Figs 25A, 28A–C, 31C, D).

Female: Malaysia, North Borneo, Kinabalu. Total length 2.9; prosoma length 1.4, width 0.7. Leg I: femur 0.6, patella 0.3, tibia 0.7, metatarsus 0.4, tarsus 0.2. Markings as in Figure 25E. Prosoma dark brown, without prominent markings. No prominent setae as in male. Opisthosoma lighter, darker than in the male. Legs laterally with dark markings. Eyes surrounded by dark rings. Chelicerae with no marking but with three small teeth on retromargin. Labium light yellow. Leg formula 1423. Epigynum and vulva as in Figure 26A–C.

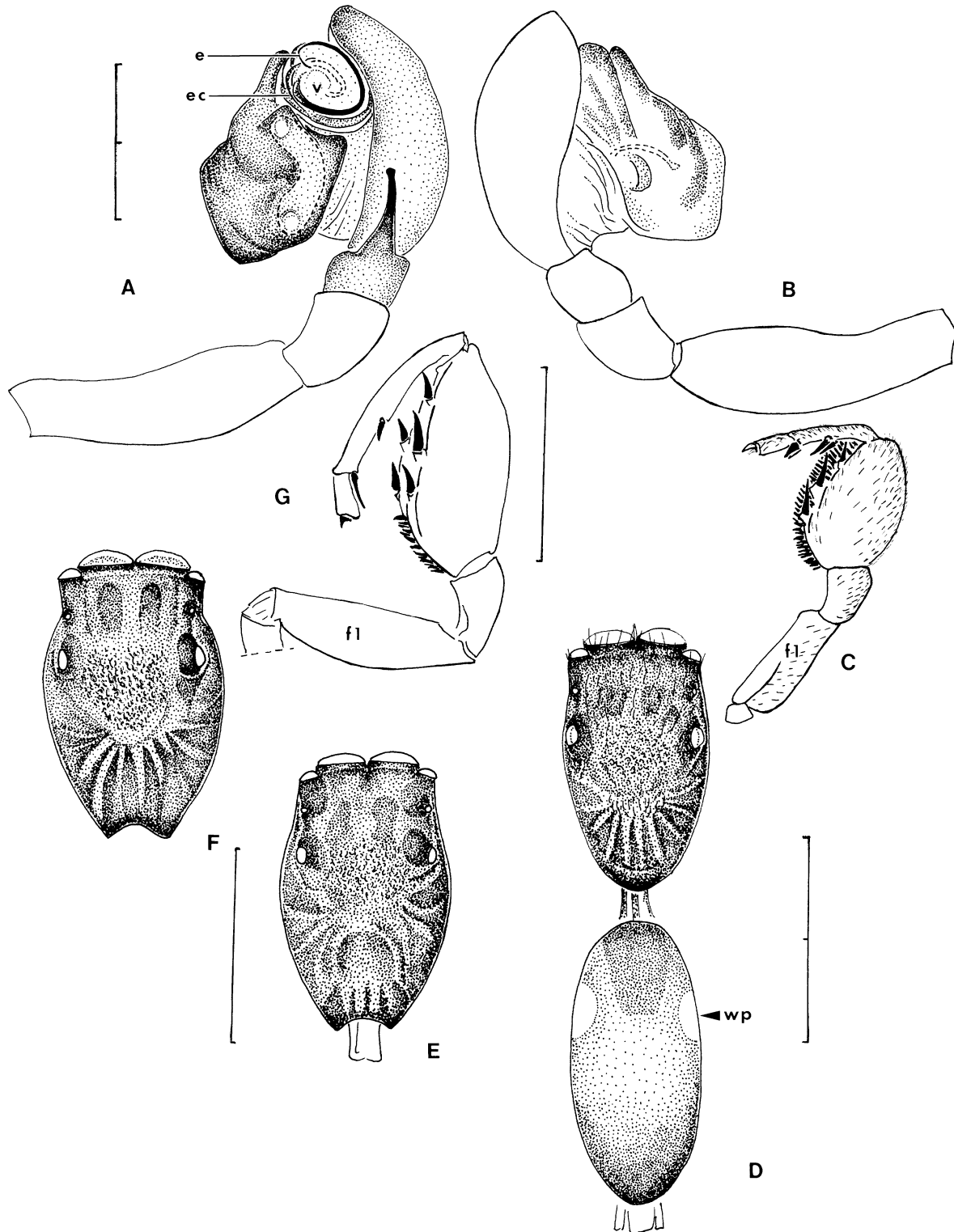


Figure 25. *Philates chelifera*. A–E, male and female from North Borneo, Malaysia (RMNH). A, male palp, retrolateral view. B, same, ectal view. C, right leg I, lateral view. D, male habitus, dorsal view. E, female prosoma, dorsal view. F, G, male lectotype from Java, Indonesia (MNHM B 2305). F, prosoma, dorsal view. G, right leg I, lateral view. Scale bars = 0.2 mm (A, B); 1.0 mm (E–G); 2.0 mm (C, D).

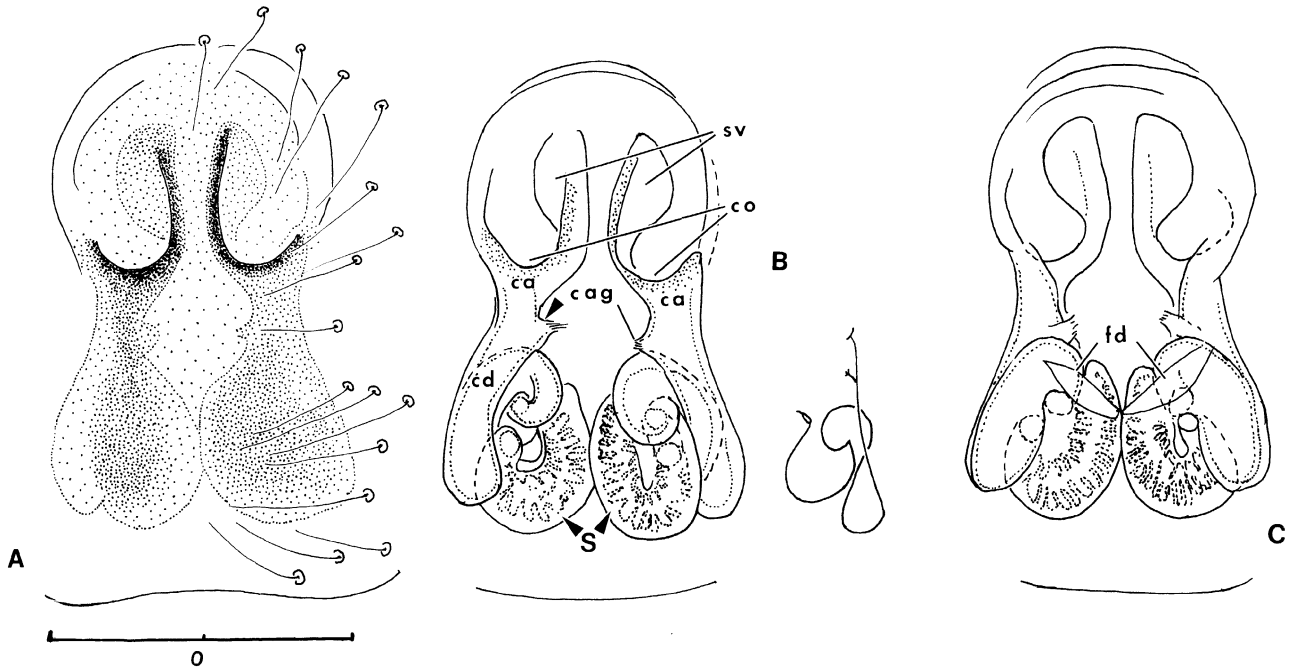


Figure 26. Female genitalia of *Philates chelifera* from North Borneo, Malaysia (RMNH). A, epigynum, ventral view. B, vulva, ventral view. C, same, dorsal view. Scale bar = 0.2 mm.

Other material examined: MALAYSIA: North Borneo, Kinabalu (500–1000 m), secondary forest canopy, SW2 Loc 46; 1♀, Fogging, leg. A. Floren, 10.3.1997; North Borneo, Kinabalu (500–1000 m), secondary forest canopy, SW3Loc62; 1♂, 9.3.1997, Leg. A. Floren, RMNH (partly on a sputter coated SEM stab).

***PHILATES SZUTSI* SP. NOV.**
(FIG. 29A–C)

Holotype: ♂ from Malaysia: North Borneo, Kinabalu (500–1000 m), canopy, SW3 Loc58, date not given on label, leg. A. Floren. Deposited in RMNH.

Etymology: Named in honour of my friend, Tamas Szűts (Hungarian Museum of Natural History).

Diagnosis: This species can be distinguished by the short, stout rta and the absence of white patches on the sides of the opisthosoma.

Male: Total length 3.7; prosoma length 1.5, width 1.0. First leg pair dissected in the specimen. Markings as in Figure 29A. Prosoma elongated, dark brown, without prominent markings except for dark rings surrounding eyes. Opisthosoma oval, elongated, dark brown, darker than the prosoma, shining, with marking. Venter light brown with yellow sides. Chelicera, labium light brown, without marking. Legs bright yellow, no black lateral markings. Leg formula: ?432, chelicera with four small teeth on retromargin. Palp:

cymbium oval, elongated. Retrolateral tibial apophysis short, broad-based, thin and projecting upward (Fig. 29C). Tegulum bilobed, path of sperm duct as in Figure 29B, C; embolus thin, short, coils once.

Female: Unknown.

Other material examined: None.

***PHILATES THALERI* SP. NOV.**
(FIG. 30A–C)

Holotype: ♂ from Malaysia: Sabah, Mt. Kinabalu, 1750 m, 27.4.1987, leg. D. Burckhardt & I. Löbl. Deposited in MHNG.

Paratype: 1♂ paratype from Malaysia: Sabah, Mt. Kinabalu, 1750 m, 22.5.1987, leg. D. Burckhardt & I. Löbl. Deposited in MHNG.

Etymology: Named in honour of Dr Konrad Thaler, who supervised my MSc thesis.

Diagnosis: This species can be distinguished by the absence of white patches on the sides of the opisthosoma and by the long tapering rta.

Male: Total length 4.7; prosoma length 2.0 width 1.4. Leg I: femur 1.3, patella 0.6, tibia 1.3, metatarsus 0.8, tarsus 0.5. Prosoma dark brown, sides darker, with dark patches in the anterior part (Fig. 30A); venter uniformly yellow. Opisthosoma longer than wide, tapering, light yellow, dorsally with inconspicuous

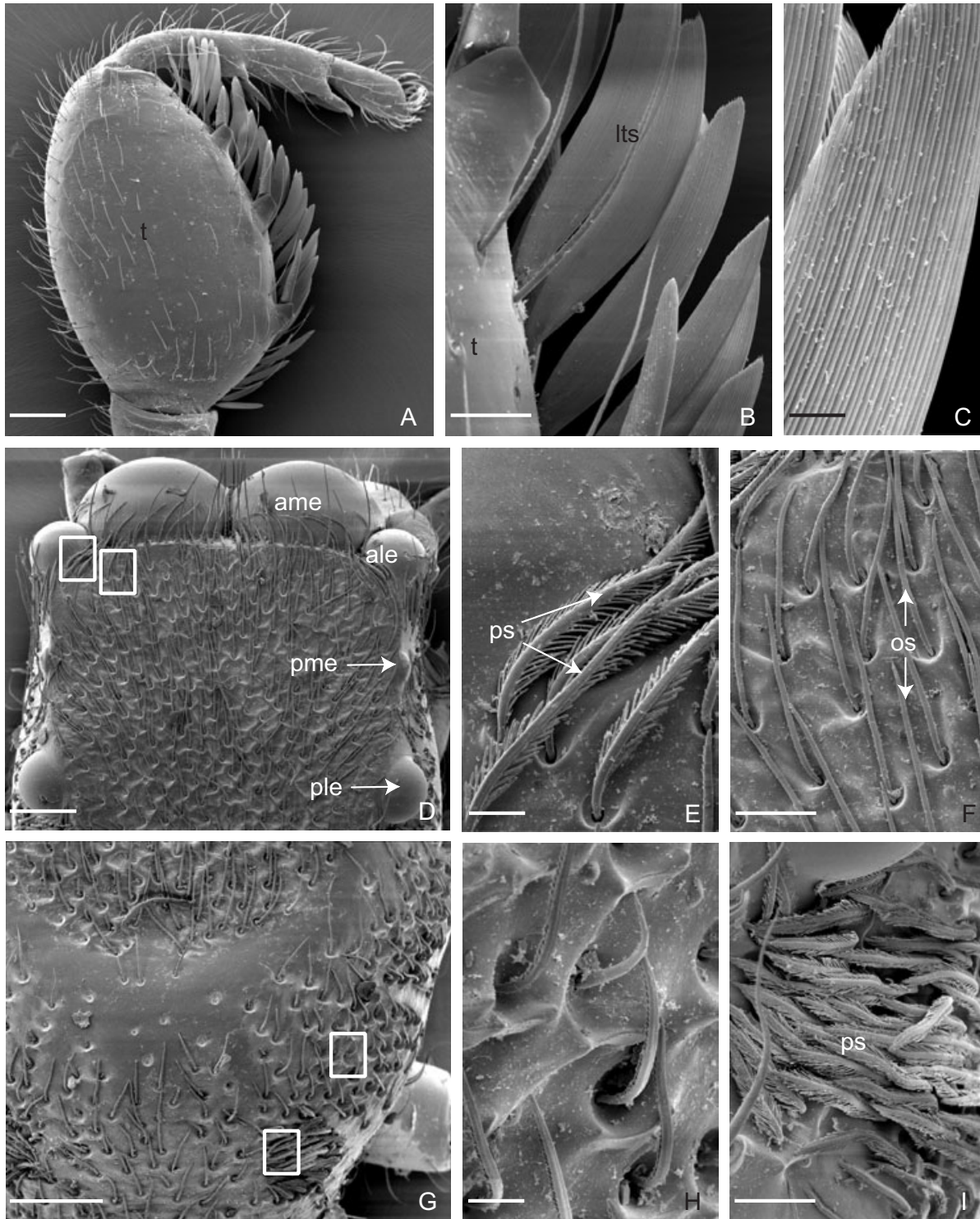


Figure 27. SEM, *Philates chelifer*, female from North Borneo, Malaysia (RMNH). A, leg I. B, lts. C, detail of B. D, prosoma, dorsal view, front section. E, F, details of D. G, prosoma, dorsal view, back section. H, I, details of G. Scale bars = 5 μm (C); 10 μm (E, H); 30 μm (B, F, I); 100 μm (A, D, G).

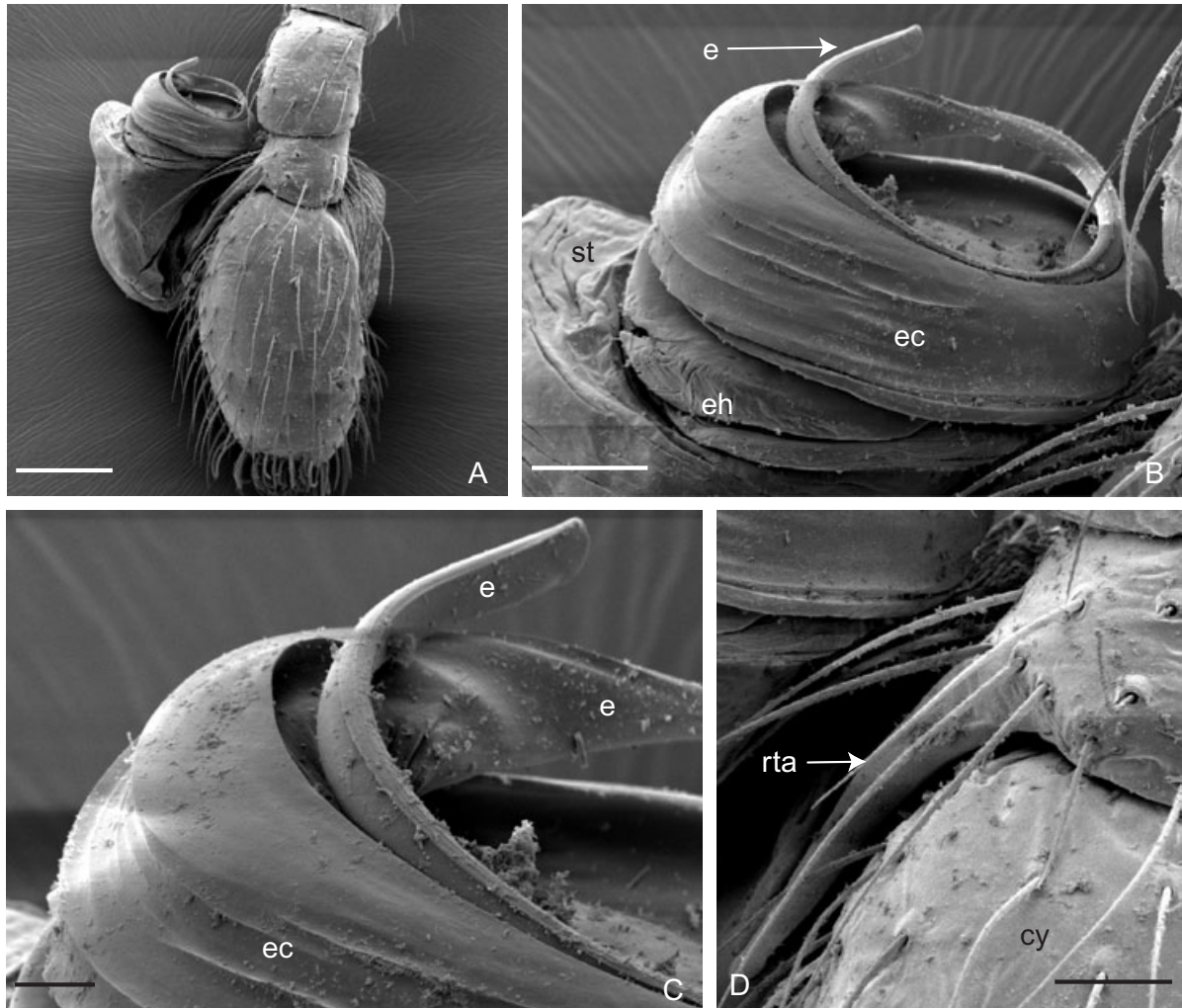


Figure 28. SEM, *Philates chelififer*, male from North Borneo, Malaysia (RMNH). A, right male palp, ventral view. B, C, Details of A. D, rta, ventral view. Scale bars = 10 μm (C); 30 μm (B, D); 100 μm (A).

dark markings; venter uniformly light yellow. Legs I–IV laterally with dark markings. Eyes surrounded by dark rings. Chelicera, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Palp: tibia short, rta tapering, pointed upward (Fig. 30A, B). Apex of cymbium with chemo-sensitive hairs. embolus short, coils 1.5 times (Fig. 30A).

Female: Unknown.

Other material examined: None.

***PHILATES ZSCHOKKEI* SP. NOV.**

(FIGS 33A, B, 34A, B, 35A–F, 36A–F, 37A–D)

Holotype: ♂ from Indonesia: Lombok Island, leg. Suharto Djojosedharmo, 8–19.1.1990, deposited in RMNH.

Paratype: 1♀, same data as holotype.

Etymology: Named in honour of Dr Samuel Zschokke, who supervised my PhD thesis.

Diagnosis: The male of *P. zschokkei* can be distinguished from that of *P. grammicus* by the presence of a white (light) transverse band (Fig. 33A), the female by the absence of a sclerotized projection (Fig. 32C). However, a light transverse band is known from all Papuan species (Zabka, 1999), making them indistinguishable from *P. zschokkei*.

Male: Total length 3.6; prosoma length 1.8, width 1.4. Leg I: femur 1.7, patella 0.8, tibia 1.5, metatarsus 0.9, tarsus 0.3 (left leg I missing). Markings as in Figure 33A. Prosoma longer than wide, broadest at the centre, raised, dark brown, without prominent markings. Opisthosoma lighter with a faintly visible transverse white line, dorsally yellow/grey, inconspic-

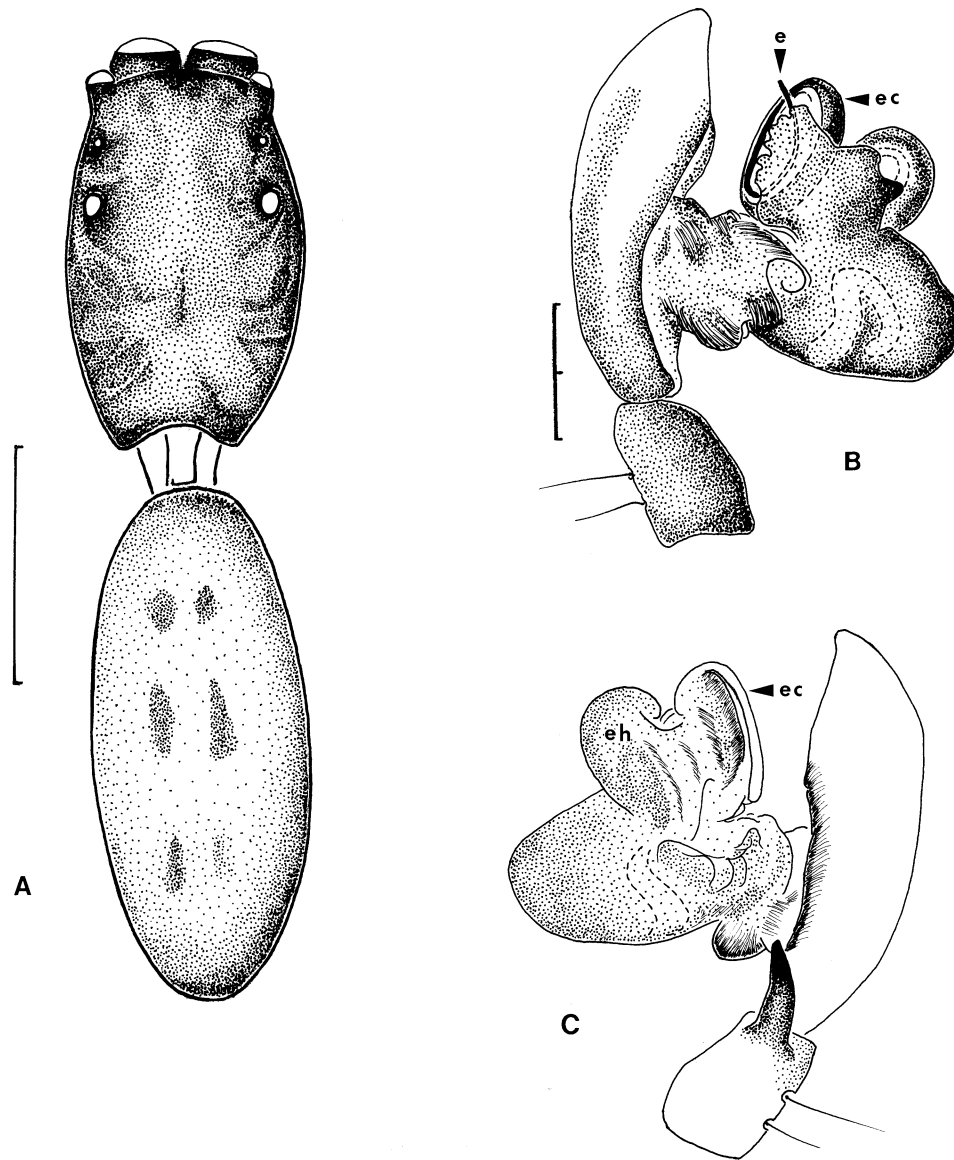


Figure 29. *Philates szutsi* sp. nov. (RMNH). A, habitus, dorsal view. B, male palpus, ectal view. C, same, retrolateral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

uous; venter uniformly yellow. Legs yellow, laterally with dark markings. Eyes surrounded by dark rings. Chelicerae and labium dark brown, with two retro-marginal teeth. Leg formula 1432, Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Palp: tibia short, rta broad-based, tilted backwards towards the cymbium (Figs 34A, 36B). Apex of cymbium with an excavation containing chemosensitive hairs (Fig. 36E, F). Embolus short, coils 1.5 times (Figs 34A, 36A, C, D); proximal end of embolus modified to a pseudo-conductor (Fig. 36A, C, D).

Female: Total length 3.8; prosoma length 1.7, width 1.1. Leg I: femur 0.7, patella 0.4, tibia 0.7, metatarsus

0.4, tarsus 0.2. Markings as in Figure 33B, description as in male. Prosoma dark brown, without prominent markings. No prominent setae as in male. Opisthosoma darker than in male. Legs laterally with dark markings. Eyes surrounded by dark rings. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Epigynum and vulva as in Figure 35A–F.

Distribution: Known only from the type locality.

Natural history: Collected from forest foliage.

Other material examined: None.

