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A revision of *Herennia* (Araneae : Nephilidae : Nephilinae), the Australasian 'coin spiders'

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Abstract. The nephilid 'coin spiders' (*Herennia* Thorell) are known for their arboricolous ladder webs, extreme sexual size dimorphism and peculiar sexual biology. This paper revises *Herennia* taxonomy, systematics, biology and biogeography. The widespread Asian *Herennia multipuncta* (Doleschall) (= *H. sampitana* Karsch, new synonymy; = *H. mollis* Thorell, new synonymy) is synanthropic and invasive, whereas the other 10 species are narrowly distributed Australasian island endemics: *H. agnarssoni*, sp. nov. is known from Solomon Islands; *H. deelemanae*, sp. nov. from northern Borneo; *H. etruscill*a, sp. nov. from Java; *H. gagamba*, sp. nov. from the Philippines; *H. jernej*, sp. nov. from Sumatra; *H. milleri*, sp. nov. from New Britain; *H. oz*, sp. nov. from Australia; *H. papuana* Thorell from New Guinea; *H. sonja*, sp. nov. from Kalimantan and Sulawesi; and *H. tone*, sp. nov. from the Philippines. A phylogenetic analysis of seven species of *Herennia*, six nephilid species and 15 outgroup taxa scored for 190 morphological and behavioural characters resulted in 10 equally parsimonious trees supporting the monophyly of Nephilidae, *Herennia, Nephila, Nephilengys* and *Clitaetra*, but the sister-clade to the nephilids is ambiguous. Coin spiders do not fit well established biogeographic lines (Wallace, Huxley) dividing Asian and Australian biotas, but the newly drawn '*Herennia* line' suggests an all-Australasian speciation in *Herennia*. To explain the peculiar male sexual behaviour (palpal mutilation and severance) known in *Herennia* and *Nephilengys*, three specific hypotheses based on morphological and behavioural data are proposed: (*1*) broken embolic conductors function as mating plugs; (*2*) bulb severance following mutilation is advantageous for the male to avoid hemolymph leakage; and (*3*) the eunuch protects his parental investment by fighting off rival males.

Introduction

The spider family Nephilidae Simon, 1894, the subject of numerous biological studies, now contains four genera according to new phylogenetic analyses (Kuntner, in press; M. Kuntner, G. Hormiga and J. A. Coddington, unpublished data): the well known pantropical *Nephila* Leach, 1815 and *Nephilengys* L. Koch, 1872, the lesser known African–Oriental *Clitaetra* Simon, 1889 and the Australasian (sub)tropical genus *Herennia* Thorell, 1877. *Nephila* and *Nephilengys* are being revised (M. Kuntner unpublished data; Australasian *Nephila* also by M. S. Harvey, A. D. Austin and M. Adams, unpublished data), *Clitaetra* contains six species and is sister to all other nephilids (Kuntner, in press) and *Herennia* is the subject of this revision. *Herennia* species exhibit extreme sexual, in particular size, dimorphism and ornate appearance (Figs 1, 14, 25–26) as well as fascinating web architecture, which typically is in the form of a ladder web closely applied to tree trunks (Figs 14, 15, 25–26). The sexual behaviour of *Herennia* is extraordinary. Males break off parts of their pedipalps and plug female epigyna with embolic parts (embolus + embolic conductor) (Figs 10*E–F*, 11, 17*A*, 18*C*, 22*E–F*). After mating, the males regularly sever their entire palpal bulb (Fig. 23*A–E*) and continue to occupy the female web as 'eunuchs' (Robinson and Robinson 1980).

Despite its interesting biology, *Herennia* has been poorly studied systematically, behaviourally and morphologically. Platnick (2005) lists four species of *Herennia* worldwide: *H. ornatissima* (Doleschall, 1859), the type of the genus ranging from India to China, Malaysia and New Guinea; *H. mollis* Thorell, 1887 from Myanmar; *H. papuana* Thorell, 1881 from New Guinea; and *H. sampitana* Karsch, 1880 from Borneo. Of these, after this revision *H. papuana* remains valid, *H. ornatissima* is revalidated and treated as a junior synonym of *H. multipuncta*, *H. mollis* and *H. sampitana* are synonyms and nine new species are described. The taxonomy has proven to be problematic, mainly as a result of scarce museum material (males with intact pedipalps are rare). A non-scientific name 'coin spiders' seems appropriate for *Herennia*, from the Latin meaning of a family of coins.

Biological observations exist for the tropical Asian *H. multipuncta*, *H. papuana* Thorell from Papua New Guinea

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and *H. etruscilla*, sp. nov. from Java. Natural history of the remaining species (in most cases known from only one or a few individuals) is unknown. *Herennia multipuncta* appears native in South Asia and Indochina (these areas apparently lacking other sympatric *Herennia*), but also occurs in Sumatra, Java, Borneo, Sulawesi, the Philippines and the Moluccas (Ambon). These latter islands are known or predicted to also harbour narrowly endemic *Herennia* species.

Although the currently available taxonomic, biogeographic and ecological data are preliminary, *Herennia* species appear to be very narrow endemics and are rare (judging from availability in museum collections). They are obligate arboricoles (see Robinson and Lubin 1979), and appear to be confined to pristine (rain) forests. A notable exception is the widespread and common *Herennia multipuncta* (Doleschall), which is synanthropic, appears to be invasive and could potentially benefit from human induced habitat destruction. *Herennia deelemanae*, sp. nov. is known from only two individuals from Sabah (Malaysian Borneo). The holotype male (Fig. 17*B–C*) was discovered as a singleton in extensive samples of a recent primary rainforest canopy-fogging inventory (evidence of potential rarity in a threatened habitat). A presumed conspecific female (Fig. 17*A*) was collected as a singleton in remote southern Sabah. More canopy-fogging spider samples are available from Borneo secondary forests, but they only contain the common *H. multipuncta* (Ch. Deeleman, personal communication).

The group Nephilinae Simon, 1894, currently catalogued in Tetragnathidae (Platnick 2005), has received considerable systematic attention resulting in a range of classification schemes (Kuntner 2002, 2003, in press; Kuntner and Hormiga 2002). Hypothesised placements for Nephilinae, *Herennia* included, have been in Araneidae (Dahl 1912; Eberhard 1982; Wunderlich 1986, 2004; Kuntner 2003; Pan *et al*. 2004) and in Tetragnathidae (Levi 1980, 1986; Levi and von Eickstedt 1989; Coddington 1990; Hormiga *et al*. 1995, 2000; Scharff and Coddington 1997; Griswold *et al*. 1998; Kuntner 2002; Kuntner and Hormiga 2002). In the context of *Clitaetra* and *Nephilengys* revisions, Kuntner (in press; unpublished data) hypothesises the clade (*Clitaetra* + (*Herennia* + (*Nephila* + *Nephilengys*))) to represent Nephilidae because the group falls into neither of the above families. Such placement is also tested here via phylogenetic analysis of most *Herennia* species and selected nephilid and non-nephilid outgroups. The first species-level phylogeny of *Herennia* allows preliminary interpretations of its phylogeography.

Materials and methods

Morphological examination

Most morphological observations and illustrations of external structures were made using a Leica MZ APO dissecting microscope (www.leica-microsystems.com, verified November 2005) with a camera lucida. For internal palpal and epigynal anatomy a Leica DMRM compound microscope with a camera lucida was used. Microscope images were taken using a Nikon DXM 1200 digital camera (www.nikon.com, verified November 2005), and assembled using the Syncroscopy Automontage software (www.syncroscopy.com, verified November 2005). Digital scanning electron microscope (SEM) photographs were taken on a Leo 1430VP scanning electron microscope (www.mwrn.com/leo/leo.htm, verified November 2005) at the Department of Biological Sciences of the George Washington University. For SEM preparation, specimens were cleaned ultrasonically for one minute, transferred to 100% ethanol overnight, dissected, submitted to critical point drying, mounted on rivets using glue and copper wire, then sputter coated.

Female genitalia and male pedipalps, if dissected, were excised using scalpels and needles. Male palpal anatomy (trajectory of the ducts) and internal female genitalic structure were examined by clearing the organs in methyl salicylate (Holm 1979) and mounting them on a temporary slide (Coddington 1983) and were illustrated under the compound microscope. In spiders with large and heavily sclerotised internal genitalia, like nephilids, this technique often produces poor results. Thus, in order to decipher the trajectory of the copulatory ducts, the epigyna were exposed to concentrated KOH for the time needed to completely digest any soft tissues. Cleared genitalia were mostly illustrated under a dissecting microscope positioned into the most informative views or further dissected to expose the details. Although this technique sometimes makes the spermathecae translucent and elucidates the trajectories within, it is often necessary to interpret the relationships of the positions where the copulatory and fertilisation ducts attach to the spermatheca lumen. Male pedipalps were expanded by exposing them to concentrated KOH for up to an hour, followed by immersion in distilled water; the process was then repeated as needed.

All measurements are in millimetres, taken using a micrometer eyepiece. Prosoma and opisthosoma length and height were measured in lateral view, the width in dorsal view; all measured at widest points (prosoma height measured at head region). Eye widths are maximum diameters of the eye lens and eye separations were measured between lenses. Leg segments were measured in detached legs. Only joints distal from the trochanter were measured, as the detached leg breaks between the trochanter and the femur. Maximum lengths of the femur, patella, tibia, metatarsus and tarsus are reported; the total of these is reported as total leg length, which corrects for overestimation if all leg joints were measured. The cheliceral formula consists of three numbers: promarginal cheliceral teeth (PCT, Fig. 6*D*); retromarginal cheliceral teeth (RCT, Fig. 6*D*); and numbers of denticles inbetween the margins in cheliceral furrow (ChD, Fig. 20*E*).

Pencil illustrations via camera lucida were kept on acid-free archival paper. Simple line illustrations were inked on Vellum film (Denril Multi-Media Vellum, Borden & Riley Paper Co. Inc., www.bordenandriley.com, verified November 2005); shaded illustrations were inked on fine-grained coquille board and further rendered with black, soft Prismacolour pencils (Sanford Corporation, Oak Brook, IL, USA, www.prismacolour.com, verified November 2005). All non-digital artwork (photographic slides included) were scanned for digital enhancement in Adobe Photoshop version 7.0 (Adobe, http://www.adobe.com/, verified November 2005), where digital microscope and SEM images were also further manipulated. All image plates were assembled and labelled in Adobe Illustrator version 10.

The species listed in the Taxonomy section are in alphabetical order after the type species; such order does not imply phylogenetic relatedness.