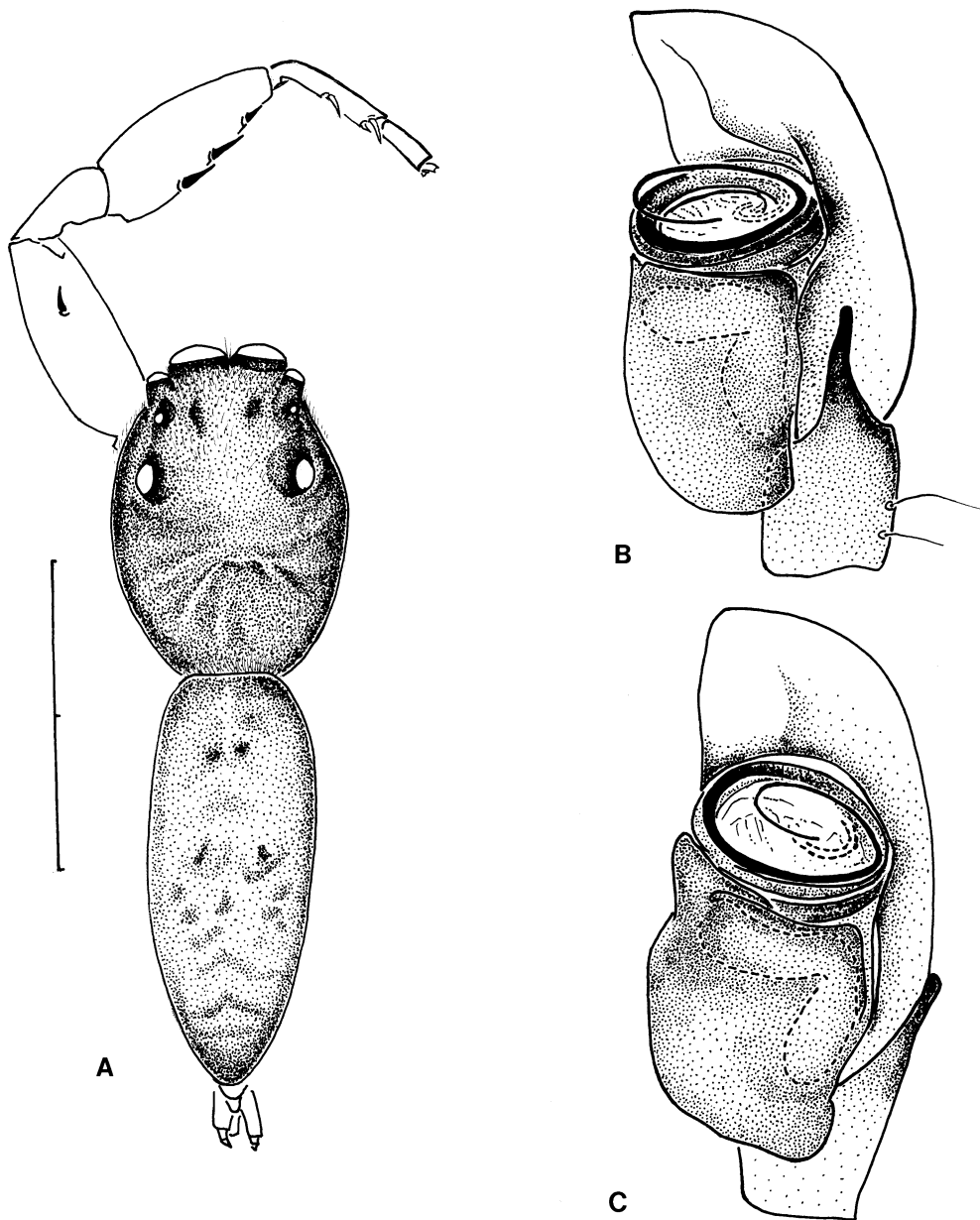


Figure 30. *Philates thaleri* sp. nov. (MHNG). A, habitus, ventral view. B, male palp, retrolateral view. C, same, ventral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

INDOMARENGO GEN. NOV.

Type species: *Indomarengo sarawakensis* sp. nov.

Etymology: Combination of Indo- (from Indonesia, where most of the species described live) + *Marengo*. It is considered feminine in gender.

Monophyly and phylogenetic placement: Monophyly remains to be tested. Autapomorphies of *I. chandra* are the constriction just below the apex of the rta (9-1) and the presence of scattered papillae (39-1).

Diagnosis: *Indomarengo* is distinguished from all other Ballinae genera as follows: (1) except for *Leikung* and *Afromarengo*, by the S-shaped path of the sperm duct (6; Figs 38D, E, 41E, F, 42A, B); (2) except for *Sadies*, *Leikung* and *Afromarengo*, by the presence of a prosomal protuberance (28; Figs 38C, 42D); (3) except for *Leikung*, of lts with a smooth surface with thin long spines (34; Figs 40E, 43C). *Indomarengo* is distinguished from *Leikung* by the presence of the following characters in the latter: tooth on anterior epigynal border (14; Figs 48E, 50A–C), raised ple (29;

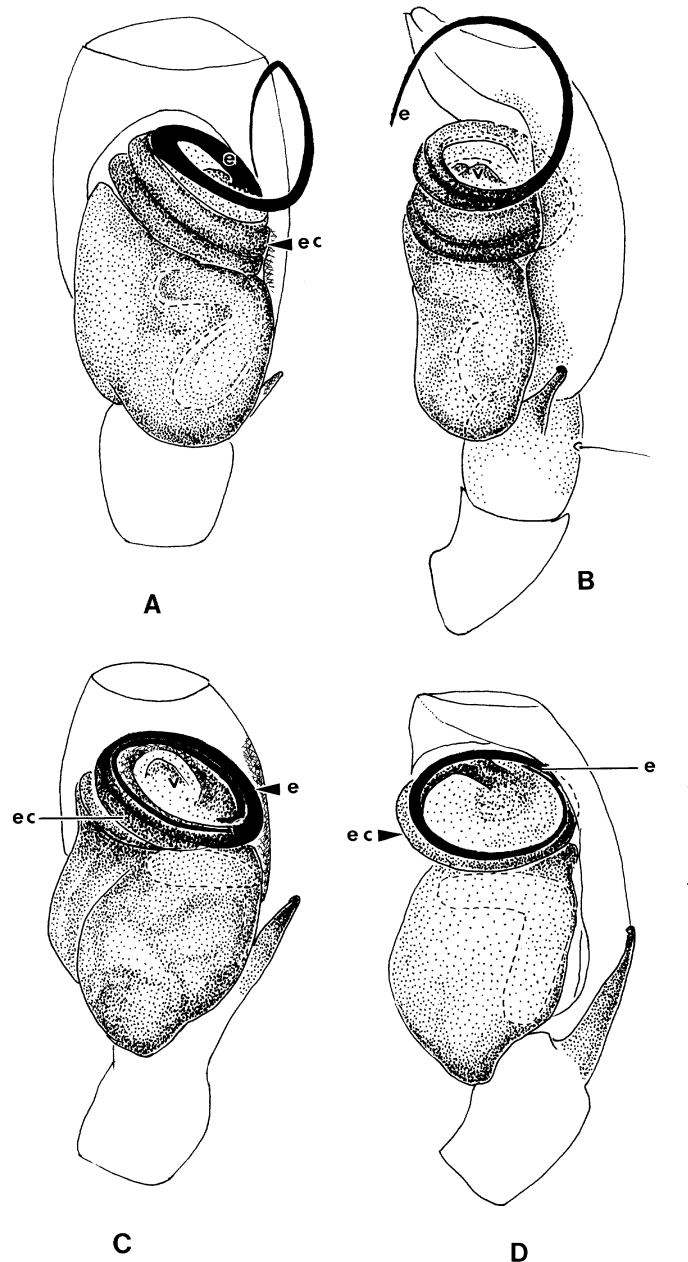


Figure 31. A, B, *Philates grammicus* (MNHN 20563/1: 3). A, male palp, ventral view. B same, retrolateral view. C, D, *Philates chelifera*, male lectotype from Java, Indonesia (MNHM B 2305). C, male palp, ventral view; D, same, retrolateral view. Scale bars = 0.2 mm.

Figs 48D, 49D, 52G and 53A), eight spines on tibia I (35; Figs 49D, 53E, 55C) and pits with sensory setae (38; Fig. 53B).

Description: See description of type species.

Composition: Three species: *I. thomsoni* (Wanless, 1978) comb. nov., *I. sarawakensis* sp. nov. and *I. chandra* sp. nov.

Distribution: Indonesia, Malaysia.

***INDOMARENGO SARAWAKENSIS* SP. NOV.**

(FIGS 4B, 38A–E, 39A–C, 40A–E, 41A–F)

Holotype: ♂ from Malaysia: Sarawak, Semengoh Arboretum, 3.4.1985, leg. C.L. Deeleman, deposited in RMNH.

Paratype: 1♀, same data as holotype. The types were collected together from the retreat shown in Figure 4B.

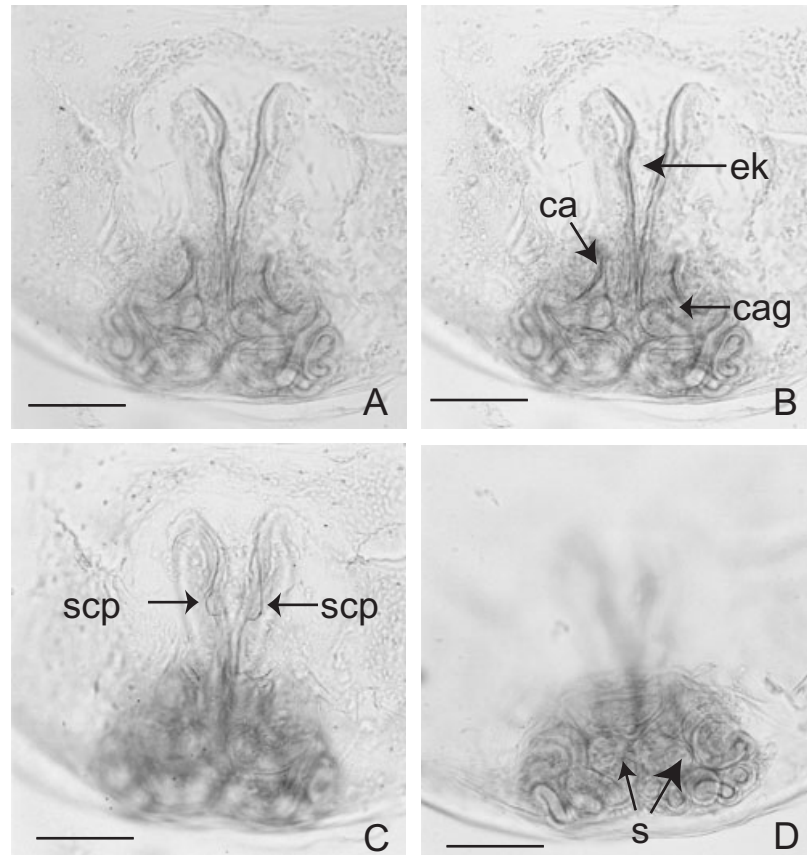


Figure 32. *Philates grammicus* (MNHN 205563/2:3). Female genitalia. A–C, ventral view. D, dorsal view. Scale bar = 0.1 mm.

Etymology: Adjective: ‘from Sarawak’, after the type locality.

Diagnosis: This species can be distinguished from its sister, *I. chandra*, by the shape and the absence of a constriction just below the apex of the rta (Figs 42B, 43A, D). The male of *I. thomsoni* is not known (Wanless, 1978). The female may be distinguished from that of *I. thomsoni* by the route of cd (Fig. 39A–C; Wanless, 1978: fig. 8b, c, d). Furthermore, *I. sarawakensis* has a rounded opisthosoma (Figs 38A, 41C), whereas *I. thomsoni* has an oval elongated opisthosoma (Wanless, 1978: fig. 8a, f).

Male: Total length 3.6; prosoma length 1.6, width 1.2. Leg I: femur 1.0 patella 0.5, tibia 0.9, metatarsus 0.8, tarsus 0.3. Markings as in Figures 38A, C, 41A–C. Prosoma dark brown, without prominent markings except for dark rings surrounding the eyes; venter dark brown. Opisthosoma round to oval, light brown, shining, with two black spots; venter yellow/grey. Specimens have what appears to be a faint transverse white band on the opisthosoma. Legs I–IV laterally with dark markings. Eyes surrounded by dark rings.

Chelicera, labium dark brown, without marking. Leg formula 1423. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Long setae on prosoma and opisthosoma (Figs 38A, C, 41A). Palp: cymbium oval, rta tilted backwards, tapering to a pointed end. Tegulum bilobed, path of sperm duct as in Figures 38D, E, 41E, F; embolus thin, long, coils more than 1.5 times (Figs 38D, E, 40A, B, 41E, F).

Variation: The male from Java, Ujung Kulon reserve: the pp appears not to be well elevated as in other specimens. Opisthosoma has a visible transverse white band and the posterior half is darker. The shape of the rta is somewhat different (Fig. 41E).

Female: Paratype: total length 3.5; prosoma length 1.6, width 1.0. Leg I: femur 0.5, patella 0.4, tibia 1.0 metatarsus 0.5, tarsus 0.3. General appearance as in male but lighter in colour. Prosoma yellow brown, without prominent markings. Opisthosoma lighter than in male. Legs laterally with dark markings. Eyes rows recurved, surrounded by dark rings. Leg formula 1423. Epigynum and vulva as in Figure 39A–C.

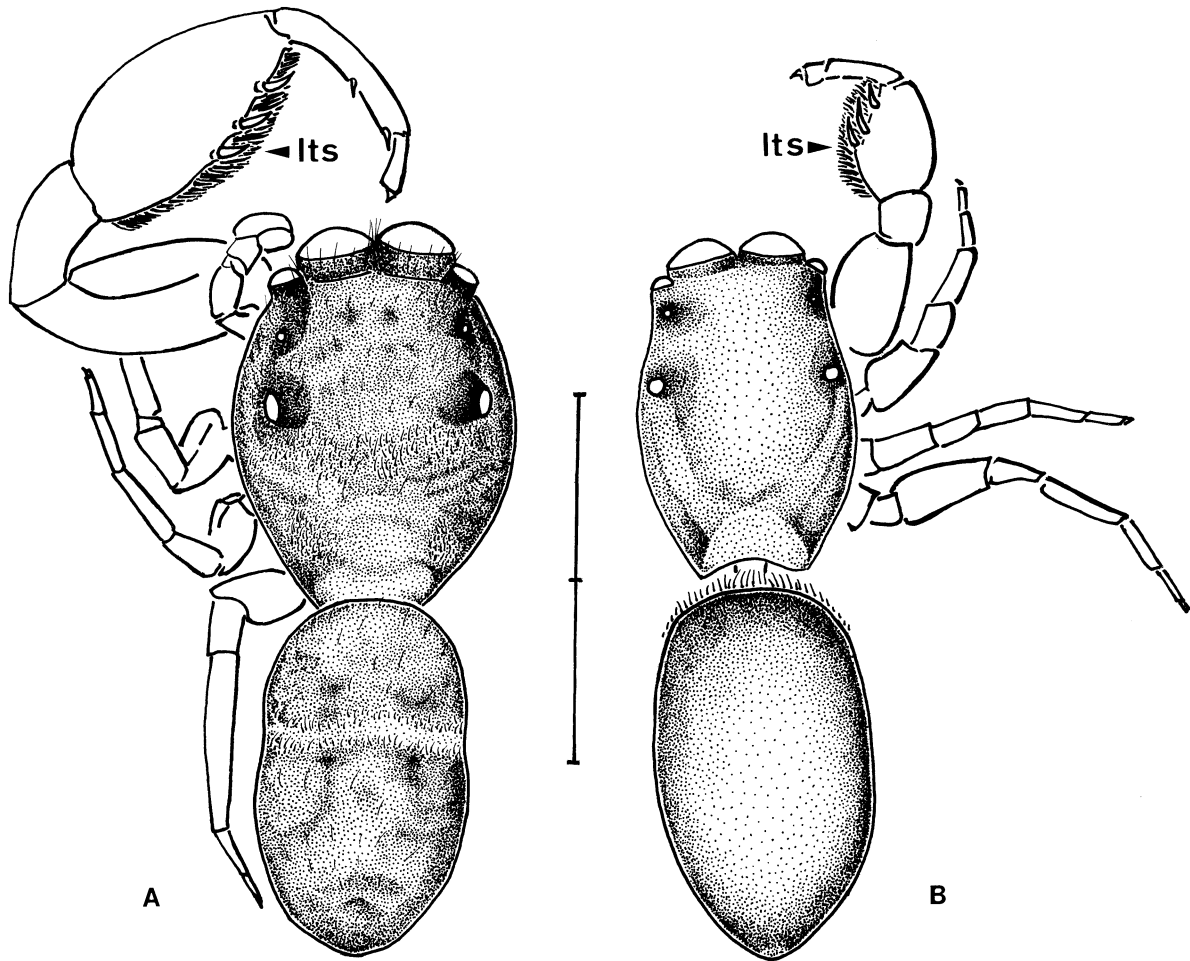


Figure 33. *Philates zschokkei* sp. nov. (RMNH). A, male, dorsal view. B, female, dorsal view. Scale bar = 2.0 mm.

Other material examined: INDONESIA: Java, West Java, Ujung Kulon reserve, fr. Leaf; 1♂, 17–19.1.1986, leg. Suharto Djojosedharmo, deposited in RMNH. Ujung Kulon reserve is a primary lowland rainforest (Deeleman-Reinhold, 2001).

INDOMARENGO CHANDRA SP. NOV.

(FIGS 42A–E, 43A–F, 44A–I)

Holotype: ♂ from Indonesia: North Sumatra, Gunung Leuser at Ketambe, submontane, 1400 m, 29.11.1984, leg. Suharto Djojosedharmo, deposited in RMNH.

Paratype: 2♂ from Indonesia: North Sumatra, Gunung Leuser at Ketambe, trail 13, 17.2.1985, leg. Suharto Djojosedharmo, deposited in RMNH (one male on a sputter-coated SEM stub).

Etymology: Chandra, used as a noun in apposition, is Sanskrit for moon. Named after my beloved aunt, Chandra Wedikkara.

Diagnosis: Although similar to *I. sarawakensis*, this species can be distinguished from its sister by the shape of the rta and the presence of a constriction just below its apex (Figs 42B, 43A, D). *I. chandra* has a rounded opisthosoma (Fig. 42E), whereas *I. thomsoni* has a oval elongated opisthosoma (Wanless, 1978: fig. 8a, f).

Male: Total length 4.5; prosoma length 2.1 width: 1.3. Leg I: femur 1.3, patella 0.6, tibia 1.3, metatarsus 0.8, tarsus 0.3. Markings as in Figure 42D, E. Prosoma light yellow/brown, without prominent markings except for dark rings surrounding eyes. Opisthosoma oval, dark brown, darker laterally, shining, no markings except for a faintly visible transverse light band. Ventral parts uniformly grey to yellow. Legs I–IV laterally with dark markings. Chelicerae and labium brown, without marking. Leg formula 1423. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Palp: cymbium oval, apical end tapering. Retrolateral tibial apophysis tilted backwards, a constriction just below

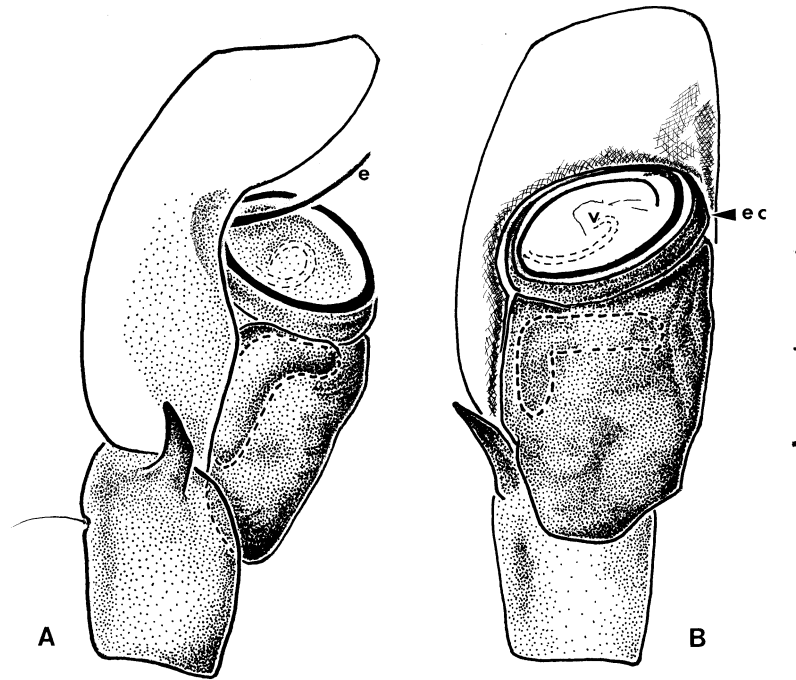


Figure 34. *Philates zschokkei* sp. nov. (RMNH). A, right male palp, retrolateral view. B, same, ventral view. Scale bar = 0.2 mm.

the apex is present (Figs 42B, 43A, D). Tegulum bilobed, path of sperm duct as in Figure 42A, B; embolus thin and long, coils more than 1.5 times (Figs 42A, B, 43A, B, E).

Variation: The two paratypes are much darker than the holotype, dark brown to black. Opisthosoma with two dorsal spots. Ventral parts dark brown to black.

Female: Unknown.

Other material examined: None.

SADIES WANLESS, 1984

Sadies Wanless, 1984: 11.

Type species: *Sadies fulgida* Wanless, 1984, by original description.

Monophyly and phylogenetic placement: Apomorphic for *Sadies* is the C-shaped path of the sperm duct (6-0), position of cag (17-1), absence (secondary loss) of enlarged tibia (31-0) and lts (33-0) and presence of leaf-like prosomal scales (37-1).

Diagnosis: *Sadies* can be separated from all other Ballinae genera by the position of cag (Figs 45C, 46A, B) and, except for *Cynapes wrighti*, by the presence of leaf-like prosomal scales (Fig. 47A, B).

Description: See Wanless (1984a).

Composition: Four species: *S. fulgida* Wanless, 1984, *S. gibbosa* Wanless, 1984, *S. seychellensis* Wanless, 1984 and *S. trifasciata* Wanless, 1984.

Distribution: All known species occur in the Seychelles and are probably endemic.

SADIES FULGIDA WANLESS, 1984 (FIGS 45A, B, C-F, 46A, B, 47A-H)

Sadies fulgida Wanless, 1984: figs 2a-f, 3a-f. 1♂ holotype (MRAC 159.955) and 1♀ allotype (MRAC 143.086) from Seychelles, Mahé, examined.

Diagnosis: Distinguished from *S. seychellensis* and *S. trifasciata* by the shape of the rta (Fig. 45B, G, H); the rta of *S. fulgida* has a broad base constricted at the centre and with a pointed end (Figs 45A, B, 47A, H; Wanless, 1984a: figs 2, 3). Wanless (1984a) proposed 'the shape of the carapace and its microsculpture' as unique for *S. seychellensis*. However, he provided no details of what he meant by these differences. The separation from *S. gibbosa* is unclear, but the shape of the rta and the enlarged tibia I are potentially useful (Wanless, 1984a: fig. 4).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

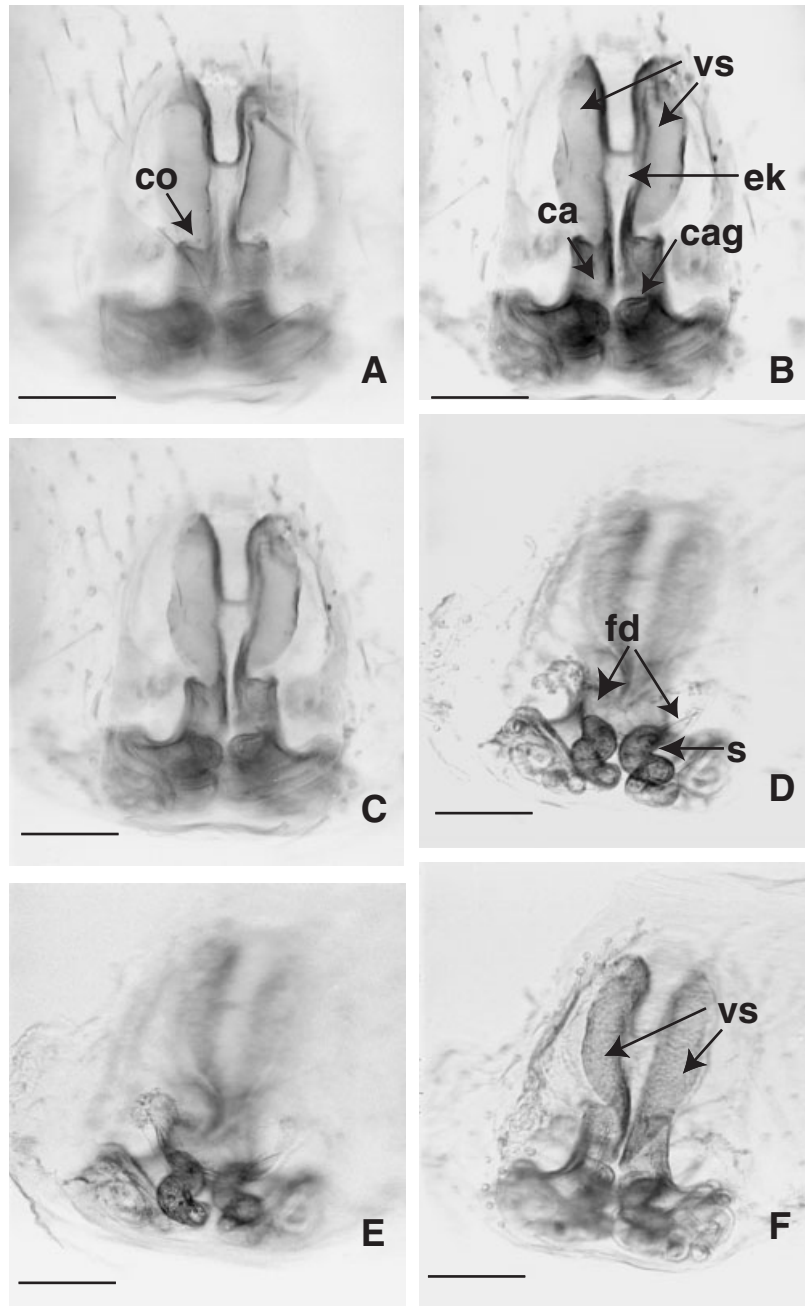


Figure 35. *Philates zschokkei* sp. nov. (RMNH). Female genitalia. A–C, ventral view. D–F, dorsal view. Scale bars = 0.1 mm.

Material examined: SEYCHELLES, Silhouette, La Passe; 1♂, 15.1.1999, leg. and det. Michael Saaristo, MZT (label: *S. seychellensis*, misidentification).

SADIES SEYCHELLENSIS WANLESS, 1984
(FIG. 45G)

'Myrmarachne' *constrictus* (Blackwall, 1877). See Saaristo (1978: figs 100–102; provisional place-

ment and first description of the male). Not examined.

S. seychellensis Wanless, 1984: 18–20, fig. 5a–f. ♂ holotype (BMNH.1952.12.17.118–122) from Seychelles, Mahé. Not examined. Paratypes: 1♂ 1♀ (MRAC 143.283), Morné Séchellois, 750–800 m, 13–17.7.1972, forêt endémique; 1♀ (MRAC 143.084), Mahé Centre, Morne Blanc, 667 m, 24–25.8.1972, forêt endémique. Examined.