The following anatomic abbreviations are used in text and figures:

AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALE	anterior lateral eyes
ALS	anterior lateral spinneret
AME	anterior median eyes
ATA	apical tegular apophysis

BH	basal hematodocha
BL	book lung(s)
CB	cymbium
CD	copulatory duct
ChD	cheliceral denticles
CO	copulatory opening
CY	cylindrical gland spigot(s)
E	embolus
EA	embolic apophysis
EB	embolus base
EC	embolic conductor
ECF	embolic conductor flap
ECG	embolic conductor groove
EC-m	embolic conductior – membranous part
EH	embolus hook
EPC	epigynal chamber
ES	epigynal septum
ESA	epigynal sclerotised arch
ETm	embolus-tegulum membrane
F	fundus
FD	fertilisation duct
Fe	femur
FL	flagelliform gland spigot(s)
m	membrane(ous)
MAP	major ampullate gland spigot(s)
mAP	minor ampullate gland spigot(s)
Me	metatarsus
N	nubbin
P	paracymbium
Pa	patella
PCT	promarginal cheliceral teeth
PI	piriform gland spigot(s)
PLE	posterior lateral eyes
PLS	posterior lateral spinneret
PME	posterior median eyes
PMS	posterior median spinneret
PPS	palpal patellar seta(e)
PSL	prosomal supracheliceral lobe
RCT	retromarginal cheliceral teeth
S	spermatheca
Sc	scutum
SD	sperm duct
ST	subtegulum
SU	sustentaculum
T	tegulum
Ta	tarsus
TCp	paired tarsal claw(s)
TCm	median tarsal claw
Ti	tibia
TO	tarsal organ
Tr	trichobothrium(a)

Specimen database

The nephilid specimen database was developed in BIOTA 1.6.0 (Colwell 1999). At least one specimen from each sample examined received a unique specimen code (a required field in BIOTA), which consisted of the two-letter genus code ('he' for *Herennia*) followed by the sample number, a letter indicating gender or stage ('f' for a female, 'm' for a male, 'j' for a juvenile) and the consecutive number within the sample. These specimen codes, matching those on specimen labels, are listed in descriptions, behavioural observations and figure captions, in order to facilitate museum voucher comparisons, if necessary. Other specimen data in BIOTA included species identification and date, gender, abundance, type status, museum depository (see museum abbreviations below) and optional notes. The locality data entered in BIOTA for each sample, if known, were: a unique locality code; locality name; district; state/province; country; elevation; latitude and longitude; and their accuracy (by convention, the word 'approx.' in this field means the approximate coordinates were found later through maps or gazetteers, not measured on the spot). If interpreted, those parts are added, in square brackets, to the original spellings. The collection data entered in BIOTA for each sample, if known, were: a unique collection code; collected by; date collected; site; and source ('label' indicating museum label and 'notes' as personal notes from the field). The nephilid specimen database, currently containing more than 4000 entries, is available from the author. Upon publication of all four nephilid revisions, the entire database will be made available electronically at http://home.gwu.edu/~kuntner.

Museum abbreviations with names of curators and/or collection managers are:

AMNH	American Museum of Natural History, New York, USA; Norman I. Platnick, Lou Sorkin.
BMNH	British Museum of Natural History, London, UK; Janet Beccaloni.
CAS	California Academy of Sciences, San Francisco, USA; Charles Griswold, Darrel Ubick.
CD	Christa Deeleman-Reinhold's collection, now in RMNH, The Netherlands.
MCSNG	Museo Civico di Storia Naturale, Genova, Italy; Giuliano Doria.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA; Gonzalo Giribet, Laura Leibensperger.
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève, Switzerland; Peter Schwendinger.
MNHN	Muséum National d'Histoire Naturelle, Paris, France; Christine Rollard.
NHMW	Naturhistorisches Museum Wien, Vienna, Austria; Juergen Gruber.
PMS	Prirodoslovni Muzej Slovenije, Ljubljana, Slovenia; Tomi Trilar.
QM	Queensland Museum, Brisbane, Australia; Robert Raven.
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; Erik J. van Nieukerken, Kees van den Berg.
SMF	Naturmuseum Senckenberg, Frankfurt, Germany; Peter Jaeger.
USNM	National Museum of Natural History (former United States National Museum), Smithsonian Institution, Washington, DC, USA; Jonathan A. Coddington, Scott Larcher, Dana M. De Roche.
WAM	Western Australian Museum, Perth, Australia; Mark Harvey.
ZMB	Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; Jason A. Dunlop.
ZMH	Zoologisches Institut und Zoologisches Museum Universität Hamburg, Germany; Hieronymus Dastych.
ZMUC	Zoological Museum, University of Copenhagen, Denmark; Nikolaj Scharff.

Phylogenetic analysis

Kuntner (in press) provided the first nephilid species-level phylogeny emphasising *Clitaetra* species. Nephilids were represented by all six known *Clitaetra* species, a selection of seven *Nephila* species emphasising the Australasian species revised by M. S. Harvey, A. D. Austin and M. Adams (unpublished data) (the type *N. pilipes, N. antipodiana, N. plumipes, N. edulis, N. clavipes, N. fenestrata, N. clavata*), two *Nephilengys* species (the type *N. malabarensis, N. cruentata*) and two