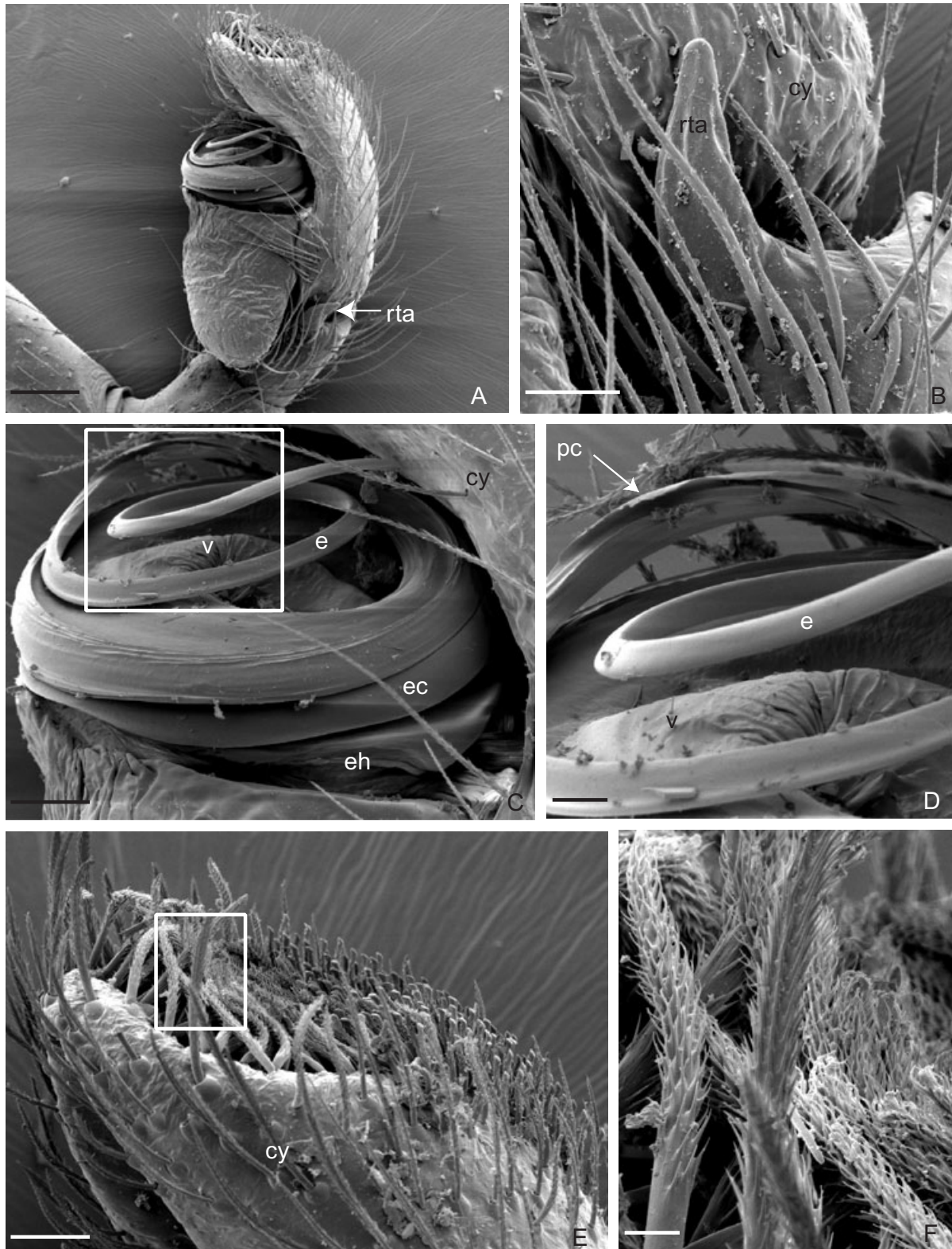


Figure 36. SEM, *Philates zschokkei* sp. nov. (RMNH). A, male palp, retrolateral view. B, detail of the rta, retrolateral view. C, ec and embolus, retrolateral view. D, pseudo-conductor. E, setae on the apex of cy, retrolateral view. F, detail of E. Scale bars = 5 µm (F); 10 µm (D); 30 µm (B, C, E); 100 µm (A).

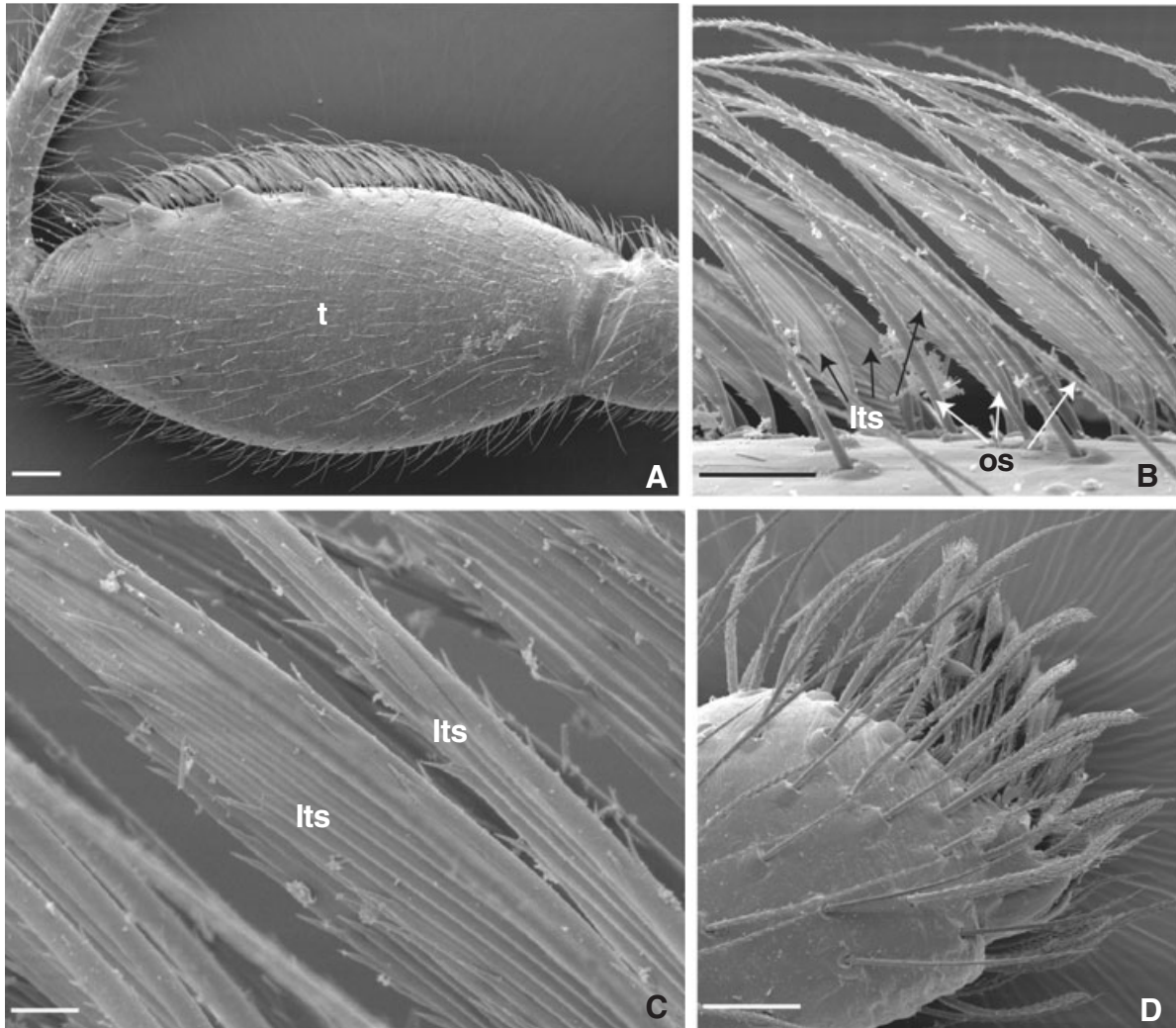


Figure 37. SEM, *Philates zschokkei* sp. nov. (RMNH). A, right tibia I, lateral view. B, lts details. C, inferior spines on lts, orientated in a distal direction. D, tip of leg I showing tarsal claw and claw tuft. Scale bars = 5 µm (C); 30 µm (B, D); 100 µm (A).

Diagnosis: Distinguished from *S. fulgida* and *S. trifasciata* by the shape of the rta (Fig. 45B, G, H), which in *S. seychellensis* gradually tapers to a pointed end (Fig. 45H; Wanless, 1984a: fig. 5). Wanless (1984a) proposed the absence of a thoracic hump and 'differences in carapace microsculpture' (though he provided no details of what he meant by the latter) as unique to *S. seychellensis*. However, I think a thoracic hump is present, though only faintly visible (pp in this study). The separation from *S. gibbosa* is unclear, but the shape of the rt and the enlarged tibia I might be of use (Wanless, 1984a: fig. 4).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

Other material examined: None.

SADIES TRIFASCIATA WANLESS, 1984
(FIG. 45H)

Sadies trifasciata Wanless, 1984: 21–22, fig. 6a–g. ♂ holotype from Seychelles, Mahé, Centre, Morne Blanc 667 m, 8–9.7.1972, PLG Benoit & JJ Van Mol (MRAC 150.961) and three from the same locality (MRAC 143.093), examined.

Diagnosis: Distinguished from *S. fulgida*, *S. seychellensis* and *S. gibbosa* by the colour pattern and shape of rta (Fig. 45B, G, H); *S. trifasciata* has a unique 3-lined pattern on the opisthosoma, a broad-based rta tapering to a beak-like end, which is con-

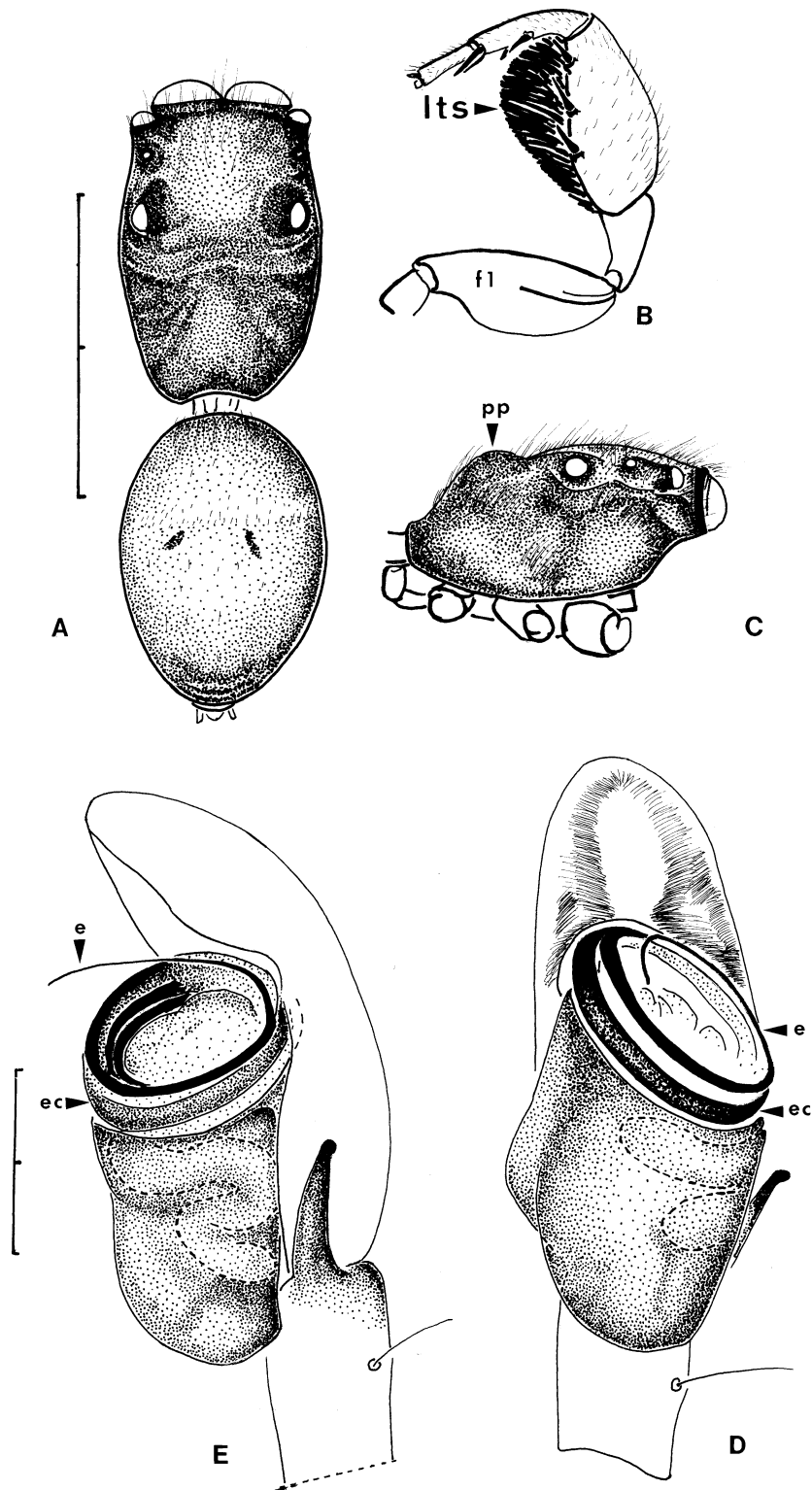


Figure 38. *Indomarengo sarawakensis* sp. nov., male from Sarawak, Malaysia (RMNH). A, habitus, ventral view. B, left leg I, lateral view. C, prosoma, lateral view. D, male palp, retrolateral view. E, same, ventral view. Scale bars = 0.2 mm (D, E); 2.0 mm (A–C).

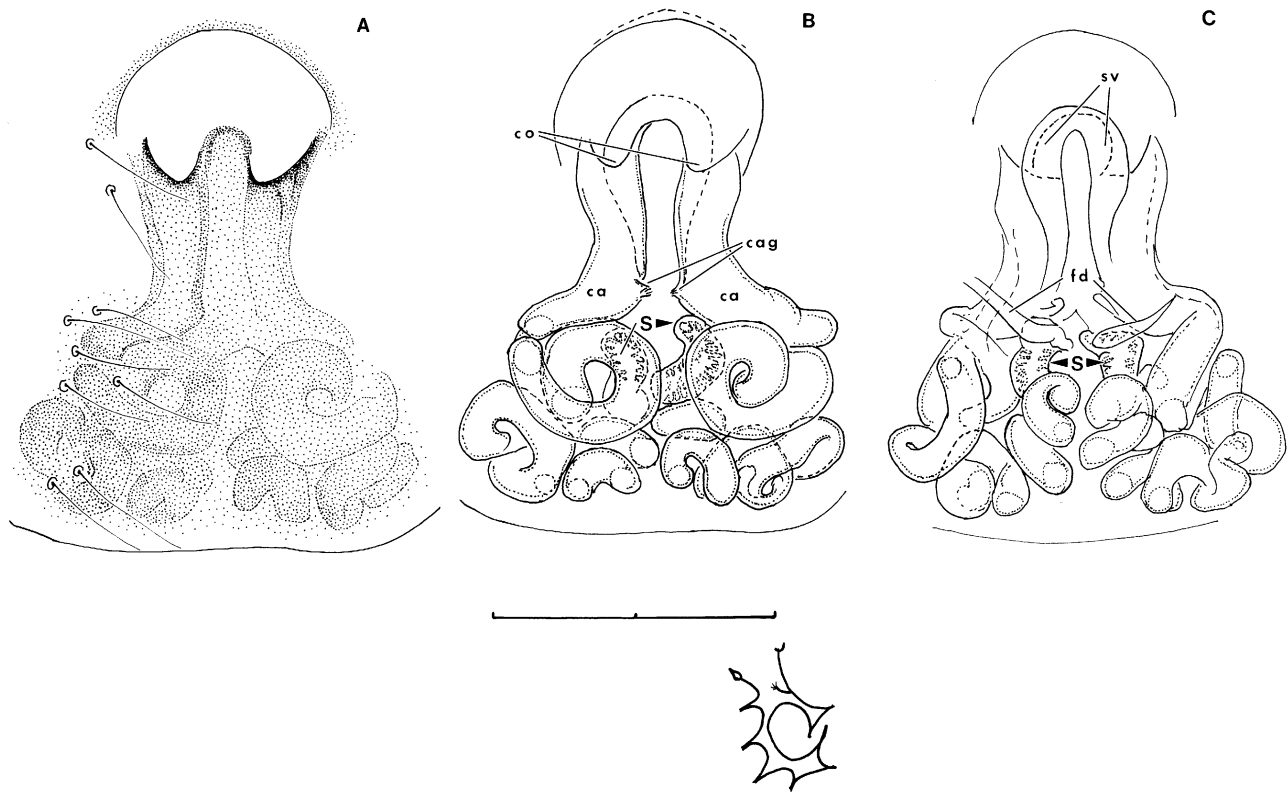


Figure 39. *Indomarengo sarawakensis* sp. nov., from Sarawak, Malaysia (RMNH). Female genitalia. A, epigynum, ventral view. B, vulva, ventral view. C, same, dorsal view. Scale bar = 0.2 mm.

stricted approximately halfway (Wanless, 1984a: fig. 6a–c).

Description: See Wanless (1984a).

Distribution: Known only from the Seychelles. Habitat data in Wanless (1984a).

Other material examined: None.

LEIKUNG GEN. NOV.

Type species: *Marengo porosa* Wanless, 1978.

Remarks: *Leikung porosa* was provisionally placed in *Marengo* by Wanless (1978), who argued that the position of the eyes and the presence of scattered papillae might justify the proposal of a new genus. He went on to say that a better understanding of Ballinae phylogeny would be required before such a proposal could be justified, mentioning the taxonomic irresponsibility of proposing genera based on a single species (Platnick, 1976; Wanless, 1978). As the most preferred hypothesis of Ballinae generic relationships suggests (Fig. 1), he was in fact correct in postulating a new genus to accommodate *Leikung porosa*.

Etymology: In Chinese mythology, Lei-Kung is the god of thunder. His skin, like that of *Leikung* spp, is believed to be perforated.

Monophyly and phylogenetic placement: Details of the female genitalia and somatic morphology are autapomorphic for this interesting genus: the presence of a tooth (to) at the anterior epigynal border (14-1), raised ple (29-1), eight spines on tibia I (35-2) and pits with sensory setae (38). Synapomorphies uniting *Leikung* and the African genus *Afromarengo* are the long embolus (5-2), absence of an epigynal septum (10-0), copulatory openings connected to each other by posterior epigynal border (13-1) and the presence of scattered papillae (39-1).

Diagnosis: *Leikung* is distinguished from all other Ballinae by the presence of a tooth on the anterior epigynal border (Figs 48E, 50A–C), raised ple (Figs 48D, 49D, 52G, 53A), eight spines on tibia I (Figs 49D, 53E, 55C) and pits with sensory setae (Fig. 53B).

Description: See the description of the type species below and Wanless (1978).

Composition: Two species: *Leikung porosa* (Wanless, 1978) and *L. kinabaluensis*.

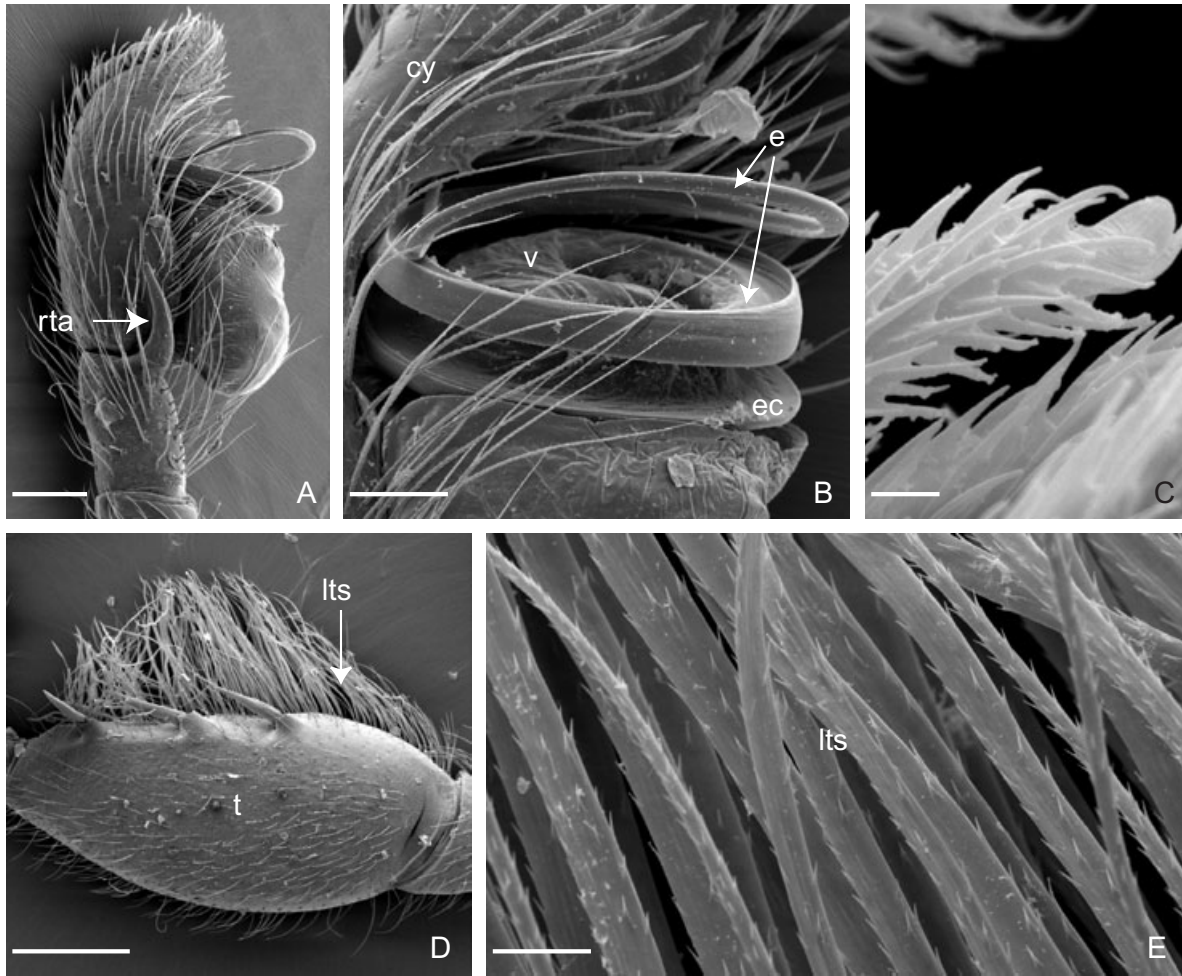


Figure 40. SEM, *Indomarengo sarawakensis* sp. nov., from Sarawak, Malaysia (RMNH). A, right male palp, retro-lateral view. B, st, ec and embolus. C, setae on the apex of cy, retrolateral view. D, right tibia I, lateral view. E, lts. Scale bars = 1 µm (C); 50 µm (B); 10 µm (E); 100 µm (A); 300 µm (D).

Distribution: Indonesia and Malaysia.

LEIKUNG POROSA (WANLESS, 1978) **COMB. NOV.**
(FIGS 4D, 48A–E, 49A–D, 51A–F, 52A–I, 53A–F,
54A–D)

Marengo porosa Wanless, 1978: 268–270, fig. 7a–g. ♀ holotype (vial 21D), 7.9.1973, BMNH, reg. no. 1977.4.29.8, from Malaysia, Frasers hill, Jeriav waterfall area and 1 ♀ paratype (vial 18 B), 6.9.1973, from the same locality, both specimens leg. A. D. Blest. Not examined.

Etymology: Refers to the porous-like structures of the prosoma (Wanless, 1978).

Diagnosis: Distinguished from *L. kinabaluensis* by details of the rta; short, sickle-shaped or bent towards the tegulum at the centre (Figs 48B, 49B, 52E, F, 54A–D).

Remarks: Material grouped here as *L. porosa* might not be conspecific. Nevertheless, the limited number of available specimens only enables the diagnosis of a single species. The recognition of populations described here as species might require additional material and probably the analysis of genetic distance.

Male: Total length 4.6; prosoma length 2.5, width 1.5. Leg I: femur 2.4, patella 1.0 tibia 1.7, metatarsus 1.3, tarsus 0.6. Markings as in Figures 48C, D, 49C, D. Prosoma oval, longer than wide, red brown, without prominent markings except for dark rings surrounding eyes. Long setae (Figs 52G, 53A). Opisthosoma round to oval, dark brown, shining, with a folium and black dots, while some specimens have a transverse whitish band (Figs 48C, 49C). Venter uniformly yellow to white, some specimens more whitish than others. Legs I–IV laterally with dark markings. Eyes in three rows (note: considered to represent four rows by Wan-

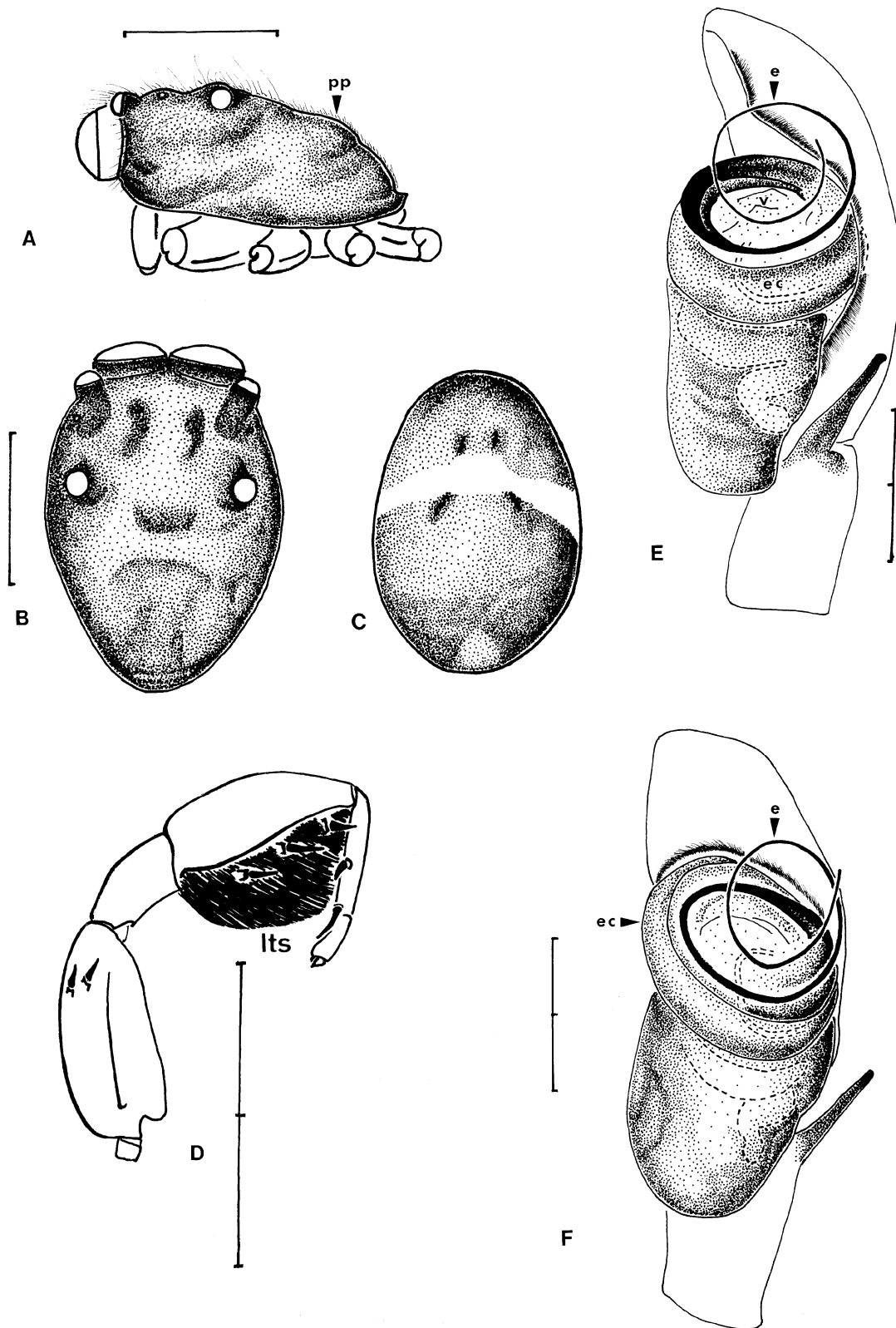


Figure 41. *Indomarengo sarawakensis* sp. nov., male from Java, Indonesia (RMNH). A, prosoma, lateral view. B, same, dorsal view. C, opisthosoma, dorsal view. D, left leg I, lateral view. E, male palp, retrolateral view. F, same, ventral view. Scale bars = 0.2 mm (E, F); 1.0 mm (A–C); 2.0 mm (D).

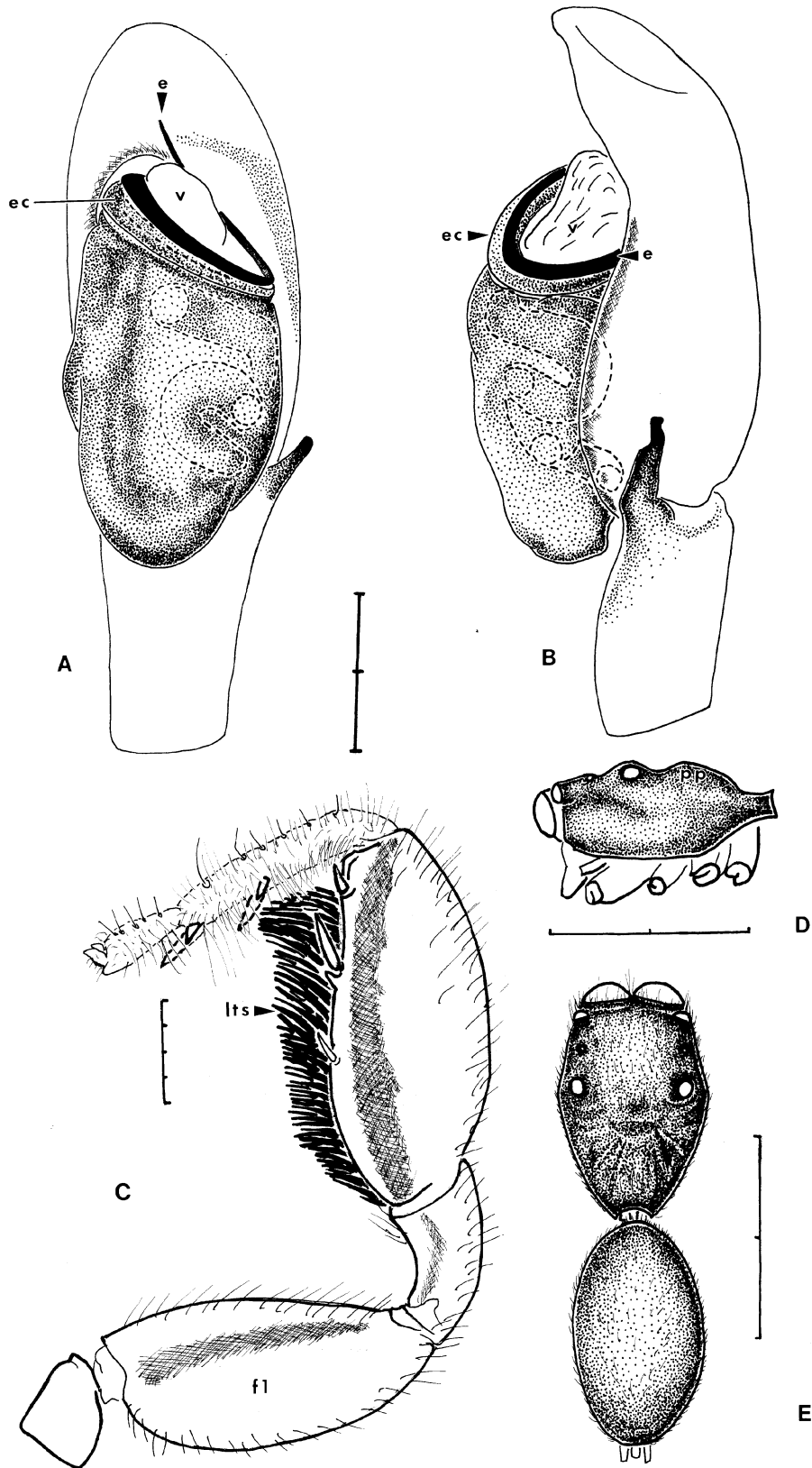


Figure 42. *Indomarengo chandra* sp. nov. (RMNH). A, male palp, ventral view. B, same, retrolateral view. C, left leg I, lateral view. D, prosoma, lateral view. E, habitus, ventral view. Scale bars = 0.2 mm (A, B); 2.0 mm (D, E); 4.0 mm (C).

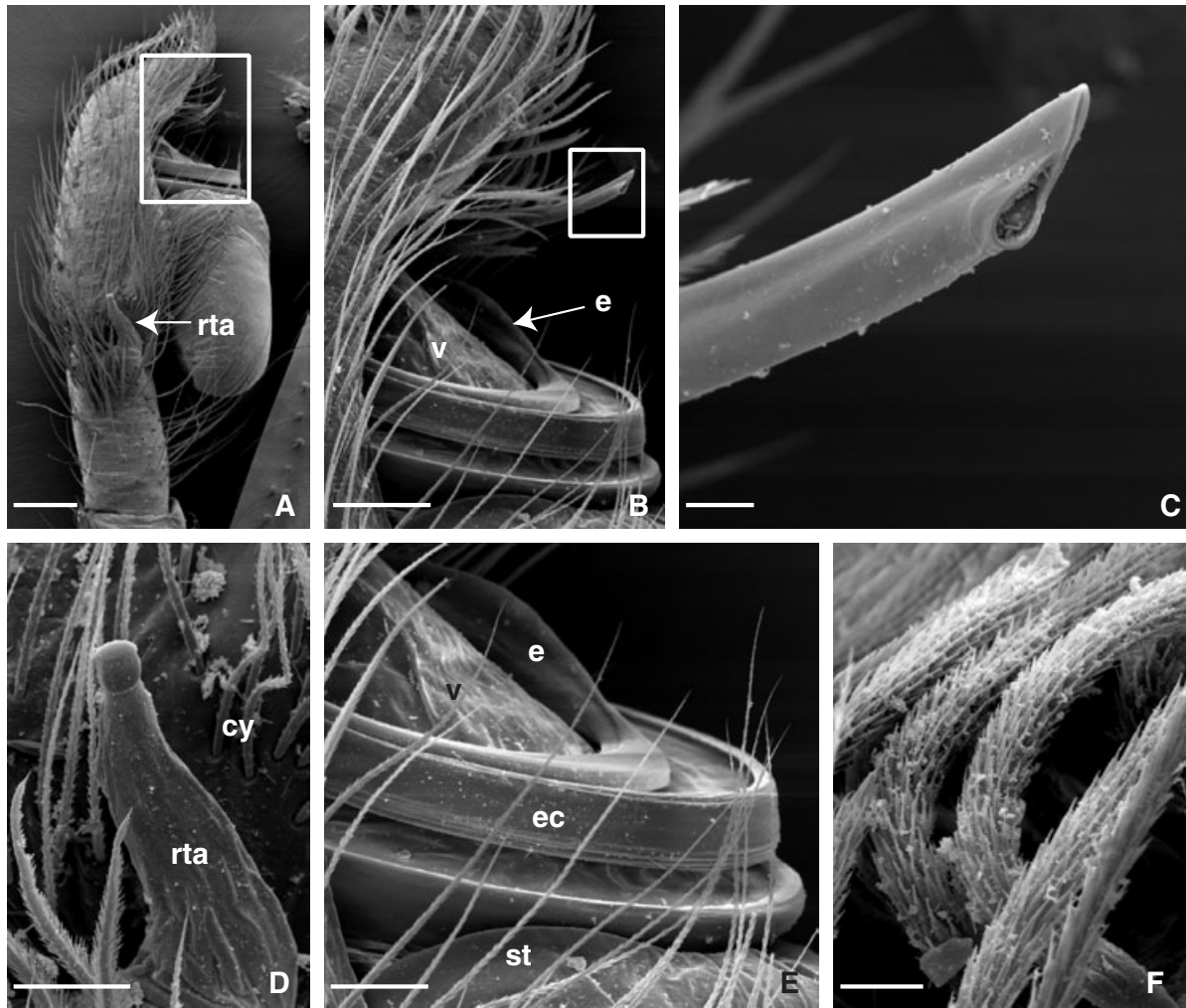


Figure 43. SEM, *Indomarengo chandra* sp. nov. (RMNH). A, right male palp, retrolateral view. B, ec and embolus, retrolateral view. C, tip of embolus, retrolateral view. D, rta, retrolateral view. E, st, ec and embolus. F, setae on the apex of cy, retrolateral view. Scale bars = 5 µm (C, F); 30 µm (D, E); 50 µm (B); 100 µm (A).

less (1978), first recurved, second and third straight and surrounded by dark rings. Chelicerae and labium dark brown, without marking. Leg formula 1432. Tibia I with 2/2/2/2 long thin spines, metatarsus I with 2/2 spines. Venter uniformly yellow. Long setae on prosoma and opisthosoma (Figs 52G, H, 53A). Porous-like structures on prosoma (Figs 52G, 53A, B). Palp: cymbium oval. Retrolateral tibial apophysis sickle-shaped, tapering to a pointed end. Tegulum bilobed, projecting outwards, anterior end gradually tapering to a pointed end, path of sperm duct as in Figures 48A, B, 49A, B; embolus thin, long, spirals more than three times (Figs 48A, B, 49A, B, 52A, B).

Female: Total length 3.7; prosoma length 2.0, width 1.1. Leg I: femur 1.1 patella 0.4, tibia 0.8, metatarsus 0.7, tarsus 0.5. Prosoma oval, longer than wide, red brown, venter lighter, without prominent markings,

no prominent setae as in male. Opisthosoma lighter than in male, two prominent yellow patches on the anterior half (absent in some specimens). Legs laterally with dark markings. Eyes surrounded by dark rings. Leg formula 1432. Tibia I with 2/2/2/2 spines, metatarsus I with 2/2 thin, long spines. Epigynum and vulva as in Figures 48E, 50A–C, 51A–F. See also the detailed description of the type in Wanless (1978).

Variation: Specimens from North Sumatra, Bohorok. Male: total length 4.0; prosoma length 2.0 width 1.3. Leg I: femur 1.5, patella 0.6, tibia 1.3, metatarsus 0.6, tarsus 0.4. Female: total length 4.0; prosoma length 2.0 width 1.4. Leg I: femur 0.5, patella 0.4, tibia 1.0 metatarsus 0.6, tarsus 0.4. Lighter in colour than the other specimens. Anterior parts of tegulum sharply tapering, end pointed. Palpal tibia relatively shorter (cf. Fig. 54A–D), rta bent towards the tegulum at the

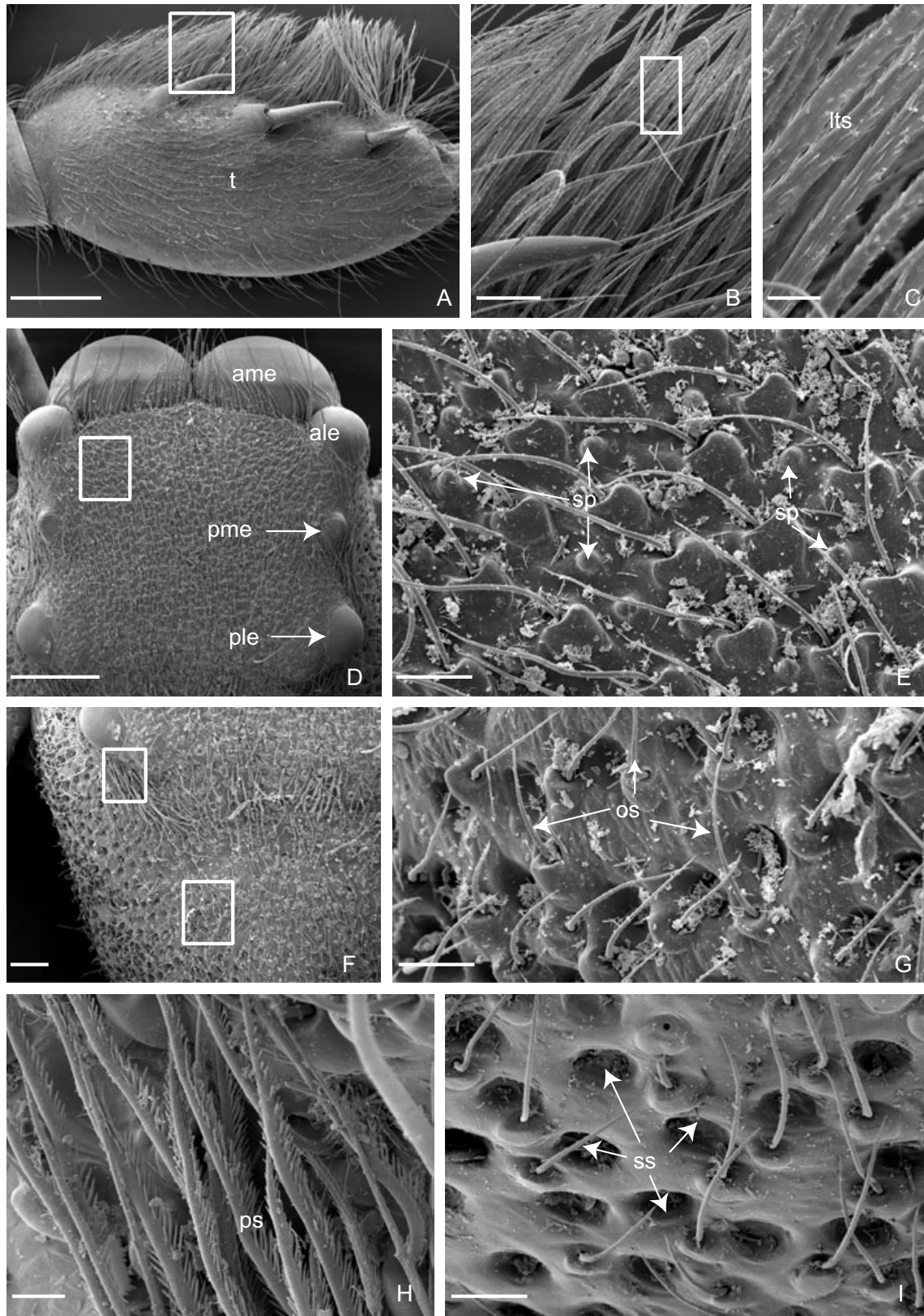


Figure 44. SEM, *Indomarengo chandra* sp. nov. (RMNH). A–C, right tibia I with lts, lateral view. D–I, prosoma, dorsal view. Scale bars = 10 µm (C); 30 µm (E, G, H, I); 50 µm (B); 100 µm (F); 300 µm (A, D).

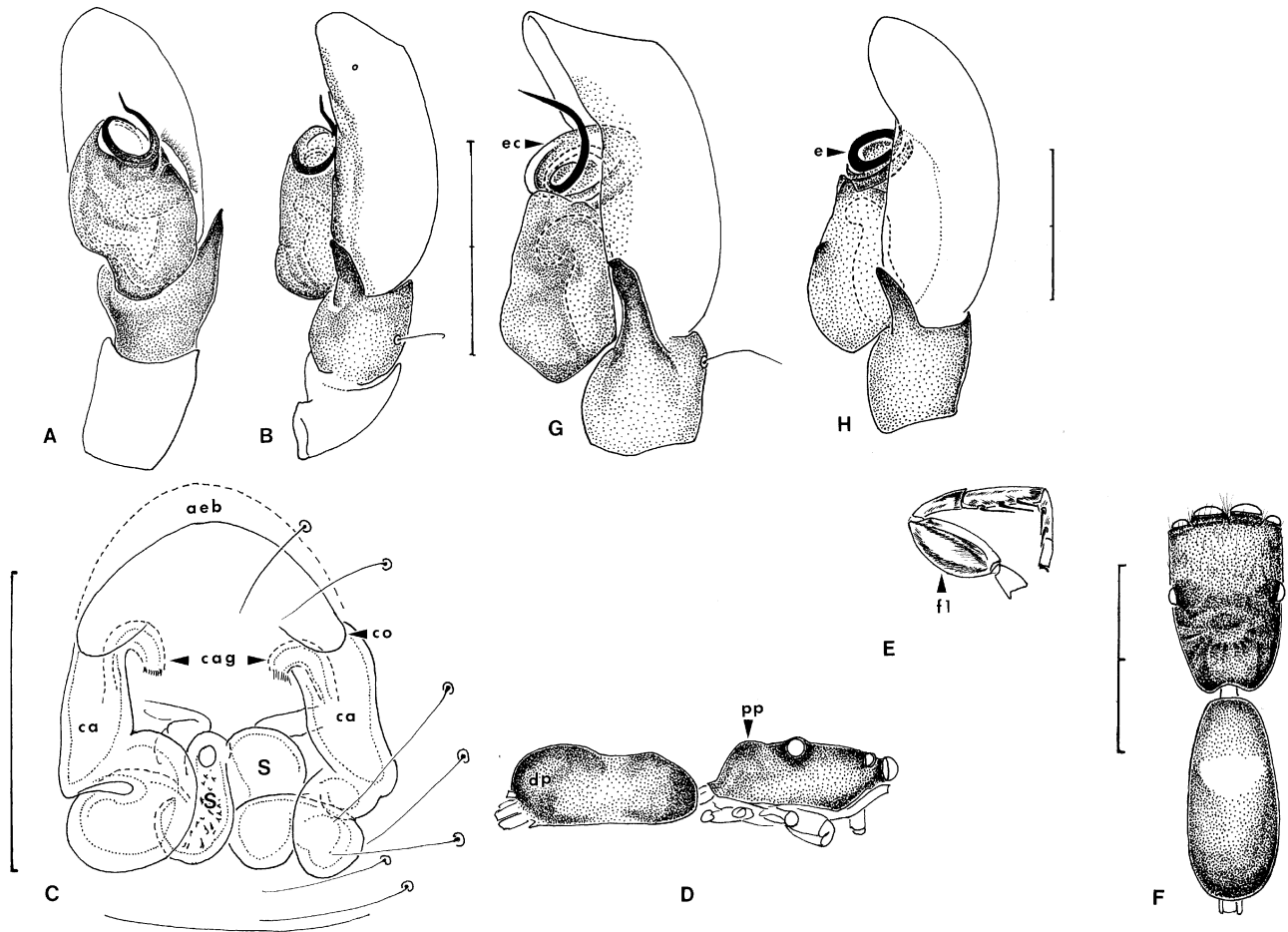


Figure 45. *Sadies* spp. A–F, *S. fulgida* from Mahe, Seychelles (male: MRAC 159.955; female: MRAC 143.086). A, left male palp, ventral view. B, same, retrolateral view. C, epigynum, ventral view. D, habitus, lateral view. E, leg I, lateral view. F, habitus, ventral view. G, *S. trifasciata*, retrolateral view of left male palp. H, *S. seychellensis*, retrolateral view of left male palp. Scale bars = 0.1 mm (C); 0.2 mm (A, B, G, H); 2.0 mm (D–F).

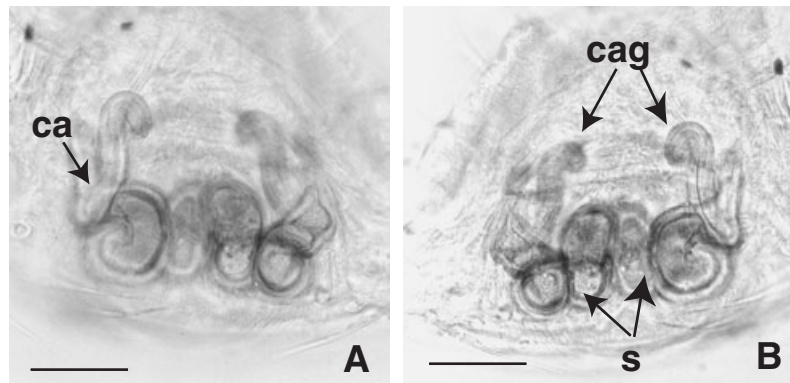


Figure 46. Female genitalia of *Sadies fulgida* from Mahe, Seychelles (MRAC 143.086). A, ventral view. B dorsal view. Scale bars = 0.1 mm.

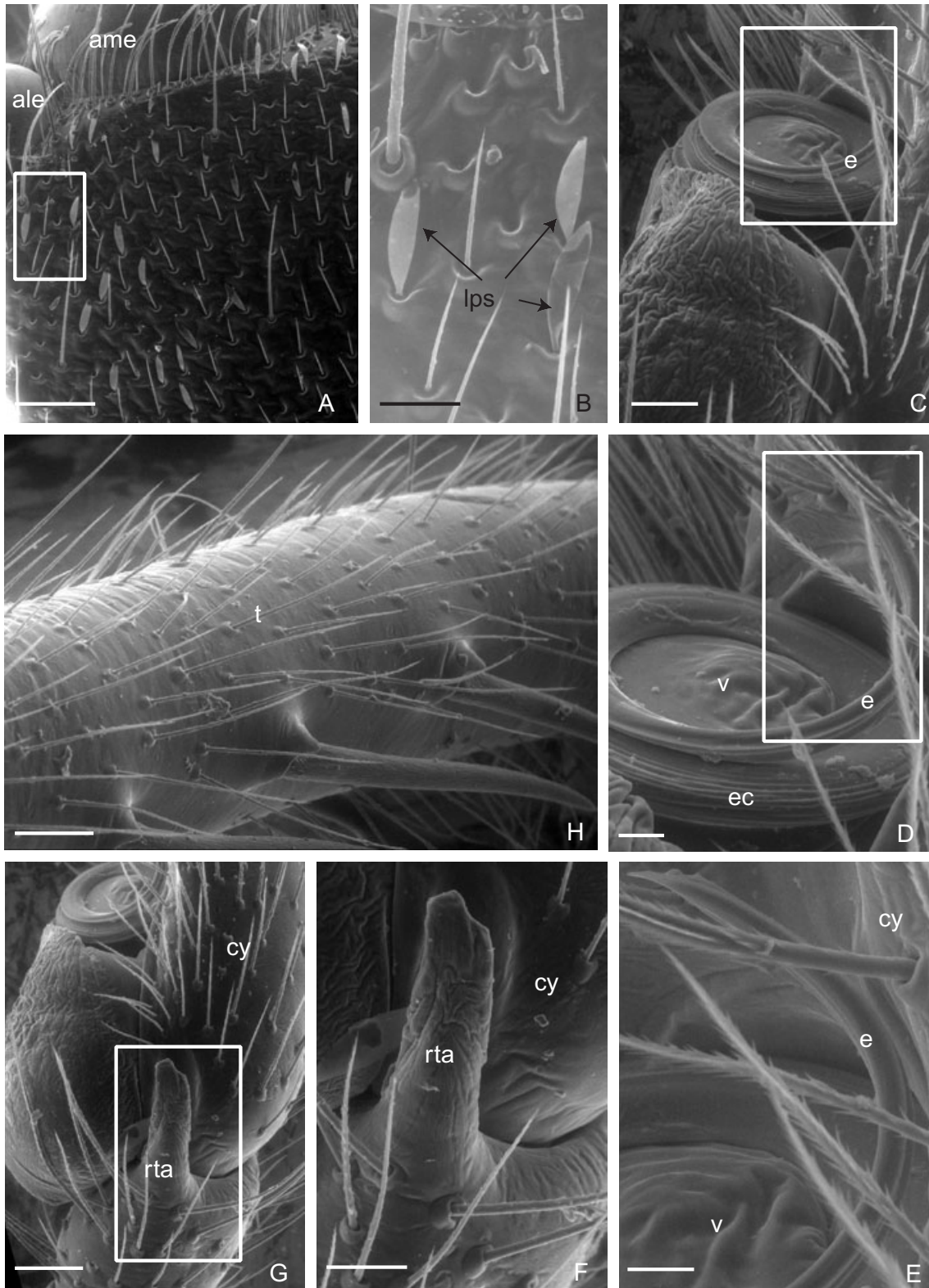


Figure 47. ESEM, *Sadies fulgida* from Seychelles, Silhouette, La Passe (MZT). A, prosoma, dorsal view. B, leaf-like prosomal scales. C, distal part of the palp, retrolateral view. D, st, ec and embolus, retrolateral view. E, embolus tip, retrolateral view. F, details of the rta, retrolateral view. G, proximal part of the palp, retrolateral view. H, tibia I, ventrolateral view. Scale bars = 10 μ m (D, E); 30 μ m (B, C, F); 50 μ m (G, H); 100 μ m (A).