Herennia species (the type *H. multipuncta*, *H. papuana*). Kuntner (in press) corroborated the monophyly of all four nephilid genera. Thus, this study uses only two species of each nephilid genus except *Herennia*: *Nephila pilipes* (type species) and *N. fenestrata* (which is sister to all other *Nephila* species in Kuntner, in press) representing *Nephila*; *Nephilengys malabarensis* (type species) and *N. cruentata* representing *Nephilengys*; *Clitaetra episinoides* (type species) and *C. irenae* (this name is here disclaimed and remains unavailable for nomenclatorial purposes; Kuntner, in press will provide the first description and diagnosis) re-testing *Clitaetra* monophyly. All *Herennia* species known from quality specimens are in this analysis, but *Herennia oz, H. milleri, H. sonja* and *H. jernej* are omitted owing to limited material. All non-nephilid outgroups from Kuntner's (in press) analysis are included here: the classical nephiline genera *Phonognatha* and *Deliochus*; the araneids *Araneus* and two *Argiope* species; the tetragnathid genera *Tetragnatha, Meta* and *Leucauge*; *Linyphia* (Linyphiidae); *Pimoa* (Pimoidae); *Steatoda* (Theridiidae); *Nesticus* (Nesticidae); *Epeirotypus* (Theridiosomatidae); *Uloborus* (Uloboridae); and *Deinopis* (Deinopidae). In total, 28 taxa were included in this analysis.

Appendix 1 lists and describes the 190 characters and character states used. The characters and their homologies, all parsimony informative, will be discussed in more detail elsewhere (M. Kuntner, G. Hormiga and J. A. Coddington, unpublished data). The phylogenetic matrix (Appendix 2) in NONA and NEXUS formats is available from the author and will be submitted to TreeBASE (http://www.treebase.org/, verified November 2005). The multistate characters were treated as unordered (Fitch 1971) to avoid unnecessary assumptions of character-state adjacency. I used NONA version 2.0 (Goloboff 1993) with parameters 'hold 1000', 'mult*500', 'max*', and 'sswap', under both 'amb –' and 'amb = ' for the cladistic analysis and WinClada 1.00.08 (Nixon 2002) to display and manipulate trees and matrices for NONA. Successive character weighting (Farris 1969) analysis was performed in NONA with the command 'run swt.run hold10000 hold/100 mult*100' (using the macro swt.run). The bootstrap values (Felsenstein 1985) were calculated in WinClada using default settings (100 replications, 'mult*10'). Bremer support or decay index values (Bremer 1988, 1994) were estimated in NONA using the commands 'hold 10000' and 'bs10'. All trees are output from WinClada and their format does not imply non-monophyly of the group Deinopoidea represented here by the two primary outgroups, *Deinopis* and *Uloborus*.

Classification

I use a combination of Linnean (ICZN 1999) and phylogenetic nomenclature (Cantino and de Queiroz 2004). A review of the debate with a rationale of such combined classification is in preparation (see also Kuntner, in press). Clade names in this study are consistent with zoological ranks up to the family level, but are precisely circumscribed following the PhyloCode (PC) articles 7, 9–11 (Cantino and de Queiroz 2004). Phylogenetic definitions (PC Article 9, Note 9.4.1) used here are node-based where 'clade (A and B)' means the least inclusive clade containing A and B. Because the PhyloCode has not taken effect and registration database has not been implemented, the names proposed here are not registered (Article 8).

Biology

The review of *Herennia* biology (see Discussion) is based on published accounts of *H. papuana* (as *ornatissima* in Robinson 1975, 1982; Robinson and Robinson 1978, 1980; Robinson and Lubin 1979) and *H. multipuncta* (as *ornatissima* in Masumoto and Okuma 1995; Murphy and Murphy 2000: 388, figs 12.1–12.2), unpublished data on *H. multipuncta* from Thailand (G. Hormiga, personal communication), as well as personal observations of *H. multipuncta* in Sri Lanka (1993) and *H. etruscilla* in Java (1996). Biology of all other species is unknown. The synthesis of '*Herennia ornatissima*' behaviours by Eberhard (1982) is based on the above-cited papers for *H. papuana*. Additional works on *Herennia* include anatomy (Roth and Roth 1984), morphological phylogenetics (Coddington 1990; Hormiga *et al*. 1995) and evolution of sexual size dimorphism (Coddington *et al*. 1997; Hormiga *et al*. 2000). Additionally, some behaviours are described here for the first time.

Taxonomy

Family **NEPHILIDAE** Simon

Subfamily **NEPHILINAE** Simon

Genus ***Herennia*** Thorell

Coin spiders

Epeira (Argyopes) Doleschall, 1859: 32 (description of *E. multipuncta* and *E. ornatissima*). – Stoliczka 1869: 236 (description of *E. mammillaris*).

Herennia Thorell, 1877: 370 (type species, by original designation, *Epeira multipuncta* Doleschall).

Herennia Karsch, 1880: 381 (description of *H. sampitana*). – Thorell, 1878: 293; 1881: 77 (description of *H. papuana*); 1887: 166 (description of *H. mollis*); 1890; Simon, 1894: 759, figs 828, 835; Roewer, 1942: 925; Bonnet, 1957: 2159; Brignoli, 1983: 241; Platnick, 1989: 306; 1993: 373; 1997: 454; 2005; Murphy & Murphy, 2000: 388.