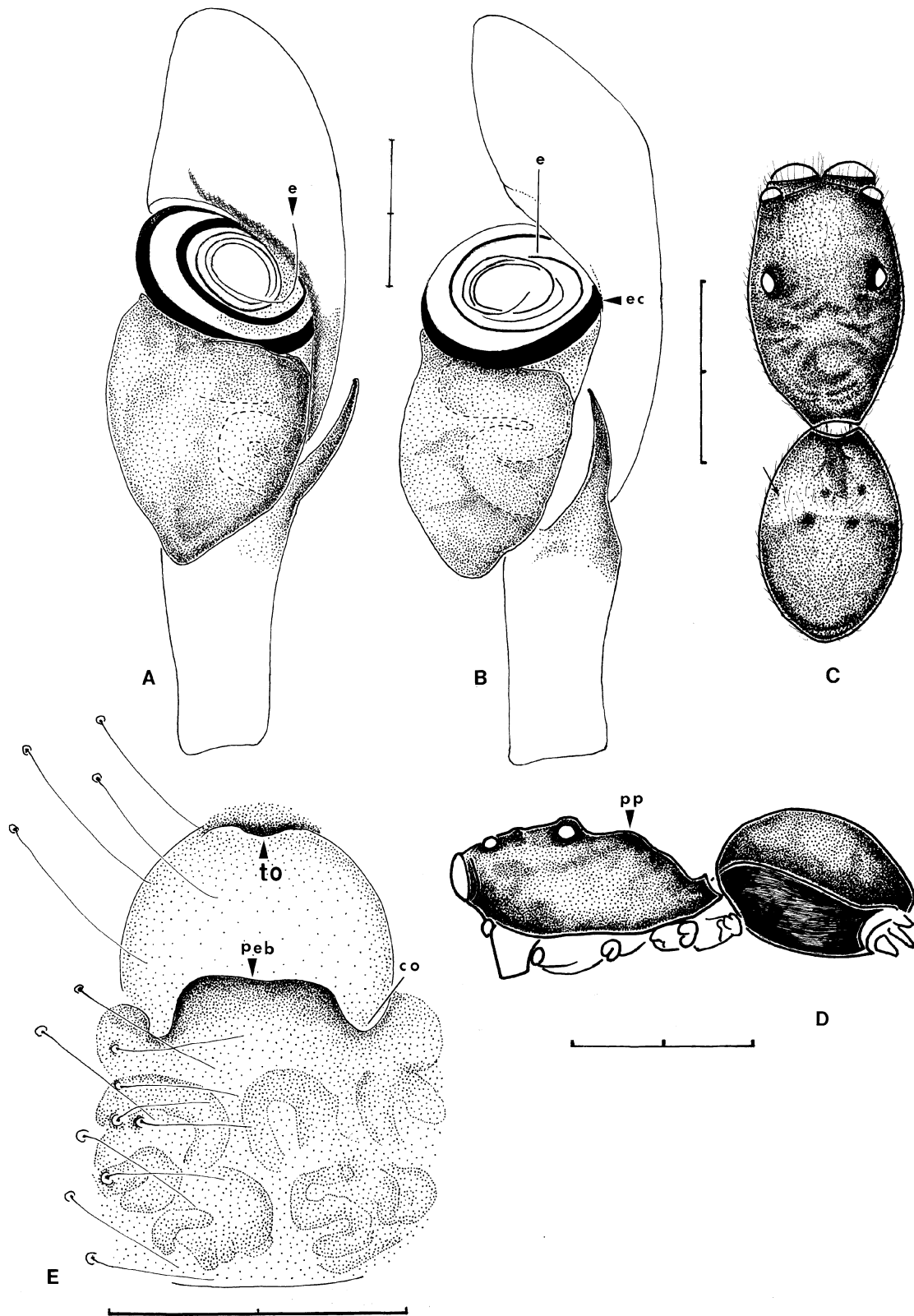


Figure 48. *Leikung porosa* from Kerinci, Sumatra, Indonesia (RMNH). A–D, male. A, male palp, ventral view. B, same, retrolateral view. C, habitus, ventral view. D, same, lateral view. E, female genitalia, epigynum, ventral view. Note the raised ple; arrow indicates the transverse white line. Scale bars = 0.2 mm (A, B, E); 2.0 mm (C, D).

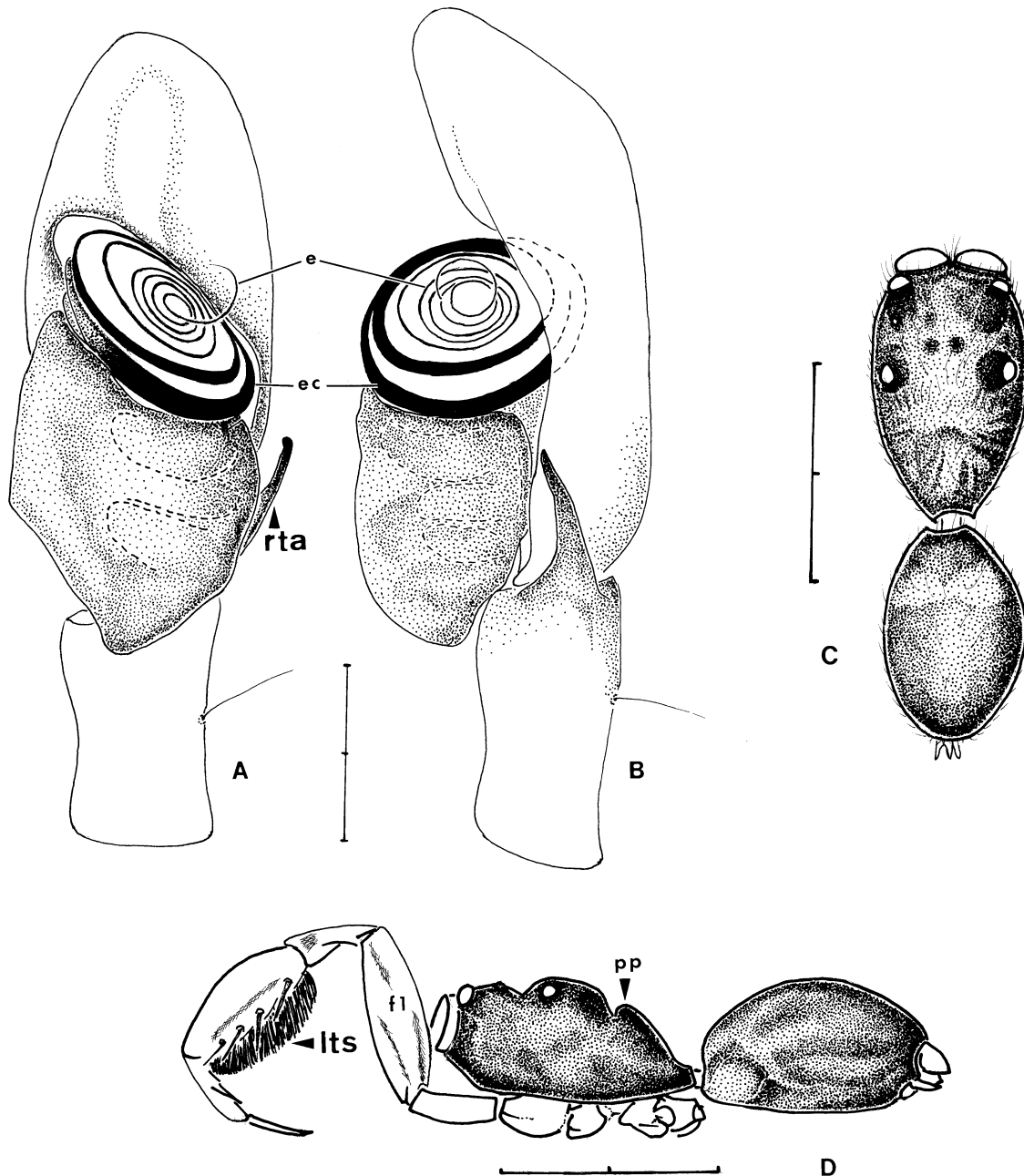


Figure 49. *Leikung porosa* from Bohorok, North Sumatra, Indonesia (RMNH). A, male palp, ventral view. B, same, retrolateral view. C, habitus, ventral view. D, habitus, lateral view. Scale bars = 0.2 mm (A, B); 2.0 mm (C, D).

centre (Fig. 54D), not sickle-shaped as in non-Bohorok specimens.

Distribution: Malaysia and Indonesia.

Other material examined: MALAYSIA: peninsular Malaysia, Genting highlands, on leaves; 1♀, 29.7.1980 leg. CL and PR Deeleman, RMNH; Templers Park; 1♂, 1.12.1990 leg. CL and PR Deeleman, RMNH; Borneo, Danum valley field sta-

tion, pitfall trap, logged forest, 1♂ 1♀, 1991?, leg. T Borghouts?, RMNH; Gunung Trus Madi, 1440 m altitude, secondary forest, 5°34.989'N, 116°29.714'E, hand catch; 1♂, 28.10.2001 leg. M. Schilthuisen & P. Koomen, Trus Madi expedition 2001 University Malaysia Sabah, BORN. INDONESIA: Sumatra, Kerinci, Seblat National Park, 800 m, near river, on leaves, 3♂ 3♀, 21–30.8.1988, leg. Suharto Djojosedharmo, RMNH; North

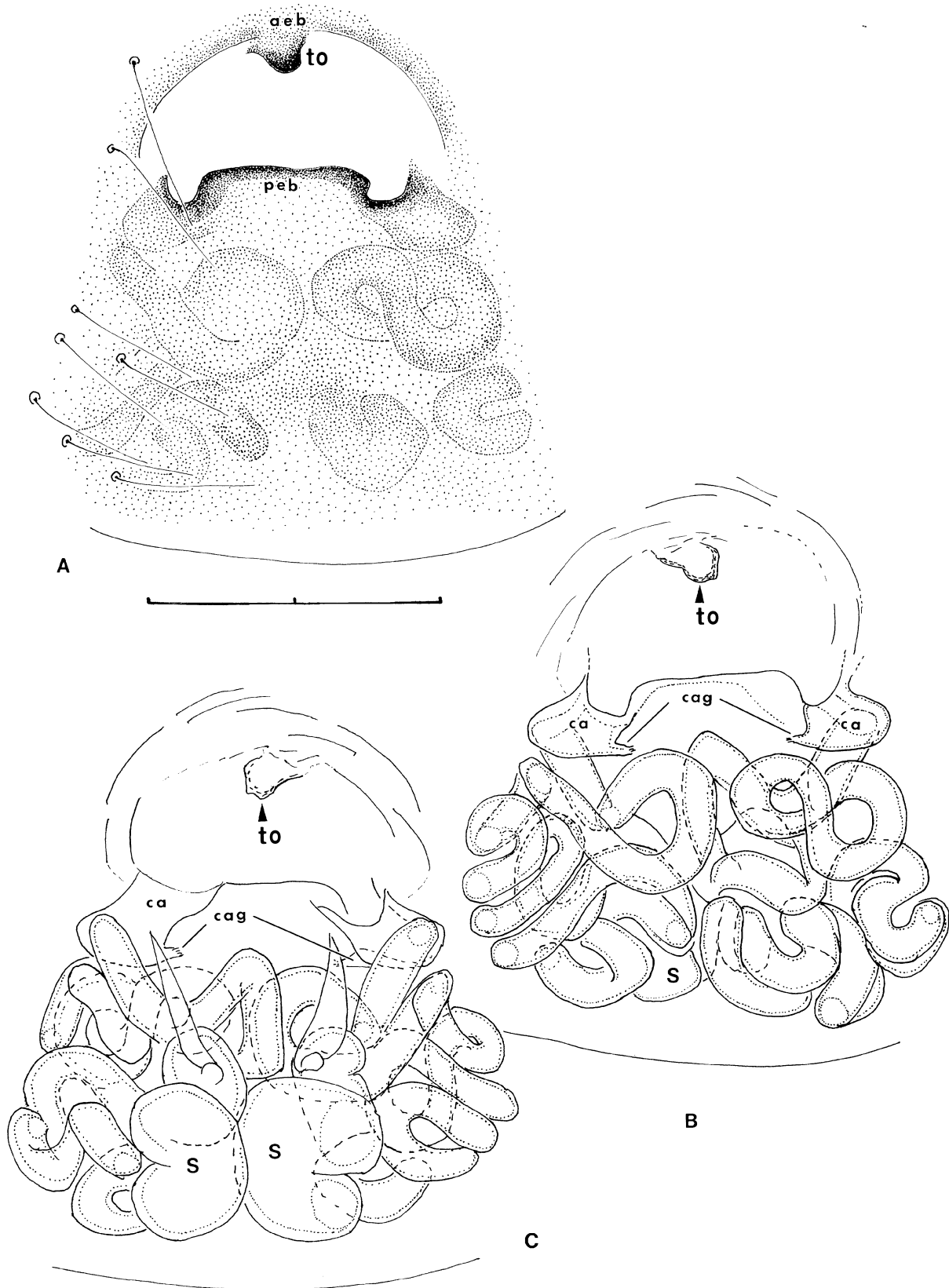


Figure 50. *Leikung porosa* from Bohorok, North Sumatra, Indonesia (RMNH). Female genitalia. A, epigynum, ventral view. B, vulva, ventral view. C, vulva, dorsal view. Scale bar = 0.2 mm.

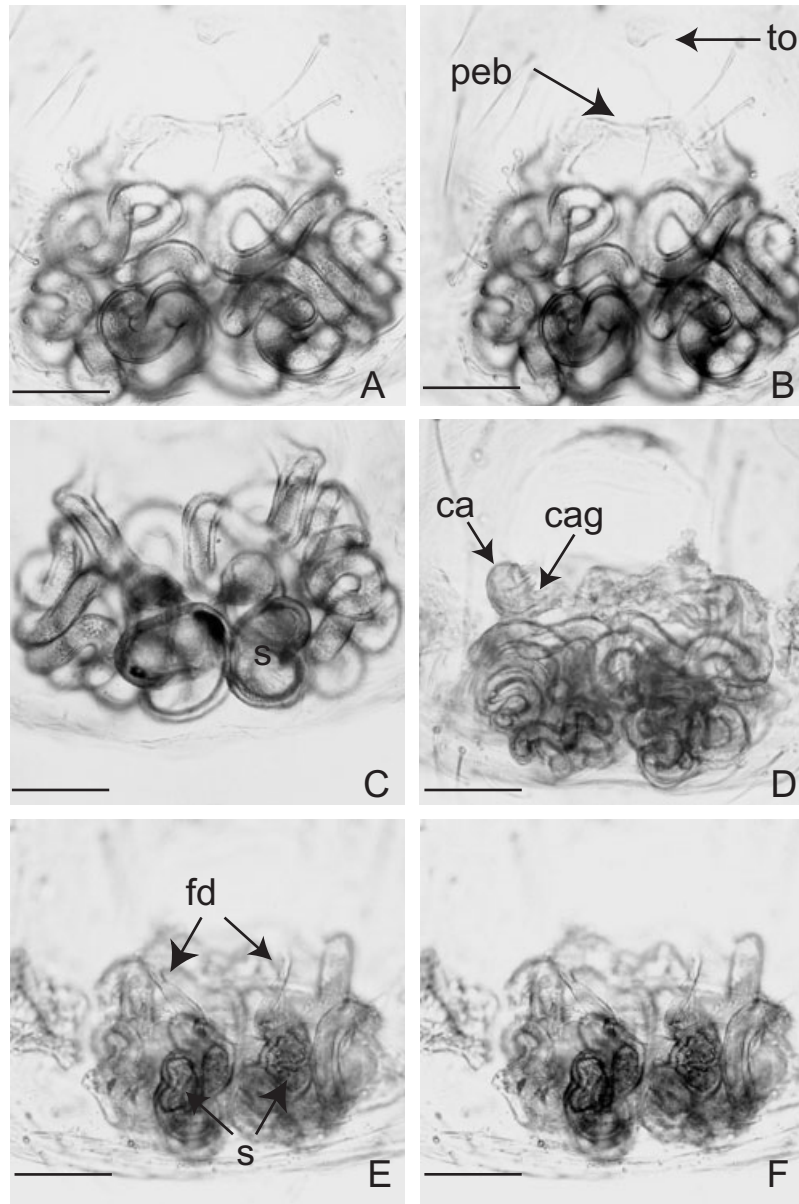


Figure 51. *Leikung porosa* (RMNH). Female genitalia. A–C, Bohorok, North Sumatra, Indonesia. D–F, Kerinci, Sumatra, Indonesia. A–D, ventral view. E, F, dorsal view. Scale bars = 0.1 mm.

Sumatra, Bohorok, Gunung Leuser National Park; 1♀, 11.6.1983, leg. CL and PR Deeleman, RMNH; North Sumatra, Bohorok, along the river, from leaves; 1♂, 14.12.1983, leg.?, RMNH; North Sumatra, Bohorok, river side; 1♂ 15.12.1983, leg.?, RMNH; North Sumatra, Bohorok, bambu nr. Center, 3.1.1984, under 'tent' rear?, 1♂ 1♀, hole in leaf, leg. 'Not given in the label', deposited in RMNH; West Sumatra, Anai, Mt. Singalang, 400–520 m, on leaves, 1♂ 1♀, 10–22.6.1994, leg. Suharto Djojosedharmo, RMNH.

***LEIKUNG KINABALUENSIS* SP. NOV.**

(FIGS 55A–G, 56A–F)

Holotype: ♂ from Malaysia: North Borneo, Kinabalu National Park, 1600 m, beating shrub, leg. P.L. Deeleman & G. Perrault, 26.6.1979, deposited in RMNH.

Etymology: Named after the type locality.

Diagnosis: Distinguished from *L. porosa* by details of the rta, which is long, wider and bent towards the tegulum at its base (Fig. 55A, G). The opisthosoma may

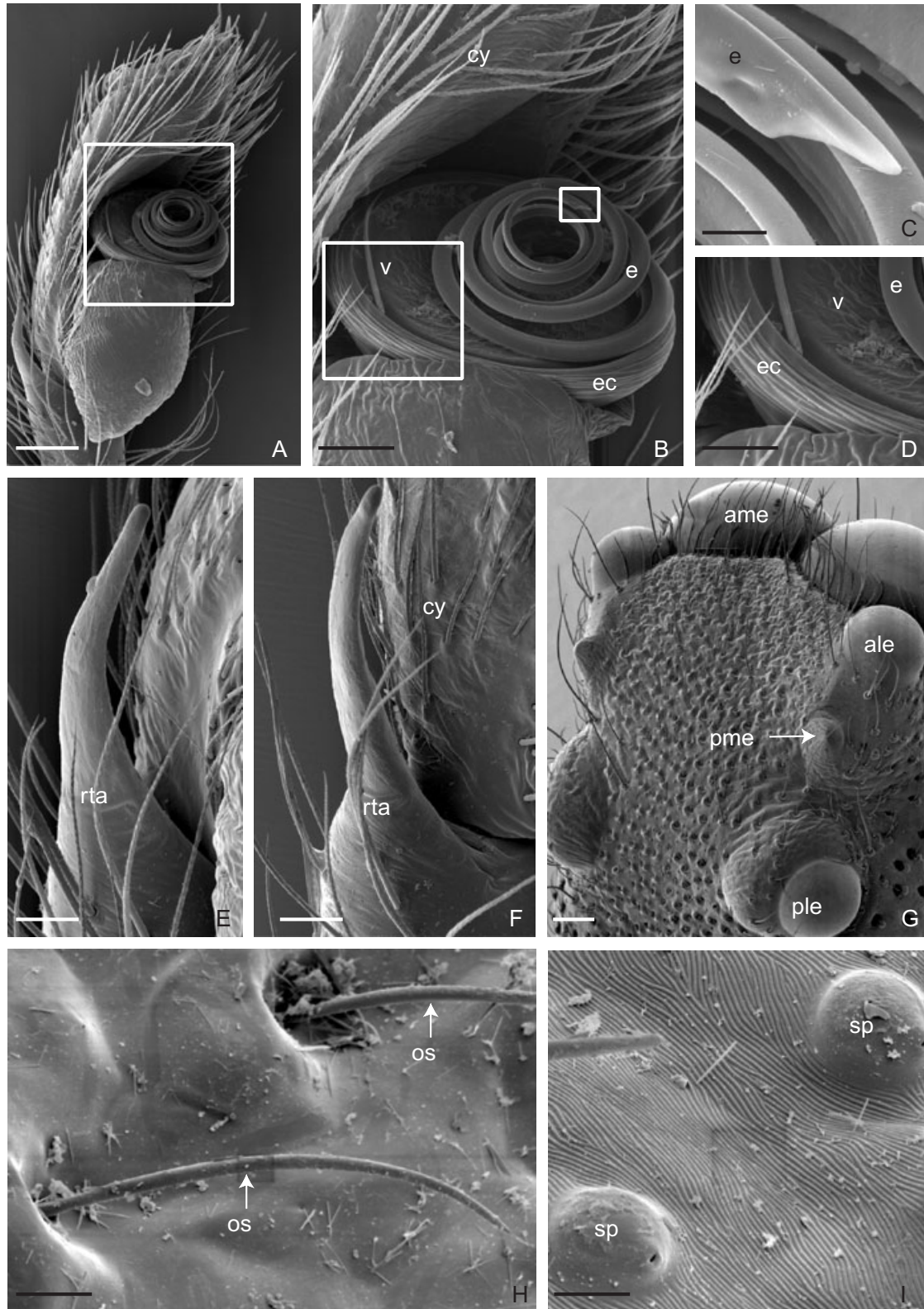


Figure 52. SEM, *Leikung porosa* (RMNH). A–E, Bohorok, North Sumatra, Indonesia. F–I, Kerinci, Sumatra, Indonesia. A right palp, retrolateral view. B, st, ec and embolus, retrolateral view. C, same, retrolateral view of embolus tip. D, same, retrolateral view of ec. E, rta. F, rta. G, dorsolateral view of prosoma. H, prosomal setae. I, sp. Scale bars = 5 µm (C, I); 10 µm (H); 30 µm (D, E, F); 50 µm (B); 100 µm (A, G).

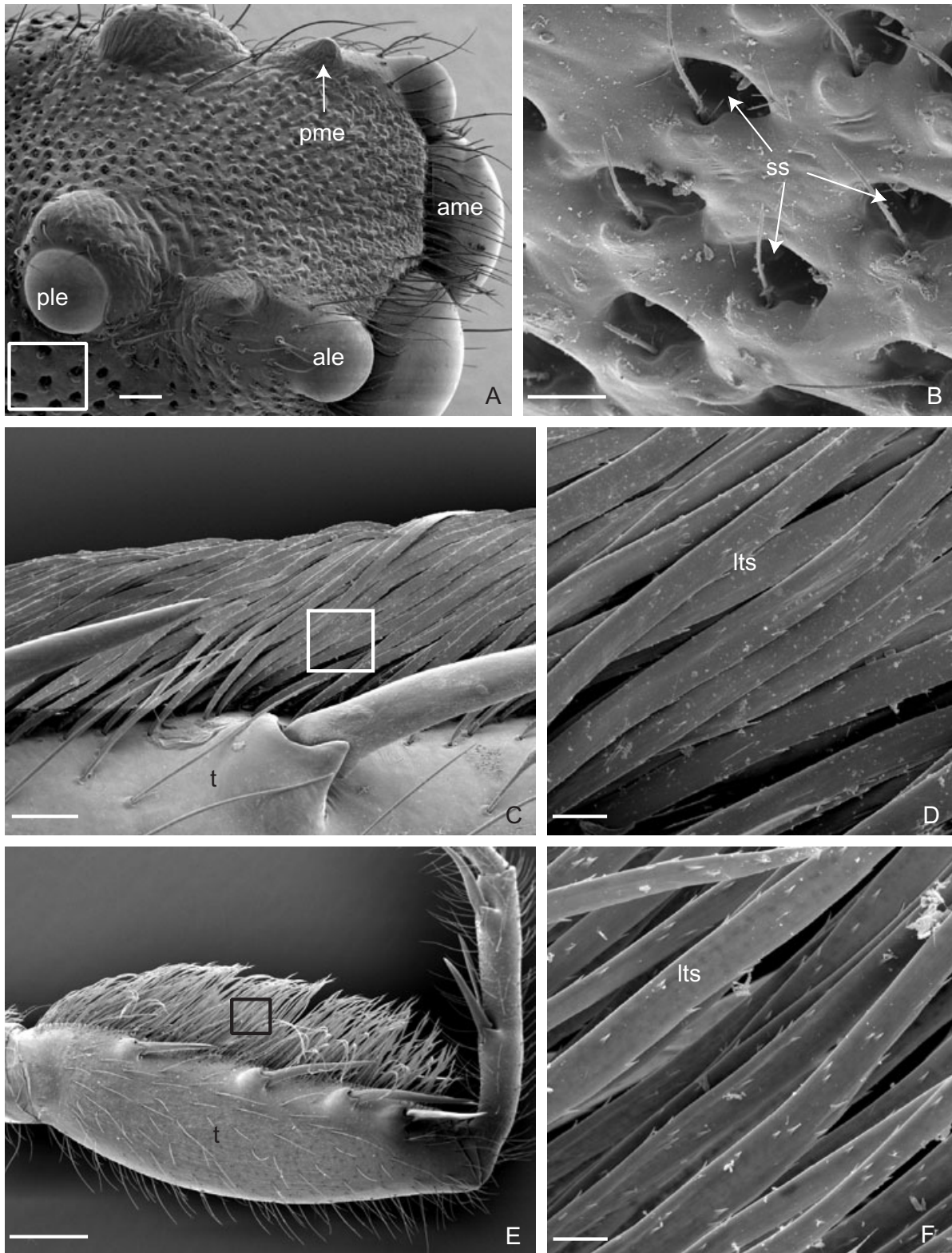


Figure 53. SEM, *Leikung porosa* (RMNH). A–D, Kerinci, Sumatra, Indonesia. E, F, Bohorok, North Sumatra, Indonesia. A, prosoma, dorsolateral view. B, prosomal pits with sensory setae, lateral view. C, tibia I, lateral view. D, lts details. E, tibia with lts. F, lts details. Scale bars = 10 µm (B, F); 50 µm (D); 100 µm (A); 300 µm (C, E).

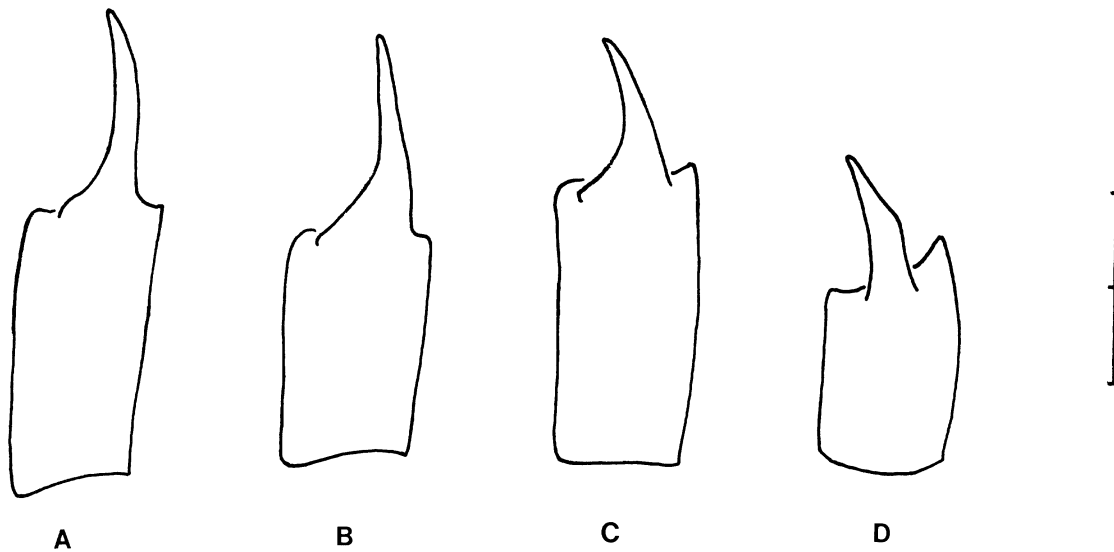


Figure 54. *Leikung porosa* (RMNH), male rta. A, Mt. Singalang, West Sumatra, Indonesia. B, C, Kerinci, Sumatra, Indonesia. D, Bohorok, North Sumatra, Indonesia. Scale bar = 0.2 mm.

be longer and tibia of leg I may not possess lts in some specimens of *L. kinabaluensis* (Fig. 55C).

Male: Total length 4.5; prosoma length 2.2, width 1.5. Leg I: femur 1.2, patella 0.4, tibia 1.3, metatarsus 0.7, tarsus 0.5. Markings as in Figure 55D, E. Prosoma raised, broad, dark brown, without prominent markings except for dark rings surrounding eyes; setae as in Figure 55D. Opisthosoma oval, elongated, shining, yellow brown, with dark marking. Transverse whitish band. Venter uniformly grey to yellow. Legs I–IV laterally without dark markings. Eyes surrounded by dark rings. Chelicera, labium dark brown, without marking. Leg formula 1423. Tibia I with 2/2/2/2 long thin spines, metatarsus I with 2/2 spines. Palp: cymbium oval, longer than wide. Retrolateral tibial apophysis large, longer than in *L. porosa*, tapering to a pointed end. Tegulum bilobed, projecting outwards, anterior end gradually tapering to a pointed end, path of sperm duct as in Figure 55A, B; embolus thin, long, coils more than four times.

Female: Total length 3.7; prosoma length 1.8, width 1.2. Leg I: femur 1.3, patella 0.5, tibia 1.1 metatarsus 0.7, tarsus 0.2. Prosoma oval, longer than wide, red brown, venter lighter, without prominent markings, no prominent setae as in male. Legs laterally with dark markings. Eyes surrounded by dark rings. Leg formula 1432. Tibia I with 2/2/2/2 spines, metatarsus I with 2/2 thin, long spines. Epigynum and vulva as in Figures 55F, 56A–F.

Variation: Specimens from East Malaysia, Kimanis road. Male: total length 3.8; prosoma length 2.0 width 1.1. Leg I: femur 1.1 patella 0.4, tibia 0.8, metatarsus

0.7, tarsus 0.5. lts absent in the holotype. Opisthosoma oval, black brown, shining, a prominent transverse whitish band present. Palp relatively smaller (Fig. 55G).

Distribution: Malaysia, Borneo.

Other material examined: MALAYSIA: East Malaysia, Kimanis road, 16 miles from Keningau, Heliplatz, 1380–1400 2♂ 1♀, 12.6.1982, leg. D. Burckhardt, MHNG.

AFROMARENGO GEN. NOV.

Type species: *Marengo coriacea* Simon, 1900.

Etymology: Afro- (after Africa, where the two described species occur) and the generic name *Marengo*. It is considered feminine in gender.

Monophyly and phylogenetic placement: Unclear. A detailed study of a large collection of material from various parts of Africa would be needed to assess monophyly. The presence of a long embolus (5-2), posterior epigynal border (13-1) and scattered papillae (39-1), and absence of an epigynal septum (10-0), unite *Afromarengo* with the South-east Asian genus *Leikung*.

Diagnosis: *Afromarengo* can be best distinguished from all other Ballinae by the presence of asymmetrical scales (32; Fig. 59C, E) and, except for *Leikung*, by the long embolus (Figs 57A–C, 58A, C, D). It can be distinguished from *Leikung* by the tooth on the anterior epigynal border (14; Figs 48E, 50A–C), eight

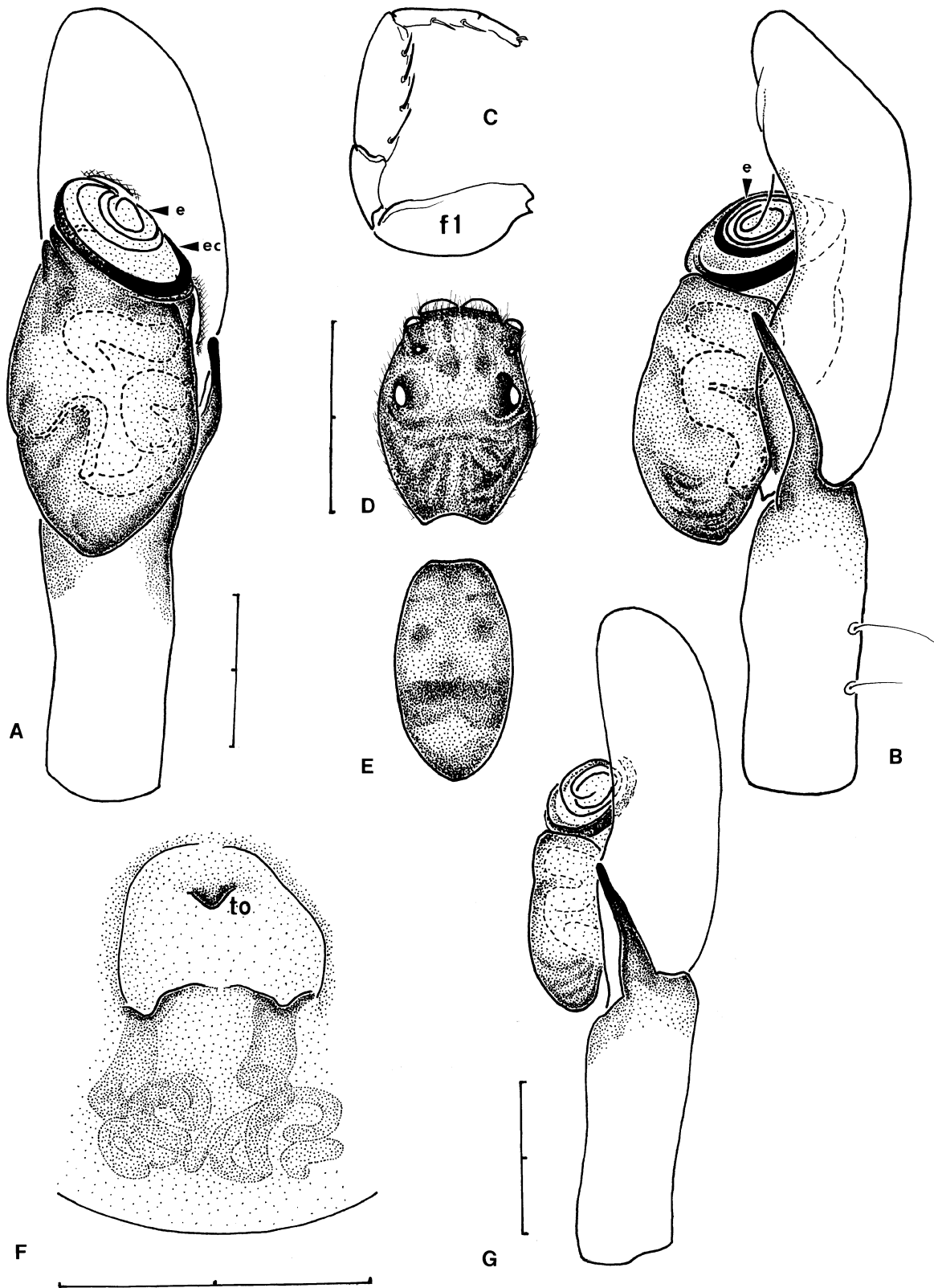


Figure 55. *Leikung kinabaluensis* (RMNH). A, male palp, ventral view. B, same, retrolateral view. C, left leg I, lateral view. D, prosoma, dorsal view. E, opisthosoma, dorsal view. F, G. East Malaysia, Kimanis road (MHNG). F, epigynum, ventral view. G, male palp, retrolateral view. Scale bars = 0.2 mm (A, B, F, G); 2.0 mm (C–E).

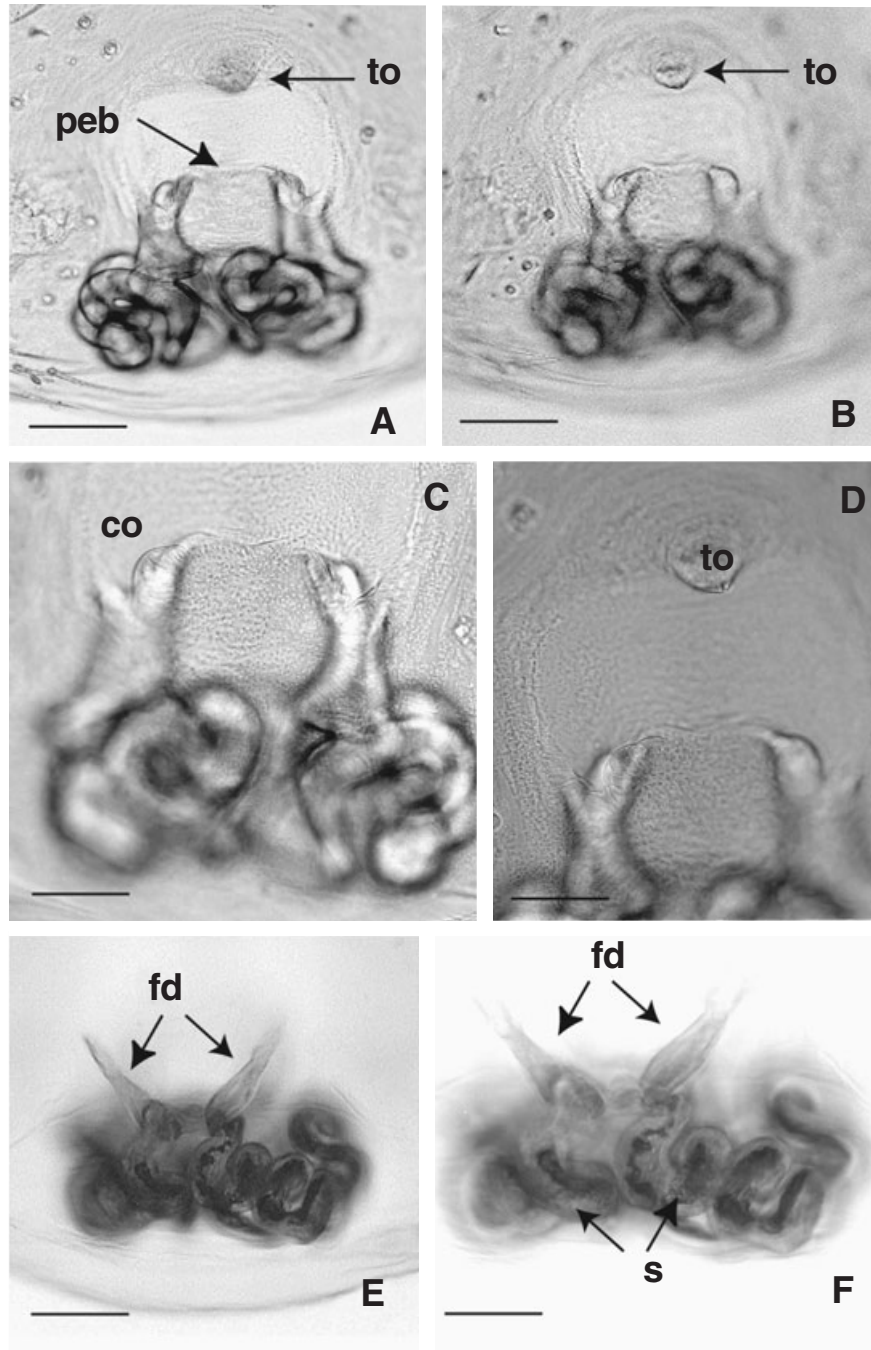


Figure 56. *Leikung kinabaluensis*, female genitalia. East Malaysia, Kimanis road (MHNG). A–D, ventral view. E, F, dorsal view. Scale bars = 0.05 (C, D, F); 0.1 mm (A, B, E, F).

spines on tibia I (35; Figs 49D, 53E, 55C) and pits with sensory setae (38; Fig. 53B) in *Leikung*.

Description: See description of type species in Wanless (1978).

Composition: Two described species, *Afromarengo coriacea* (Simon, 1900) comb. nov. and

A. lyrifera (Wanless, 1978) comb. nov. (new combinations from *Marengo*). There may be many more undescribed species (Benjamin, unpublished data).

Distribution: Known from Angola, Kenya, Tanzania, South Africa and Zaire.

AFROMARENGO CORIACEA (SIMON, 1900) COMB. NOV.
(FIGS 4C, 57A–C, 58A–D, 59A–F)

Marengo coriacea Simon, 1900: 401, ♂ lectotype from Natal, South Africa in MNHN 20184, examined.

Marengo kibonotensis Lessert, 1925: 439, figs 15–17 (♀ holotype from Kenya in NRS, not examined). Proposed as a synonymy of *M. coriacea* by Wanless (1978); see remarks below.

Marengo coriacea Lawrence, 1947: 36, fig. 22 (♀ from Durban, Natal, South Africa, not examined).

Marengo coriacea Roewer, 1965: 31, fig. 26a–e.

Marengo coriacea Wanless, 1978: 261 fig. 1a–j, pl. 1a–c.

Diagnosis: Distinguished from *A. lyrifera* by the latter's cylindrical opisthosoma. The rta appears to be long and thin in *A. coriacea*, short and stout in *A. lyrifera* (Wanless, 1978: figs 1f, i; 2e, f).

Remarks: I doubt the synonymy of *M. kibonotensis* Lessert, 1925, from Kenya, which, judging from illustrations of the female type given by Lessert (1925: figs 15–17) appears to be different from *A. coriacea*. Furthermore, *Afromarengo* spp. can most easily be distinguished by details of the male palp, for example by the shape of the rta. However, I refrain from making any further taxonomic changes until a detailed study of a large collection of material is undertaken.

Description: *Afromarengo coriacea* has been described in detail (Lawrence, 1947; Wanless, 1978; Wesolowska & Russell-Smith, 2000) and is not treated further here. Description of males from Kenya (HMNH 274):

total length 3.3; prosoma length 1.6, width 1.0. Leg I: femur 1.0 patella 0.3, tibia 1.0 metatarsus 0.6, tarsus 0.2. Prosoma uniformly dark black, sides lighter, venter uniformly black. Opisthosoma longer than wide, dark brown, venter uniformly black. Legs I–IV with lateral dark markings. Eyes surrounded by dark rings. Chelicerae, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Palp: cymbium oval, longer than wide. Retrolateral tibial apophysis large, tapering to a pointed end (Fig. 57B, C). Tegulum bilobed, projecting outwards, anterior end gradually tapering to a pointed end, path of sperm duct as in Figure 57A–C, embolus thin long, coils more than four times (Fig. 57A, C).

Distribution: Known from Kenya, Tanzania, South Africa and Zaire.

Other material examined: KENYA: Gala estate, 2♂, 15–20.3.2001 leg. S. & L. Mahunka, HMNH 274; Tana river, Sankuri (25 km north of Garissa); 1♂, 18.10.1977, leg. V. Mahnert, det. Wanless 1984, MHNG (77/24).

MARENGO G. & E. PECKHAM, 1892

Marengo G. & E. Peckham, 1892: 66. Simon, 1900: 400–401. Simon, 1901: 488, 502. Sherriffs, 1931: 538–539. Wanless, 1978: 231–296. Zabka, 1999.

Type species: *Marengo crassipes* Peckham & Peckham, 1892, by original description. Single adult female specimen in MCZ, not examined.

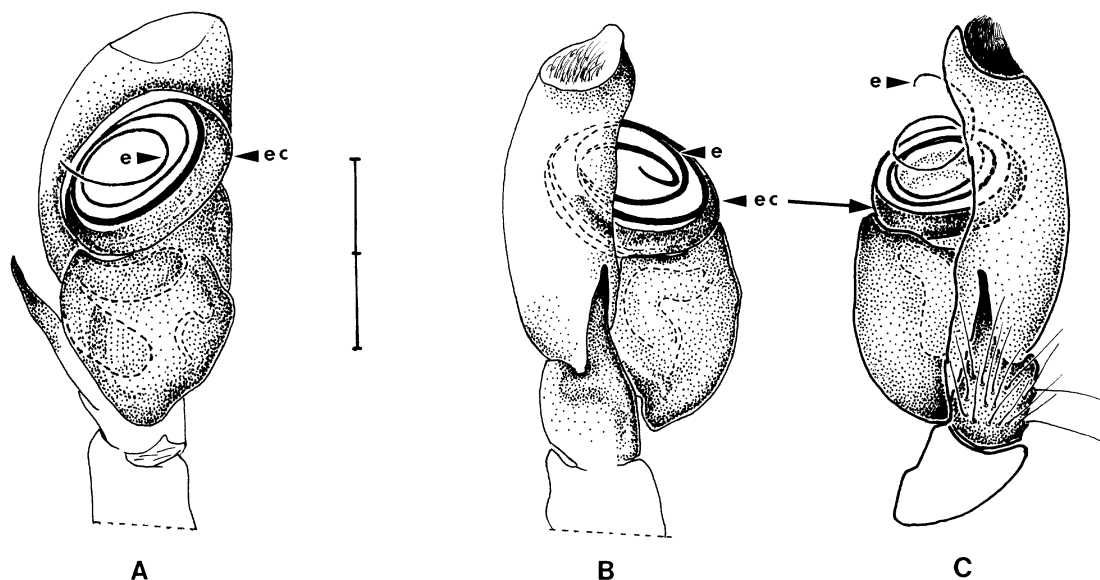


Figure 57. *Afromarengo coriacea*, male. A, B, Natal, South Africa (MNHN 20184). A, right male palp, ventral view. B, same, retrolateral view. C, Kenya (HMNH), left male palp, retrolateral view. Scale bar = 0.2 mm.

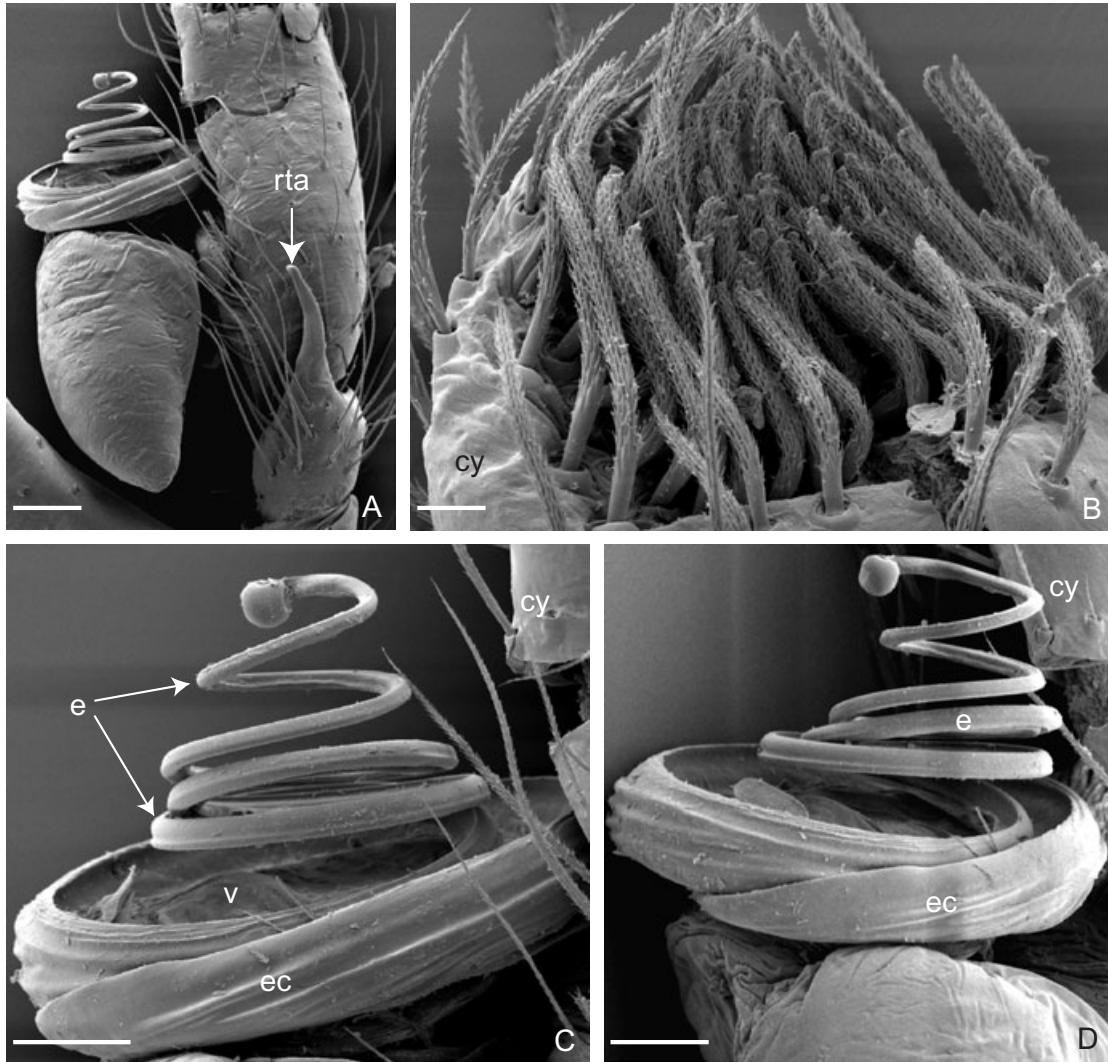


Figure 58. SEM *Afromarengo coriacea*, male from Kenya (HMNH). A, left male palp, retrolateral view. B setae on the apex of cy, retrolateral view. C, ec and e, retrolateral view. D, ec and embolus, ventral view. Scale bars = 10 μm (B); 30 μm (C, D); 50 μm (A).

Remarks: Peckham & Peckham (1892) established *Marengo* to accommodate a single species, *Marengo crassipes*, from Sri Lanka (Ceylon). They diagnosed the genus based on nongenital morphology and the colour of a single female specimen. The appearance of the specimen led them to denote the genus as 'ant-like'. According to the original description, the genus can be diagnosed by the flat prosoma, eye position and the enlarged femur I and tibia I. However, none of these characters are synapomorphic for *Marengo*. Simon (1900, 1901) redefined *Marengo* and described four more species. Lessert (1925) added a further species, *M. kibonotensis*. *Marengo* was one of the few salticid genera to be revised and redefined by Wanless (1978). He revised the genus to include seven species, three of them new. *Philates* was synonymized with

Marengo, *M. nitida* with *M. crassipes*, and *M. kibonotensis* with *M. coriacea*. The genus was once more redefined and the scope broadened by Zabka (1999), based on five newly described species from Papua New Guinea. Wanless (1978) and Zabka (1999) progressively broadened the original definition of the genus to make placement of newly described species possible. As a result, prior to the present study *Marengo* was on its way to becoming something of a polyphyletic wastebasket.