Diagnosis

Herennia differs from all non-nephilid spiders by the striated cheliceral boss in both sexes (Figs 6*B*, 20*A–C*). *Herennia* females differ from all other nephilid genera by the warty carapace (Figs 5*B*, *D–F*, 19), wider than long sternum (except in *H. tone* and *H. gagamba*), lobed abdomen (Figs 1*A*, *C–D*, 8*A–C*, 9*A–B*, *E*, 10*A–D*, 14, 16*A–B*, 22*A–B*, 25*A–B*, 26*A–B*, 27*A*, *C*, 28*A*, 29*A–B*, *D–E*, 31*A–B*) and the epigynum with distinct ventral chambers divided by a septum (Figs 2*A–B*, 10*E–F*, 11, 16*C*, *G*, 17*A*, 22*E–F*, 27*B*, *D–E*, 28*B–C*, 29*C*, 31*C–D*). *Herennia* males differ from all other nephilid genera by the presence of a conspicuous apical tegular apophysis (Figs 4*A*, *E*, 12*A–B*, *E*, 13*B–E*, 17*B*, 18*A–B*, 30*A*, *C*) and an embolus hook (Figs 4*C–E*, 18*A*, 30*C*). They further differ from males of *Nephila* and *Clitaetra* by the large and complex sigmoidally shaped embolic conductor with an extensive proximal membrane (Figs 4*A–C*, 12*A–E*, 13, 18, 30, 17*B–C*) and from males of *Nephilengys* by the shape of distal embolic conductor part, which has a flap (Figs 4*A–B*, 11*B*, *F*, 12*A*, *C*, *E*, 13*C–E*, 17–18) (absent only in *H. papuana*, Fig. 30). Webs of *Herennia* are built tightly against tree trunks (Figs 14*A–B*, 25, 26*A*), rocks or walls (Figs 14*C*, 15), such that the orb plane follows the substrate shape. The hub-cup (Figs 14*A–B*, 15, 25*B*), where the spider rests, touches the substrate. The *Herennia* web has 'pseudo radii' (Robinson and Lubin 1979), which run parallel vertically through the orb (Figs 25*A*, 26*A*) and do not run through the hub.

Description

Female

General somatic morphology illustrated in *H. multipuncta* (Fig. 1). Live females are cryptic dorsally (Figs 14, 25, 26*A*), but colourful (red, orange) ventrally (Fig. 26*B*).

Prosoma. No carapace humps or spines (except very short ones on top of warts, Fig. 19*F*). Head region low and narrow, thoracic region wide (Figs 1*A–C*, 5*A–C*, 14, 19*A*, *D*, 20*A*). Carapace warty, edge ridged (Figs 5*B–F*, 19). Carapace covered with numerous white and thin, hair-like setae (Figs 5, 19). No tapeta in secondary eyes. Lateral eyes (Figs 1*B–C*, 5*A–C*, 19*A*, *D–E*) not widely separated from medians. Lateral eyes on a joint tubercle, slightly separated. PLE equal in size (*H. multipuncta, H. papuana*) or larger than PME (*H. tone, H. agnarssoni, H. milleri*). Cheliceral boss with numerous striae (Figs 6*B*, 20*A–C*). Sternum wider than long (or as wide as long in *H. tone*). Sternal humps I to III conspicuous (Fig. 6*E*), hump IV inconspicuous, unpaired anterior hump absent. Cheliceral formula ranges from 3/3/25 (*H. papuana*) through 3/4/30 (*H. milleri*) to 4/4/15 (*H. agnarssoni*).

Appendages. Leg formula 1, 2, 4, 3, except in *H. jernej* (1, 2 = 4, 3). Femoral spines I, II short, except in *H. jernej* and *H. tone*. Femur I with a prolateral row of thin hair-like setae (Figs 5*B*, *D*, 19*A–B*, *D*). Sustentaculum present, hidden within other setae (Fig. 7*A–D*), or alternatively inconspicuous or absent in *H. etruscilla* (Fig. 21*C*), *H. papuana* and *H. milleri*. Prolateral tibiae with a paired lyriform organ (Fig. 21*A–B*).

Opisthosoma (Figs 1*A*, *C–D*, 8–9, 10*A–D*, 14, 16*A–B*, *D–E*, 22*A–D*, 25–26, 27*A–C*, 28*A*, 29*A–B*, 31*A–B*) dorsoventrally flattened, laterally more or less lobed, posteriorly truncated. Opisthosoma entirely covered with many rows of large and small sclerotisations. Spinnerets uniformly of the typical nephiline form (Figs 7*E–F*, 21*D–F*; observed in *H. multipuncta, H. etruscilla, H. papuana*) (see also Hormiga *et al*. 1995): ALS with 'normal PI field' where the PI spigot base is nearly as long or longer than the shaft (Griswold *et al*. 1998: ch. 69, fig. 48B), the major ampullate spigot and a nubbin; PMS with a sparse aciniform field, and a nubbin; PLS with the aggregate spigots embracing the flagelliform and with the two cylindrical spigots of normal size, the mesal being peripheral.

Epigynum (Figs 2*A–B*, 10*E–F*, 11, 16*C*, *G*, 17*A*, 22*E–F*, 27*B*, *D–E*, 28*B–C*, 29*C*, 31*C–D*) with a pair of ventral rounded chambers divided by a septum (may be inconspicuous) and laterally positioned copulatory openings. Oval spermathecae attached to the ventral body wall and juxtaposed or barely separated, with gland pores all over their surface (Figs 2*C–D*, 18*D*, 31*E*). Copulatory ducts massive, round and heavily sclerotised, fertilisation ducts short. A heavily sclerotised medial arch present in the inner epigynum (Figs 2*C–D*, 18*D*, 31*E*), which can extend laterally (Fig. 31*E*), corresponding to external epigynal sclerotisations.

Male

General somatic morphology illustrated in *H. multipuncta* (Fig. 3) and *H. etruscilla* (Figs 23–24). Live males are orange or red (Fig. 25*A*).

Prosoma (Fig. 3*A–C*) pear-shaped, cephalic region low. Prosoma highest in the middle. Labium wider than long, as in Fig. 3*D*. Both eye rows slightly recurved, eyes roughly equidistant. Large AME extending anteriorly over clypeus (Figs 3, 23*A–E*). Lateral eyes on a tubercle, not juxtaposed, and not widely separated from the medians. Tapeta absent from secondary eyes. Cheliceral boss striated.

Appendages (Fig. 23*C–D*, *F*). legs long and slender, with long spines on femora and tibiae. Leg formula 1,2,4,3.

Opisthosoma (Figs 3, 24) round, dorso-ventrally flattened, with a dorsal scutum. Scutum with two pairs of apodemes and numerous smaller sclerotisations. Venter with inconspicuous rows of median and lateral sclerotisations. Book lung covers not grooved, but with sculptured cuticle (Fig. 24*A–B*). PLS black, other spinnerets pale. One or two pairs of white spots lateral to the spinnerets. Epiandrous gland spigots in a row, roughly divided in two lateral groups (Fig. 24*C–D*).

Pedipalp (Figs 4, 12–13, 17–18, 30) with a short globular cymbium, a rectangular paracymbium with an invagination, a large flat or globular tegulum containing the sperm duct, an apical tegular apophysis (Figs 4*A*, *E*, 12*A–B*, *E*, 13*B–E*, 17*B*, 18*A–B*, 30*A*, *C*), a prominent and separate subtegulum, and a massive sigmoidal-shaped embolic conductor enveloping the embolus (see Diagnosis). The embolus and the embolic conductor separated from the tegulum and from each other by an extensive membrane (Fig. 30*D–E*). A single macroseta present on the distal part of the palpal patella. Embolus base with an apophysis (Figs 4*C*, 30*C–E*). Embolus (Figs 4*C–E*, 30*C–E*) long and fairly thin (but not filiform as in *Nephila*), with a distal hook.

Monophyly

Herennia monophyly is supported by the following unambiguous synapomorphies (see phylogenetic results): ridged carapace edge (character 3/state 1); carapace warts (8/1); wider than long sternum (22/1); lobed abdomen (53/1); truncated abdomen tip (55/1); abdominal sigillae (63/1); spotted dorsum (66/1); lateral epigynal chamber openings (77/1); apical tegular apophysis (129/1); hooked embolus (155/1); and presence of pseudoradii (174/1). Ambiguous synapomorphies include also (ACCTRAN) short and stout femoral macrosetae (40/1), oval spermathecae (87/2), rounded apical paracymbium (121/0), flat embolus tip (157/0), the apparent absence of body shake (scored only in *H. papuana*; 186/0) and (DELTRAN) carapace edge with hair-like setae (4/1), presence of sternal tubercle IV (29/1), epigynal septum (78/1), ridged embolic conductor edge (142/1), rectangular orb web (160/1) and bulbus detachment or eunuch behaviour (185/1).

Phylogenetic definition

The genus *Herennia* is defined as the least inclusive clade containing the species *H. multipuncta* (the type), *H. papuana, H. etruscilla* and *H. deelemanae*. This definition avoids the other newly described *Herennia* species as specifiers because they are currently known from females only.

Composition

The genus contains eleven species, of which nine are newly described: *H. agnarssoni*, sp. nov. (Solomon Islands); *H. deelemanae*, sp. nov. (Malaysia (Sabah)); *H. etruscilla*, sp. nov. (Indonesia (Java)); *H. gagamba*, sp. nov. (Philippines (Luzon)); *H. jernej*, sp. nov. (Indonesia (Sumatra)); *H. milleri*, sp. nov. (Papua New Guinea (New Britain, Rossel Island)); *H. multipuncta* (Doleschall) (South and South-east Asia); *H. oz*, sp. nov. (Australia (Northern Territory)); *H. papuana* Thorell (Papua New Guinea); *H. sonja*, sp. nov. (Indonesia (Kalimantan, Sulawesi)); and *H. tone*, sp. nov. (Philippines (Negros)).

Distribution

Tropical and subtropical Asia and Australasia (Fig. 32).

Taxonomic history

In 1877, Thorell described the new genus *Herennia* and designated *Epeira multipuncta* Doleschall as the type species. He synonymised *H. ornatissima* with *H. multipuncta* and described a female of this species from Sulawesi, which, he claimed, was an intermediate form between the Javan (*Epeira multipuncta* Dol.) and the Ambonese form (*E. ornatissima* Dol.). Thorell (1877: 370) believed *Herennia* to be close to the araneid *Argiope*.

Simon (1894: 757–759, figs 828, 835) erected the nephiline group Herennieae to contain only *Herennia*. He redescribed *Herennia* (1894: 759), erroneously noting (*contra* Thorell 1877) that the type species was *H. ornatissima*. Simon (1894: 758) agreed with Thorell (1877, 1887, 1890) that *Epeira multipuncta* Doleschall and *E. ornatissima* Doleschall were two forms of the same species. However, he ignored Thorell's (1877, 1887) synonymisation of *H. ornatissima* with *H. multipuncta* and simply noted (p. 758) that he preferred the name *ornatissima* over *multipuncta*. Thorell (1877), as the first reviser, designated *H. multipuncta* as type species of *Herennia*.