Monophyly and phylogenetic placement: The monophyly of *Marengo* is supported by the presence of white patches on lateral sides of the opisthosoma (23-1) and marked sexual dimorphism (41-1). However, of the five species currently placed in *Marengo*, only *M. crassipes*

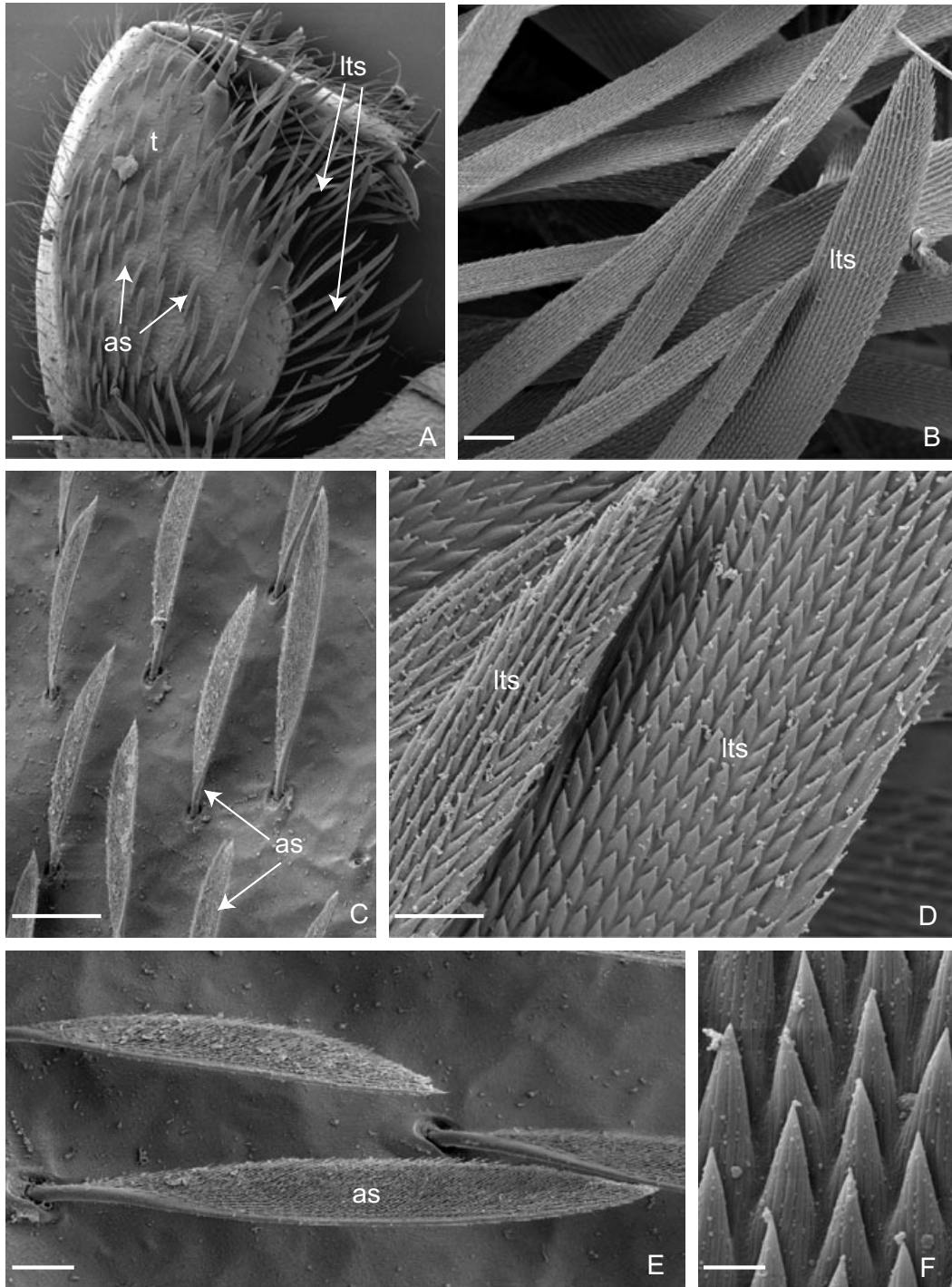


Figure 59. SEM *Afromarengo coriacea*, male from Kenya (HMNH). A, left tibia I, lateral view. B, lts. C, asymmetrical scales. D, details of lts. E, details of asymmetrical scales. F, surface of lts with inferior spines orientated in a distal direction. Scale bars = 1 μ m (F); 5 μ m (D); 10 μ m (B, E); 30 μ m (C); 100 μ m (A).

and *M. deelemanae* are known from both sexes. The monophyly of *M. crassipes* is supported by the presence of a concave ec (3-0) and presence of lts with a surface ribbed with prominent spines (34-1). *M. crassipes*,

M. inornata and *M. striatipes* all possess epigynes that look very different from each other. Additionally, *M. striatipes* does not have an enlarged femur 1. Thus, the monophyly of *Marengo* remains to be tested.

Diagnosis: Distinguished from *Ballus*, *Baviola*, *Colaxes*, *Cynapes* and *Sadies* by the presence of lts (**33**; Figs 61A, 63E, F, 64C, D, 68E, G). Distinguished from all other Ballinae, except for *Philates chelifera*, by the absence of cag (**16**; Figs 62A–D, 66C, D, 67C, 68C, D) and from *P. chelifera* by the presence of an enlarged femur I (**30**; Figs 61A, 65A, D, 68A, G).

Description: See the description of the type species below and Wanless (1978).

Composition: Five species: *M. crassipes*, *M. deelemanae* sp. nov., *M. inornata*, *M. nitida* and *M. striatipes*.

Distribution: India: Kerala. Sri Lanka: Colombo, Kandy, Talawakele, Knuckles Range, Galle. Thailand: Pran Buri.

MARENGO CRASSIPES G. & E. PECKHAM, 1892 (FIGS 60A–C, 61A, B, 62A–D, 63A–F, 64A–D, 65D–F)

Marengo crassipes Peckham & Peckham (1892): 66, pl. v, fig. 4a–c, 1♀ lectotype from Sri Lanka, in MCZ, not examined.

M. crassipes Simon, 1901: 492, fig. 578. 1♀ from Sri Lanka (MNHN 15223), Central Province, Kandy, examined.

M. crassipes Wanless, 1978: 264–266, figs 3a–f, 4a; pls 1e, f, 2a–c, e.

Diagnosis: The female may be distinguished from those of all other known *Marengo* spp. by the presence of two pairs of white spots on the lateral sides of the opisthosoma (Fig. 61A; females of *M. nitida* are unknown). The male is separated from that of *M. nitida* by the thin, tapering and relatively longer rta (Figs 60C, 63B, 65F) and from that of *M. deelemanae* by the surface of lts, which is ribbed with numerous prominent spines. Males of *M. inornata* and *M. striatipes* are unknown.

Male: Sri Lanka, Kandy (MNHN 20405), total length 3.3; prosoma length 1.7, width 1.2. Leg I: femur 0.8, patella 0.3, tibia 0.9, metatarsus 0.6, tarsus 0.2. Markings as in Figures 60A, 65D. Prosoma dark reddish-brown to black-yellow, sides darker, with dark patches in front just behind ame and white patches just below the ple, venter uniformly yellow. Opisthosoma longer than wide, light brown to dark brown, dorsally with inconspicuous dark spots, laterally with a conspicuous oval spot, venter uniformly light yellow. Legs I–IV laterally with dark markings. Eyes in three rows, first recurved, second and third straight and surrounded

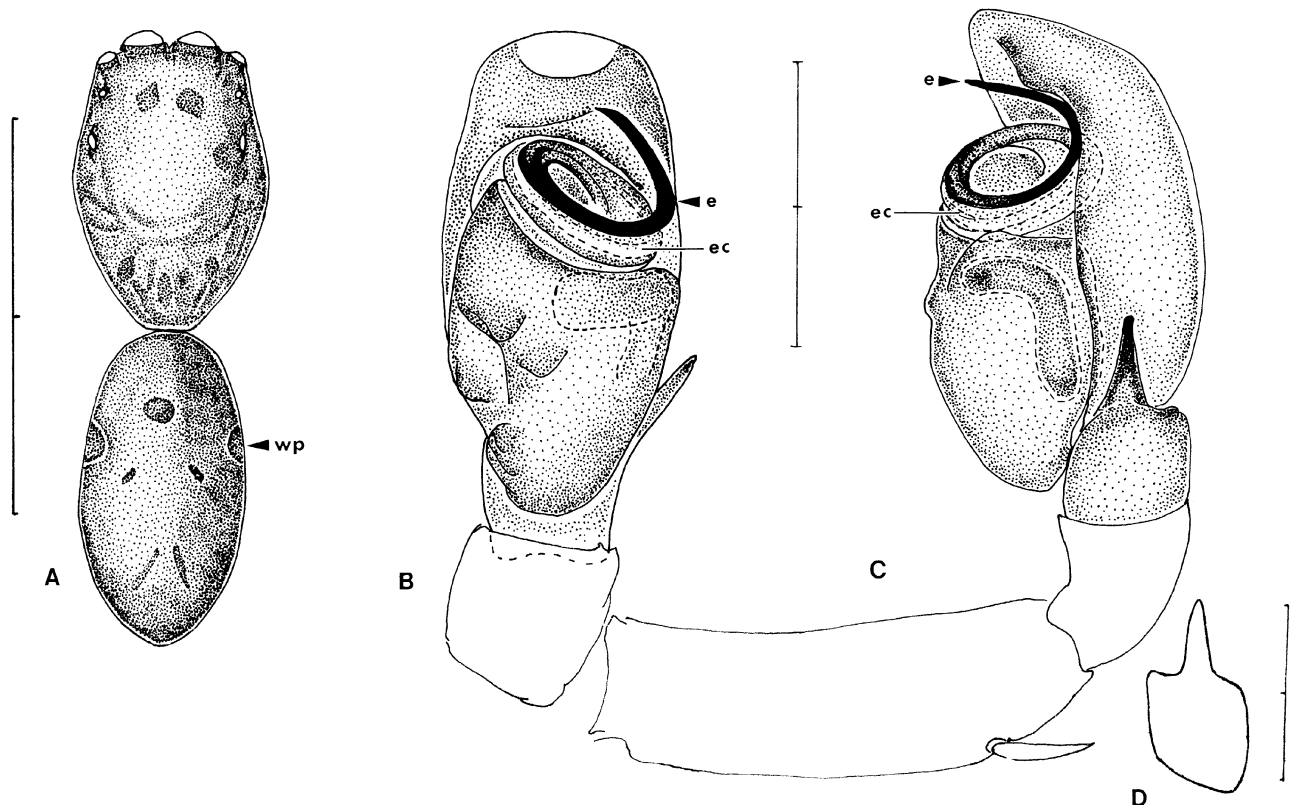


Figure 60. *Marengo crassipes* from Talawakele, Sri Lanka. A, male habitus, dorsal view. B, left male palp, ventral view. C, left male palp, retrolateral view. D, rta, male from Kandy (ZMUC 236). Scale bars = 0.2 mm (B–D); 2.0 mm (A).

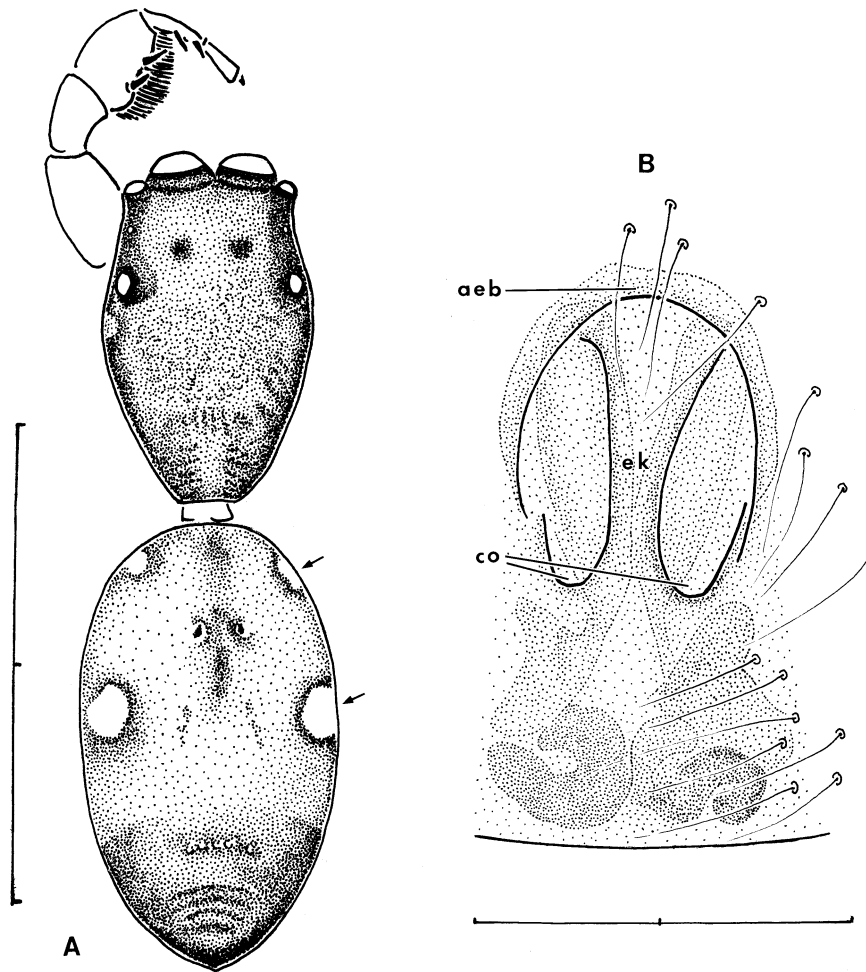


Figure 61. *Marengo crassipes* from Talawakele, Sri Lanka. A, female habitus, dorsal view. B, epigynum, ventral view. Arrows = white patches. Scale bars = 0.2 mm (B); 2.0 mm (A).

by dark rings. Chelicerae, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Palp: tibia short, rta slender, tapering to a pointed end (Figs 60C, 63B, 65F). Cymbium oval, tip excavated, setae as in Figure 63C, D. Bulb bilobed, embolus short, coils 1.5 times (Figs 60B, C, 63A, 65E, F).

Female: From Talawakele. Total length 3.3; prosoma length 1.3, width 0.8. Leg I: femur 0.7, patella 0.2, tibia 0.5, metatarsus 0.4, tarsus 0.2. Prosoma dark reddish-brown, sides darker, dark patches in front and white patches just below the posterior lateral eyes (Fig. 61A). Opisthosoma light brown, dorsally with inconspicuous dark spots, darker median line, laterally with two conspicuous white oval spot at the beginning and end of the anterior opisthosomal half (Fig. 61A). Setae as in Figure 64A. Legs I–IV laterally with dark markings. Epigynum and vulva as in Figures 61A, 62A–D.

Remarks: I have collected both sexes of *M. crassipes* from the same locality (Talawakele) and I am sure that they are conspecific. The figures in this study are all based on material from Talawakele. However, I am not sure if the MNHN material is conspecific. The opisthosomal markings of male specimens differ from those of specimens collected by myself.

Distribution: Known only from Sri Lanka; appears to be widespread in the central highlands.

Other material examined: SRI LANKA: Kandy, 1♂ (MNHN 20405); locality unknown, 14♀ and 1 juvenile, UMO, ex jar 1808; 1♀ det. O. P. Cambridge, UMO, jar 1795; Kandy, 1♂ (ZMUC 236), Coll. Rea Sherriffs, Tilg. 20.11.1960; Kandy, 3♀ and 2 juveniles (ZMUC 230), Coll. Rea Sherriffs, Tilg. 20.11.1960; Central Province, Talawakele, 1100 m, 2♂ 3♀, leg. Suresh P. Benjamin, 19.8.1996, NMB; Central Province, Knuckles Range, Deenston (approximately 7°19'N, 80°51'E),

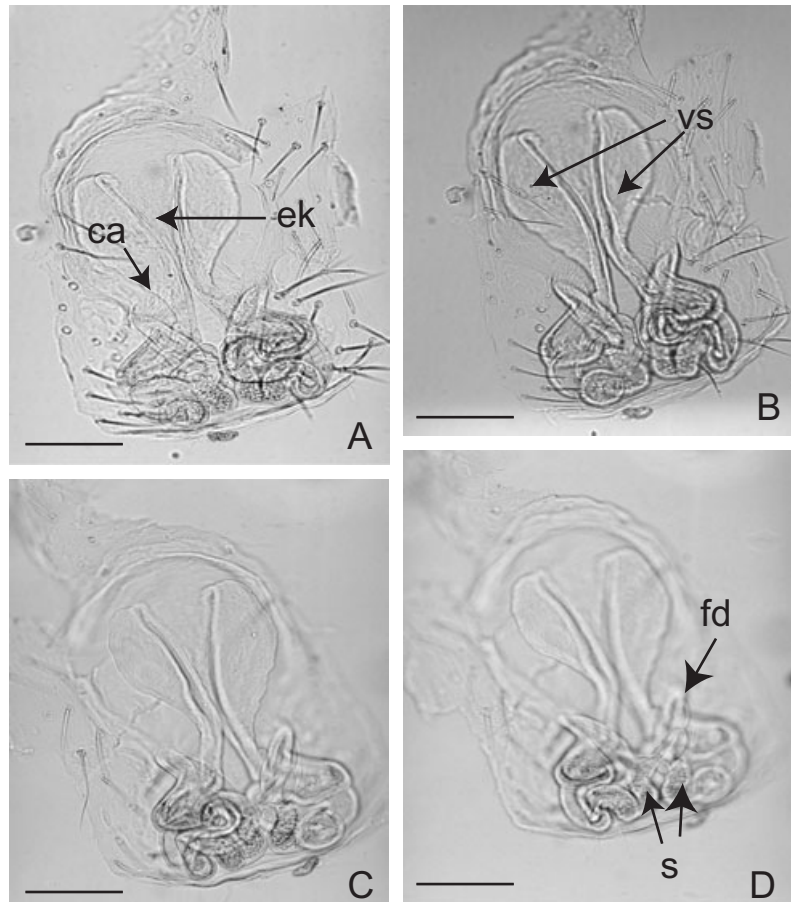


Figure 62. *Marengo crassipes* from Talawakele, Sri Lanka. Female genitalia. A, B, ventral view. C, D, dorsal view. Scale bars = 0.1 mm.

1100 m; 1♂ leg. Suresh P. Benjamin, 11.3.1998, MHNG; Central Province, Knuckles Range, along the Rattota–Ilukkumbura road, 900 m, 1♂ and 1♀ leg. Suresh P. Benjamin, 1–30.6.2003, MHNG.

MARENGO NITIDA SIMON, 1900
(FIG. 65A–C)

M. nitida Simon, 1900: 401 (1♂ lectotype from Sri Lanka, Southern Province, Galle, in MNHN 20415, examined).

M. nitida Simon, 1901: 488, figs 574–576.

M. nitida Sherriffs, 1931. Material difficult to trace. The single male from Rae Sherriffs' collection, labelled '*Marengo nitida* (Simon) Kandy' is considered to be a male specimen of *M. crassipes*.

M. crassipes Wanless, 1978: 266 (misidentified as a synonym of *M. crassipes*).

Diagnosis: The male of *M. nitida* is distinguished from that of *M. crassipes* by the thick, stout rta (Fig. 65C). Further, they can be separated by the different opisthosomal markings.

Male: Total length 3.1; prosoma length 1.6, width 1.1. Leg I: femur 0.8, patella 0.4, tibia 0.9, metatarsus 0.7, tarsus 2. Markings as in Figure 65A. The single male specimen examined was darker than *M. crassipes*. Prosoma dark brown, sides darker, with dark patches in front just behind the ame and white patches just below the ple. Opisthosoma rounded to oval, light brown, dorsally with inconspicuous dark spots, laterally no markings. Legs I–IV laterally with dark markings. Eyes in three rows, first recurved, second and third straight and surrounded by dark rings. Chelicera, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/1 spines. Palp: tibia short, rta short, stout (Fig. 65C). Cymbium oval, tip excavated, bulb bilobed, embolus short, coils 1.5 times (Fig. 65B, C).

Female: Unknown.

Remarks: Simon (1900) listed the type locality as Kandy although Galle appears on the museum labels

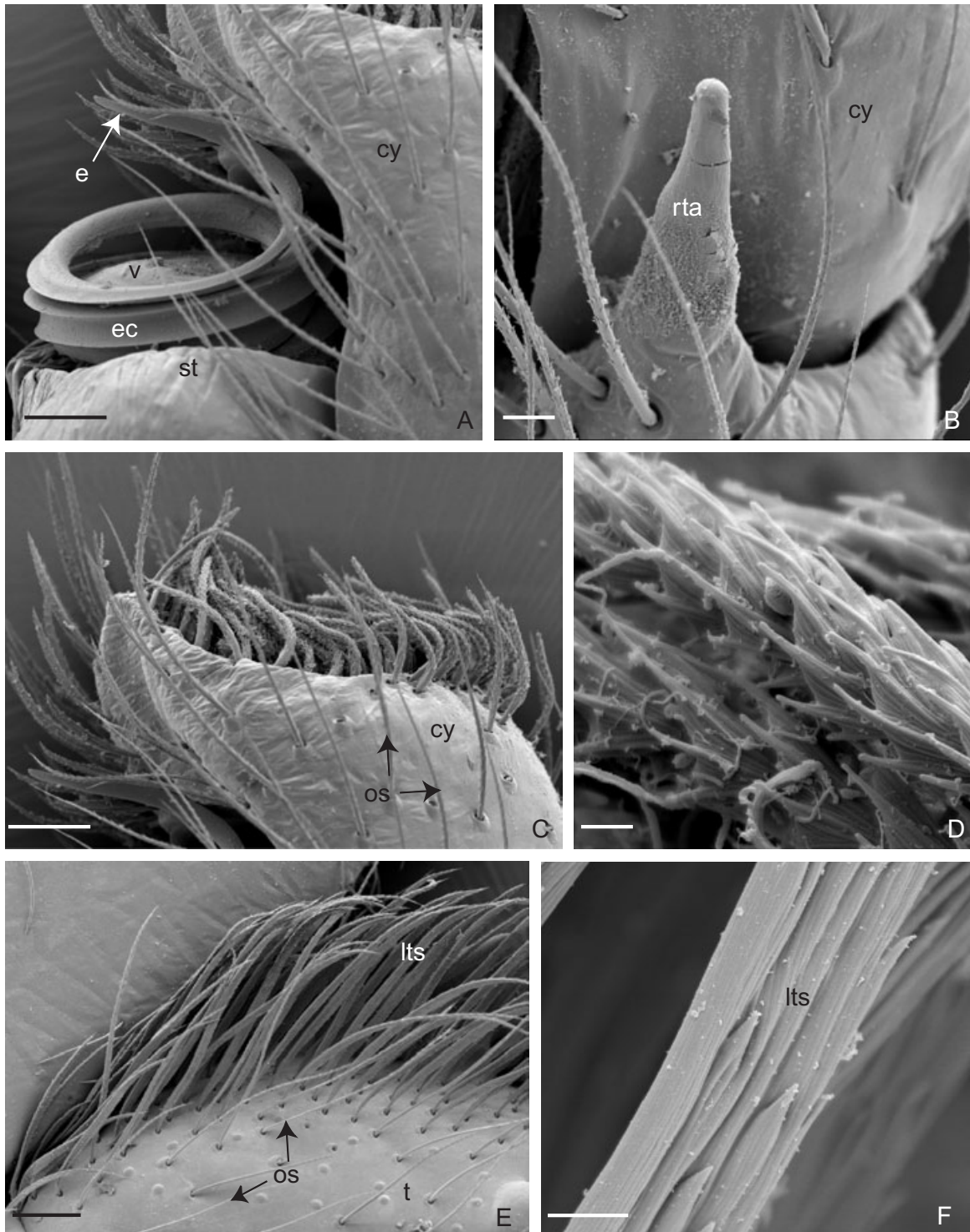


Figure 63. SEM, *Marengo crassipes*, male from Talawakele, Sri Lanka. A, male palp, retrolateral view, details of ec and embolus. B, rta. C, setae on the apex of cy, retrolateral view. D, detail of C. E, right tibia I, lateral view. F, detail of E. Scale bars = 1 μ m (D); 3 μ m (F); 10 μ m (B); 30 μ m (A, C); 50 μ m (E).

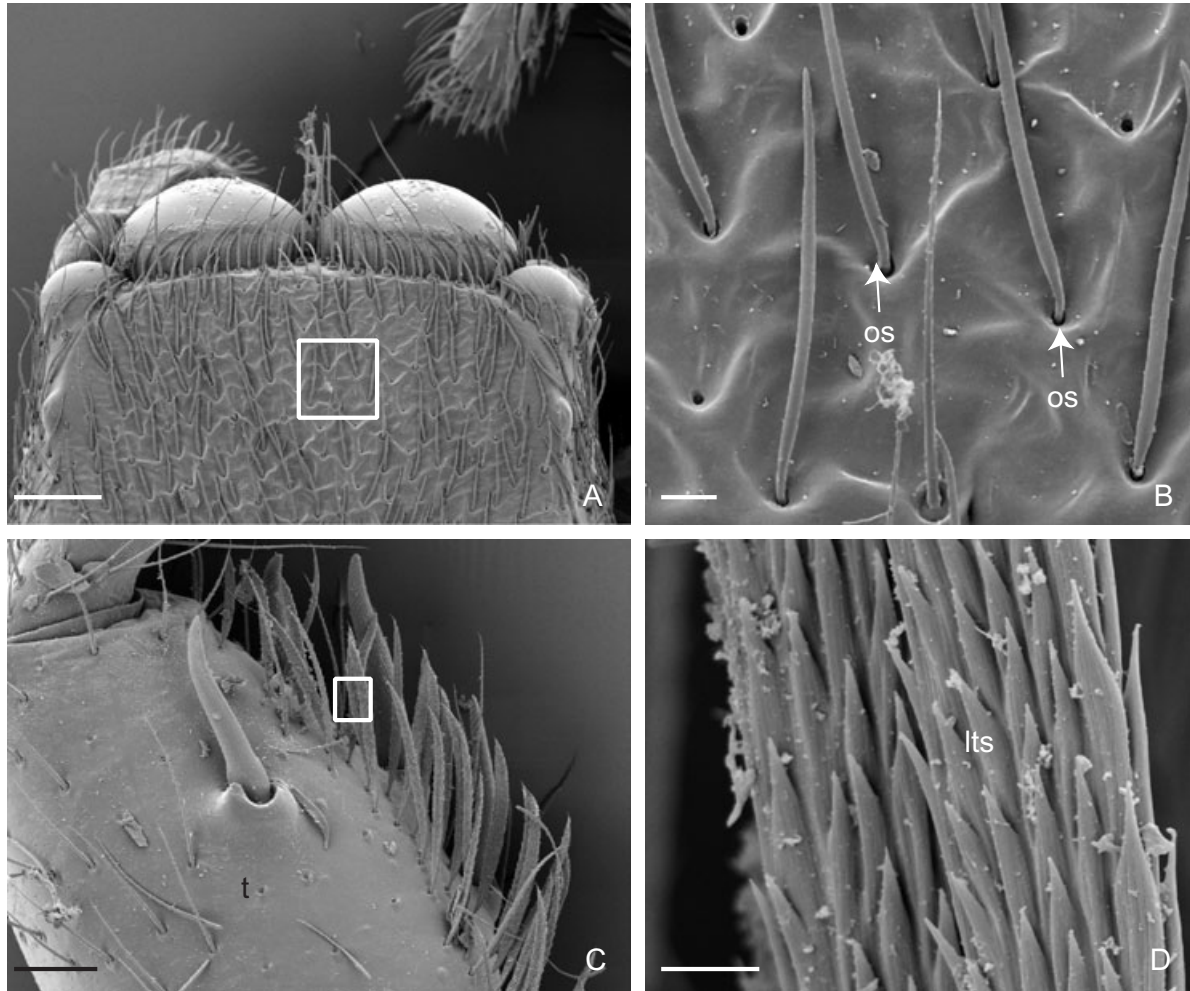


Figure 64. SEM, *Marengo crassipes*, female from Talawakele, Sri Lanka. A prosoma, dorsal view. B, detail of A. C, right tibia I, lateral view. D, detail of C. Scale bars = 3 μ m (D); 10 μ m (B); 50 μ m (C); 100 μ m (A).

(the original labels give no details of the exact locality). Simon (1901: 574a) illustrated a specimen that has a round opisthosoma similar to the material from Galle.

Distribution: Known only from the original locality in Sri Lanka. Doubtful records from India: Kerala, Travancore and Koyencolam (Sherriffs, 1931).

Other material examined: None.

MARENGO INORNATA (SIMON, 1900)
(FIG. 66A–D)

Philates inornatus Simon, 1900: 403. 1♀ lectotype (MHNH 21411) from Sri Lanka, Central Province, Kandy, examined.

Marengo inornata Wanless, 1978: 267–268, fig. 6a–e.

Diagnosis: The female is distinguished from those of all other *Marengo* spp., except for *M. striatipes*, by the lack of any marking on the opisthosoma (Fig. 66A), and from *M. striatipes* by the latter's raised prosoma and slender femur I (Fig. 67A).

Female: Lectotype (MHNH 21411): Total length 3.8; prosoma length 3.0 width 1.5. Leg I: femur 0.6, patella 0.3, tibia 0.4, metatarsus 0.3, tarsus 0.2. Habitus (Fig. 66A) as in *M. crassipes* except for the absence of prominent markings. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. The female of *M. inornata* is re-described in detail by Wanless (1978: fig. 6a–e). Epigynum and vulva as in Figure 66B–D.

Distribution: Known only from the original locality in Sri Lanka.

Other material examined: None.

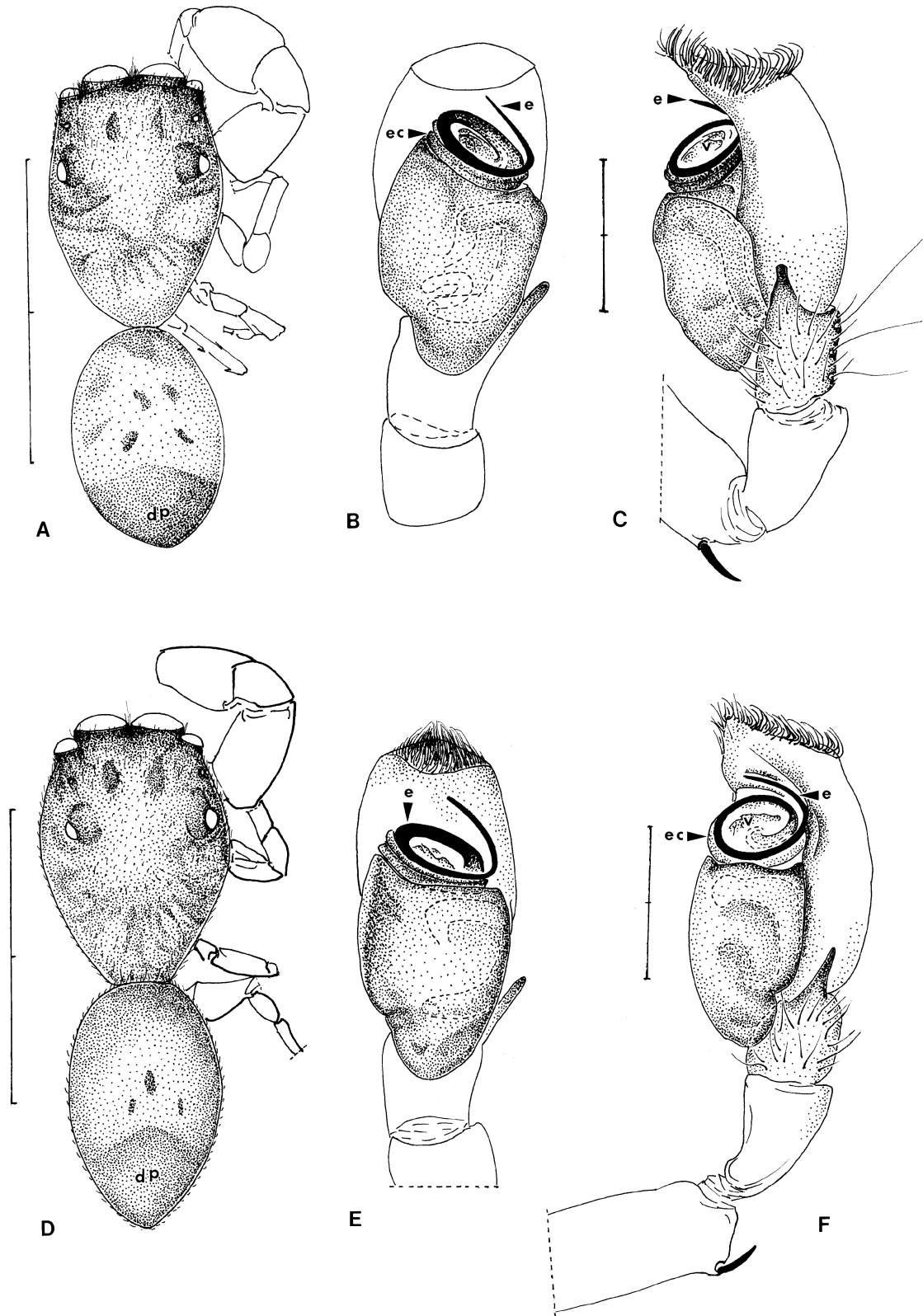


Figure 65. A–C, *Marengo nitida* (MNHN 20415). D–F, *M. crassipes* (MNHN 20405). A, male habitus, dorsal view. B, male palp, ventral view. C, same, retrolateral view. D, male habitus, dorsal view. E, male palp, ventral view. F, same, retrolateral view. Scale bars = 0.2 mm (B, C, E, F); 2.0 mm (A, D).

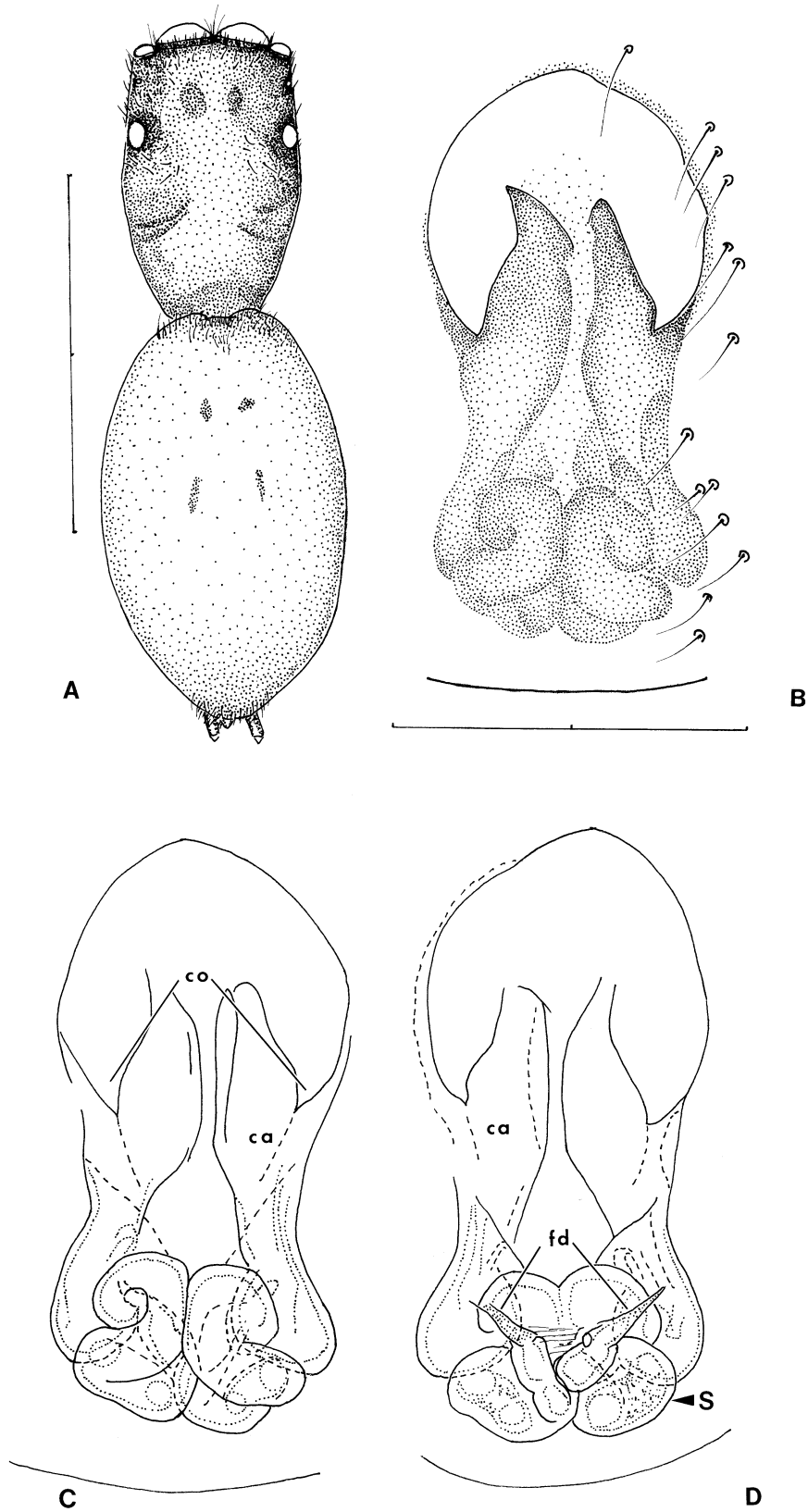


Figure 66. *Marengo inornata* (MNHN 21411). A, habitus, ventral view. B, epigynum, ventral view. C, vulva, ventral view. D, same, dorsal view. Scale bars = 0.2 mm (B–D); 2.0 mm (A).

MARENGO STRIATIPES SIMON, 1900
(FIG. 67A–C)

M. striatipes Simon, 1900: 400. 1♀ lectotype MNHN 16268, from Sri Lanka, Western Province, Colombo, designated as lectotype by Wanless (1978), examined. *M. striatipes* Sherriffs, 1931. Material difficult to trace, the single female from Rae Sherriffs' collection (ZMUC 213), labelled '*Marengo striatipes* (Simon) Colombo' is not conspecific with type material. *M. striatipes* Wanless, 1978: 267, fig. 5a–d.

Diagnosis: Distinguished from all other *Marengo* by the raised prosoma and slender femur I (Fig. 67A; Wanless, 1978: fig. 5a, b).

Female: Lectotype (MNHN 16268): Total length 2.6; prosoma length 1.2, width 0.8. Leg I: femur 0.6, patella 0.2, tibia 0.5, metatarsus 0.4, tarsus 0.2. Markings as in Figure 67A. Prosoma longer than wide, broadest and sharply raised at the centre (Wanless, 1978: fig. 5b), dark brown, without prominent markings. Opisthosoma oval, uniformly yellow, dorsally with inconspicuous. Legs laterally with dark markings, femur I not enlarged. Eyes surrounded by dark rings. Epigynum and vulva as in Fig. 67B. *M. striatipes* is re-described in detail in Wanless (1978: fig. 5a–d).

Male: Unknown.

Distribution: Known only from the original locality in Sri Lanka. Doubtful records from India: Kerala, Travancore and Koyencolam (Sherriffs, 1931).

Other material examined: 1♀ and 1 juvenile from Colombo, in ZMUC (label: *Marengo striatipes* (Simon) Colombo; kat. nr. 213; does not specify the exact locality or collection date), not conspecific with type material.

MARENGO DEELEMANAE SP. NOV.
(FIGS 68A–G, 69A–G)

Holotype: ♂ from Thailand: Prov. Prachuap Khiri Khan, Pran Buri, Khao Sam Roi Yot National Park, leg C. L. Deeleman, 31.12.1988, deposited in RMNH.

Paratype: 1♀, same data as holotype.

Etymology: Named in honour of Christa L. Deeleman-Reinhold in recognition of her services to arachnology.

Diagnosis: The female of *M. deelemanae* is separated from those of all other *Marengo* spp. by the markings of the opisthosoma (Fig. 68G). The male is separated from that of *M. nitida* by the latter's thin, tapering and relatively longer rta (Fig. 68E) and from that of *M. crassipes* by the latter's surface of lts, ribbed with numerous prominent spines (Figs 63E, F, 64C, D).

Male: Holotype: total length 2.8; prosoma length 1.3, width 0.8. Leg I: femur 0.7, patella 0.2, tibia 0.7, metatarsus 0.5, tarsus 0.2. Markings of specimen as in Figure 68G. Prosoma dark reddish-brown to black-yellow, sides darker, with dark patches in front just behind the anterior median eyes and white patches just below the posterior lateral eyes; venter uniformly yellow. Setae as in Figure 68G. Opisthosoma longer than wide, light brown to dark brown, laterally with a conspicuous oval spot. Legs I–IV laterally with dark markings. Eyes in three rows, first recurved, second and third straight and surrounded by dark rings. Chelicerae, labium and dorsal parts lighter in colour. Leg formula 1432. Tibia I with 2/2/0/2 spines, metatarsus I with 2/1 spines. Palp: Cymbium oval, elongated. Rta short, broad-based, projecting upward (Fig. 68E). Tegulum bilobed, path of sperm duct as in Figure 68E, F; embolus thin, short, coils once (Fig. 68B, E, F).

Female: Paratype: total length 2.7; prosoma length 1.3, width 0.8. Leg I: femur 0.5, patella 0.3, tibia 0.7, metatarsus 0.3, tarsus 0.2. Markings as in Figure 68A. Prosoma dark reddish-brown to black, without prominent markings or setae. Opisthosoma light black, dorsally with two conspicuous spots. Legs laterally with dark markings. Eyes in three rows, first recurved, second and third straight and surrounded by dark rings. Chelicerae, labium and dorsal parts lighter in colour. Leg formula 4321. Tibia I with 2/2/0/2 spines, metatarsus I with 2/2 spines. Epigynum and vulva as in Figure 68B–D.

Distribution: Known only from the type locality, secondary forest bordering limestone outcrop, young mangrove (Deeleman-Reinhold, 2001).

Other material examined: None.

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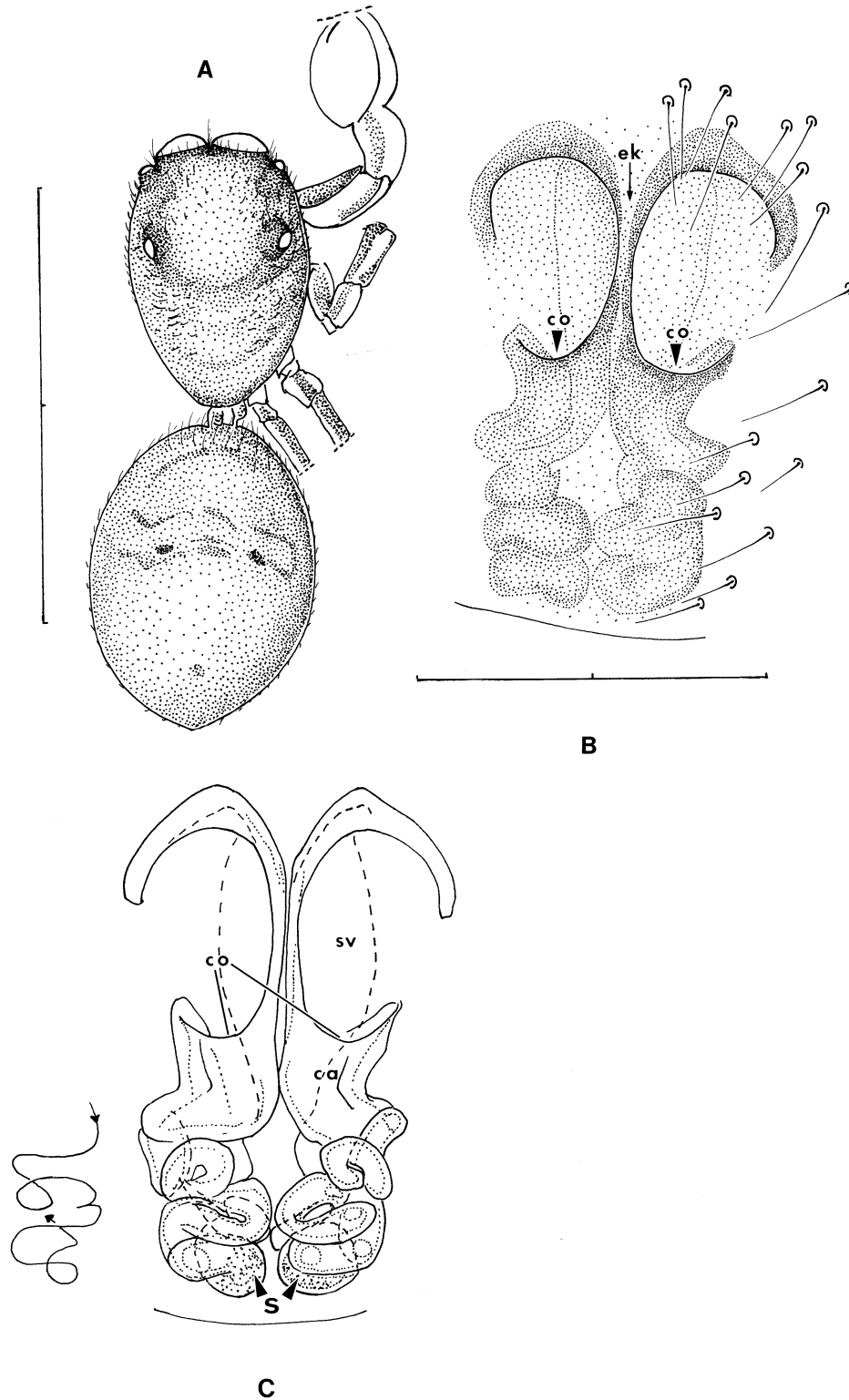


Figure 67. *Marengo striatipes* (MNHN 16268). A, habitus, ventral view. B, epigynum, ventral view. C, vulva, ventral view. Scale bars = 0.2 mm (B, C); 2.0 mm (A).

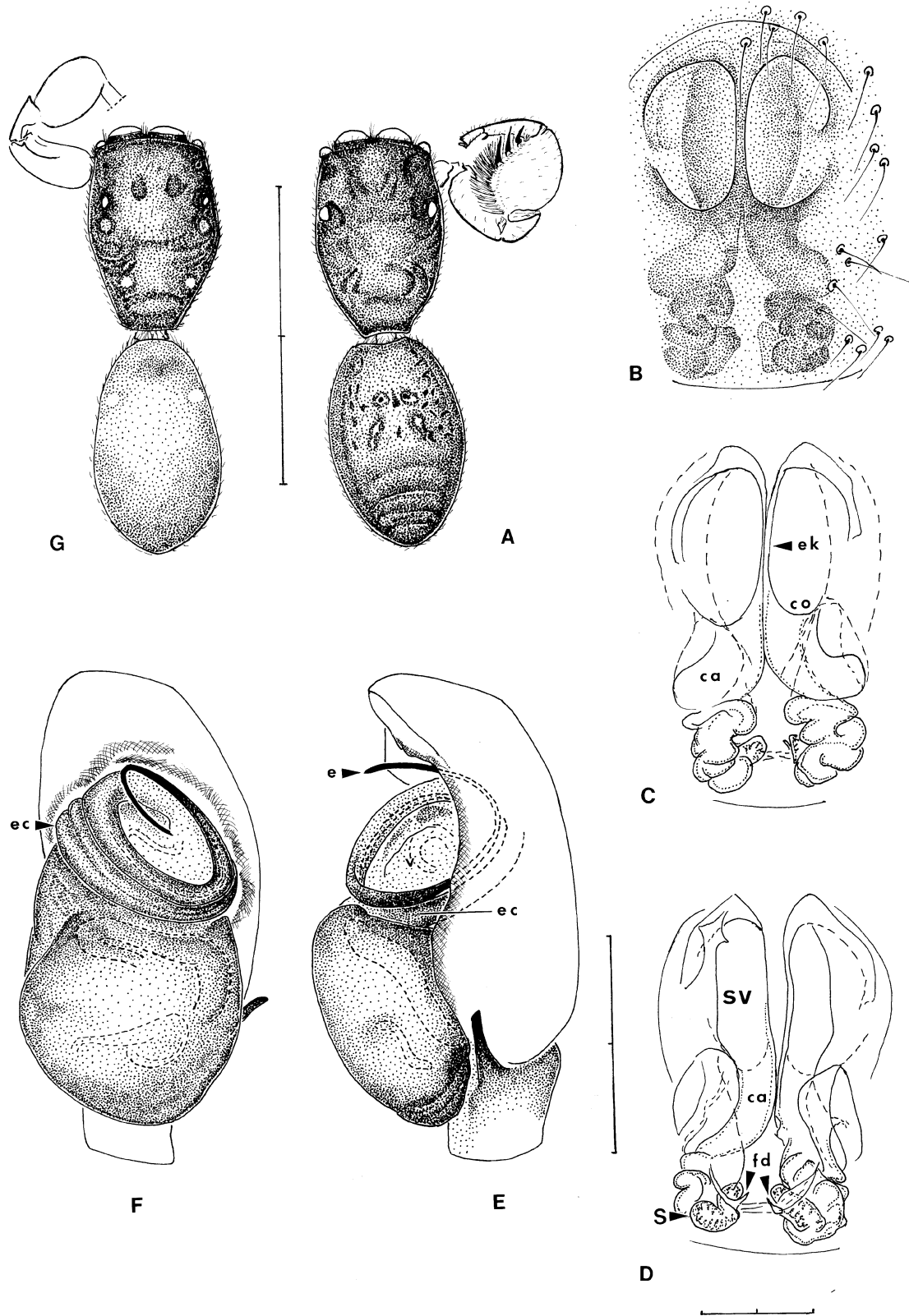


Figure 68. *Marengo deelemanae* sp. nov. (RMNH). A–D, female. E–G, male. A, habitus, ventral view. B, epigynum, ventral view. C, vulva, ventral view. D, same, dorsal view. E, male palp, retrolateral view. F, same, ventral view. G, habitus, ventral view. Scale bars = 0.2 mm (B–F); 2.0 mm (A, G).

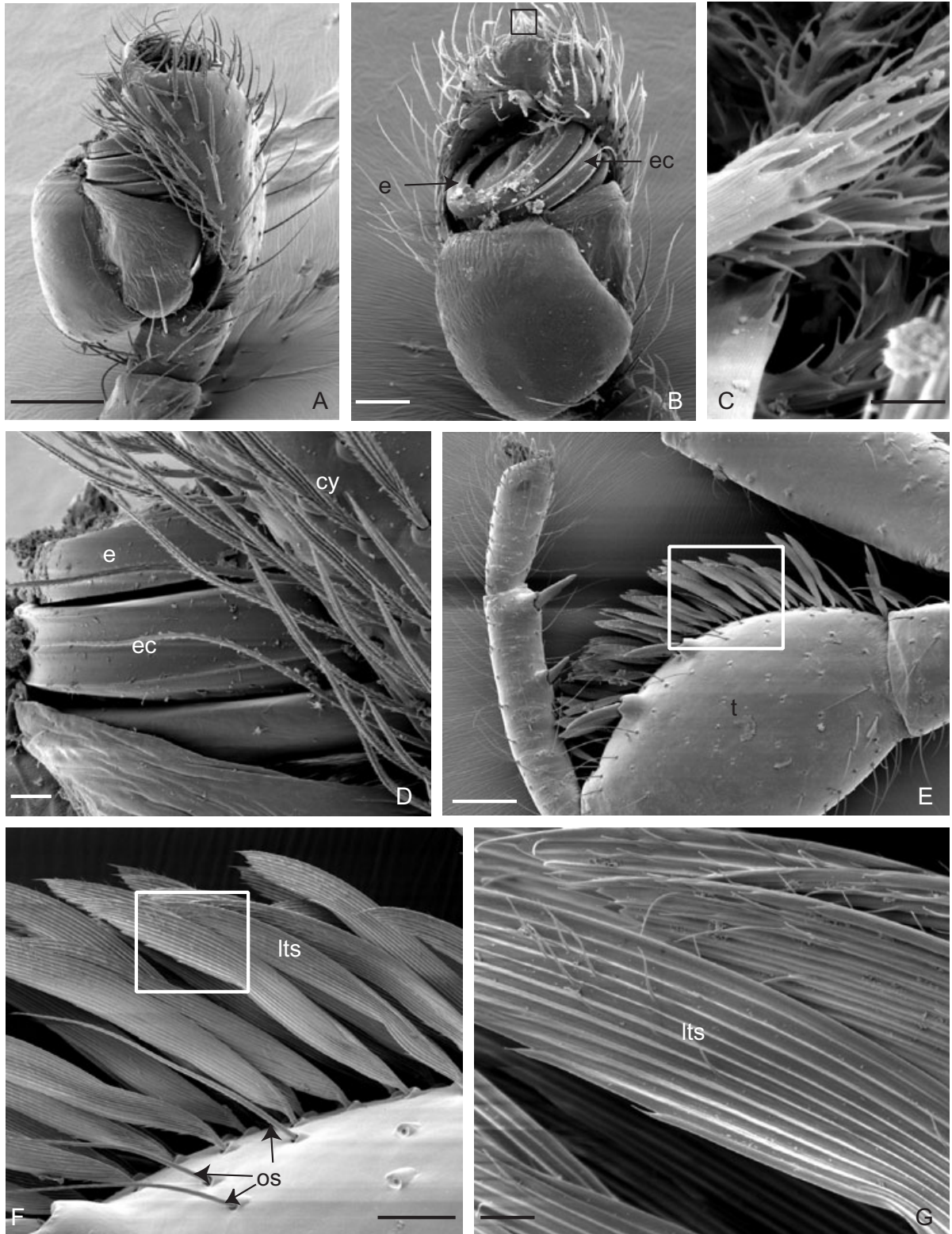


Figure 69. SEM, *Marengo deelemanae* sp. nov. (RMNH). A, right male palp, retrolateral view. B, same, ventral view. C, setae on the apex of cy, retrolateral view. D, ec and embolus, retrolateral view. E, right tibia I, lateral view. F, detail of E. G, inferior spines on lts, orientated in a distal direction. Scale bars = 3 μ m (C); 5 μ m (G); 10 μ m (D, E); 30 μ m (F); 50 μ m (B); 100 μ m (A).

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