Simon (1894: 759, figs 828, 835) also redescribed *H. ornatissima*. However, the figure of the male pedipalp (fig. 828) certainly depicts another species (close to *H. papuana*) and the figure of the female (fig. 835) cannot be associated with any species treated here.

Remarks

Simon's misapplication of *Herennia ornatissima* versus *H. multipuncta* has gone uncorrected in all spider catalogues (Roewer 1942; Bonnet 1957; Platnick 1989, 1993, 1997, 2005) and has thus misled all *Herennia* nomenclature since. Works on South and South-east Asian spiders (e.g. Tikader 1982: 106; Murphy and Murphy 2000: 388) and on spider systematics (e.g. Hormiga *et al*. 1995) correctly identify the species but misapply the name.

Other authors misidentified their organisms. Chrysanthus (1971: 41) redescribed *H. papuana* (as *H. ornatissima*) from New Guinea (the epigynum figure (fig. 86) was printed upside down). Likewise, Robinson (1975, 1982), Robinson and Robinson (1978, 1980) and Robinson and Lubin (1979) worked on *H. papuana*, not *H. ornatissima*. Eberhard (1982) also probably referred to *H. papuana,* not *H. ornatissima.*

In her illustrated guide to the genera of Australian orb-weavers, Davies (1988: plate 18) provided illustrations of unidentified *Herennia* species. The figures of the female from Australia's Northern Territory are *H. oz*, sp. nov. and those of the male from Papua New Guinea are *H. papuana*. However, although all figures faithfully represent the illustrated objects (both specimens examined here), the male pedipalp figures are unfortunate in depicting an expanded and damaged organ. Unexpanded pedipalps of *H. papuana* exhibit a dramatically different morphology. Furthermore, the labelling of the palpal sclerites, in the same plate, is incorrect. The sclerite labelled 'embolus' is the broken-off part of the sclerotised embolic conductor, and the sclerite labelled 'tegular apophysis' is in fact the embolus, which had been broken-off at the tip. Hormiga *et al*. (1995: fig. 5J) redrew this damaged pedipalp from Davies (1988).

Etymology

Herennia is feminine in gender (Bonnet 1957: 2159). However, Thorell's (1877: 370) original explanation of etymology reads: '*Herennius*, nom. propr. Latinum'. Perhaps the name refers to the Roman Caesar *Herennius Etruscus*, the son of *Herennia Etruscilla*. Searches on '*Herennius*' or '*Herennia*' consistently point to old Roman coins of the 'Family *Herennia*'. Perhaps these Roman coins, which may resemble the flat and lobed abdomen of the spider *Herennia* were the source of Thorell's name derivation. The non-scientific name, coin spiders, introduced here, follows this presumed analogy. See also *H. etruscilla* etymology.

Key to the species of *Herennia* (females)

1. First femur with prolateral group of long spines (Figs 16*A–B*, 27*C*, 31*B*) 2
   First femur without prolateral group of long spines 4
2. Epigynum with a prominent anterior border (Fig. 27*D*); Philippines . . . . . *H. gagamba*, sp. nov.
   Epigynum with a weak anterior border (Figs 16*C*, 31*C–D*) . . . 3
3. Epigynum with thick lateral sclerotised edge (Fig. 16*C*); Solomon Islands . . . . . *H. agnarssoni*, sp. nov.
   Epigynum with thin lateral sclerotised edge (Fig. 31*C–D*); Philippines . . . . . *H. tone*, sp. nov.
4. Carapace with a central yellow V-shaped mark on dark background (Figs 1*C*, 14*A–C*, 27*A*, *C*) 5

Carapace without such mark. 7

5. Epigynum with round chambers and thin septum (Figs 2*A–B*, 27*B*). 6
   Epigynum with oval chambers and strong septum (Fig. 27*E*); Sumatra . . . . . *H. jernej*, sp. nov.
6. Sclerotised epigynal edge lateral and posterior to the chambers extensive (Fig. 2*A–B*); South and South-east Asia . . . . . *H. multipuncta* (Dol.)
   Sclerotised epigynal edge lateral and posterior to the chambers thin (Fig. 27*B*); Kalimantan, Sulawesi. . . . *H. sonja*, sp. nov.
7. Epigynum round, with weak septum (Fig. 17*A*); North Borneo . . . . . *H. deelemanae*, sp. nov.
   Epigynum wide, with conspicuous septum (Figs 16*G*, 18*C*, 28*B–C*, 29*C*) 8
8. Epigynum with oval chambers (Figs 18*C*, 28*B–C*) 9
   Epigynum with round chambers (Figs 16*G*, 29*C*) 10
9. Epigynum with thick lateral sclerotised edge (Fig. 18*C*); Java. . . . . *H. etruscilla*, sp. nov.
   Epigynum with thin lateral sclerotised edge (Fig. 28*B–C*); Australia . . . . . *H. oz*, sp. nov.
10. Epigynal septum thick (Fig. 29*C*); Papua New Guinea . . . . . *H. papuana*, Thorell
    Epigynal septum thin (Fig. 16*G*); New Britain . . . . . *H. milleri*, sp. nov.

Key to the species of *Herennia* (males)

NB: Males of *H. agnarssoni,* sp. nov., *H. gagamba*, sp. nov., *H. jernej,* sp. nov., *H. milleri,* sp. nov., *H. oz*, sp. nov., *H. sonja,* sp. nov., and *H. tone,* sp. nov. are unknown.

1. EC thin (Fig. 30*A–B*); Papua New Guinea. *H. papuana*, Thorell
   EC broad, with a subdistal apophysis (Figs 4*A–B*, 12–13, 17*B–C*, 18*A–B*) 2
2. EC subdistal apophysis prong-like (Fig. 18*A–B*); Java. . . . . *H. etruscilla*, sp. nov.
   EC subdistal apophysis flap-like (Figs 4*A–B*, 12–13, 17*B–C*, 18*A–B*) 3
3. Distal EC longer than wide (Figs 4*A–B*, 12–13); South and South-east Asia. . . . . *H. multipuncta* (Dol.)
   Distal EC wider than long (Fig. 17*B–C*); North Borneo . . . . . *H. deelemanae*, sp. nov.

Herennia multipuncta (Doleschall)

(Figs 1–15)

Epeira (Argyopes) multipuncta Doleschall, 1859: 32, pl. 11, fig. 1, description of female (from Java).

Epeira (Argyopes) ornatissima Doleschall, 1859: 32, pl. 1, fig. 5, description of female (from Ambon).

Epeira (Argyopes) mammillaris Stoliczka, 1869: 236, pl. 20, fig. 12, description of female (from Assam).

Herennia multipuncta Thorell, 1877: 370 (first reviser); 1890: 101.

Herennia sampitana Karsch, 1880: 381, description of female (from Kalimantan). **Syn. nov.**

Herennia mollis Thorell, 1887: 166, description of female (from Myanmar). **Syn. nov.**

Herennia ornatissima Simon, 1894: 759, figs 828, 835 (description of male and female). – Roewer, 1942: 925; Bonnet, 1957: 2159, 2160; Tikader, 1982: 106, figs 202–204 (description of female); Platnick, 1989: 306; 1993: 373; 1997: 454; 2005; Hormiga *et al*., 1995: 334, fig. 11A-F; Murphy & Murphy, 2000: 388, figs 12.1, 12.2.

Material examined

Type material. Type(s) of *E. multipuncta* do not exist, description based on artwork, deposited in RMNH.

Presumed holotype female of *E. ornatissima* in RMNH labelled ‘coll. Doleschall Amboina *Epeira ornatissima* Dol.’ from Maluku, Ambon Island [3°38′S, 128°7′E] — he077/f1, with numbers 5550 and 1159 on separate labels, examined.

Type(s) of *E. mammillaris* were not found.

Holotype female of *H. sampitana* from Sampit, Borneo [Kalimantan, 2°31′S, 112°57′E] — he089/f1 in ZMB dry collection, examined.

Type(s) of *H. mollis* were not found.

Additional material examined. **China:** Hainan Island, Sanya [Yaxian], 18°16′N, 109°29′E, 5.vi. 1983 — he056/f1 (♀ USNM). **India:** Ootacmund [Udagamandalam], 11°24′N, 76°41′E (coll. Hampson) — he093/f1 (♀ BMNH); Assam, 4 mi W Kochugaon, 26°33′N, 90°3′E, 50 m, 17.x. 1961 (coll. Ross & Cavagnaro) — he012/f1 (♀ CAS); Kerala, Periyar Lake, 9°31′N, 77°12′E, 900m, 23.iii. 1962 (coll. Ross & Cavagnaro) — he014/f1 (2♀ CAS), he014/m1 (♂ CAS); Trivandrum, 8°30′N, 76°56′E, ii.1896 — he094/f1 (3♀ BMNH); Maharashtra, 20 mi N Bombay, 19°15′N, 72°50′E, 50 m, 21.i.1962 (coll. Roos & Cavagnaro) — he011/f1 (♀ CAS); Tamil Nadu, Alagarkoil, 21 km NE Madurai, 10°5′N, 78°13′E, 27.xii.1989 (coll. V & B Roth) — he018/f1 (♀ CAS), he018/j1 (Immature CAS), he001/m1 (♂ CAS), he002/m1 (♂ CAS); 5 km W Rajapalayam, Ayyanar Falls, 9°27′N, 77°30′E, 350 m, xi.1979 (coll. W Eberhard) — he038/f1 (♀ MCZ), he046/m1 (♂ MCZ). **Indonesia:** Java [no loc. data] — he060/f1 (♀ MNHN) — he064/f1 (♀ MNHN) — he067/f1 (♀ MNHN); Java, Tjibodas [Cibodas], 6°43′S, 107°2′E, 1907 (coll. T Barbour) — he035/f1 (♀ MCZ); Jawa Barat, Buitenzorg [= Bogor], 6°35′S, 106°47′E — he066/f1 (♀ MNHN) — he092/f1 (10♀ NHMW), he092/m1 (♂ NHMW); (coll. J Barbour) — he033/f1 (3♀ MCZ), he045/f1 (2♀ MCZ); 1909 (coll. O Bryant) — he034/f1 (7♀ MCZ); (coll. Palmer & Bryant) — he020/f1 (3♀ MCZ); 800 ft, 6.iii.1909 (coll. Palmer & Bryant) — he036/f1 (♀ MCZ); Propinsi Kalimantan Selatan, Aranio Dist., Tiwingan Village, 3°33′S, 115°2′E, 100 m, 9.x.i1996 (coll. M Kuntner) — he048/f1 (♀ USNM); Sulawesi [no further data], 2°24′S, 120°18′E — he061/f1 (3♀ MNHN); Nord Celebes [no further data], 0°45′N, 122°0′E (coll. Putz) — he084/f1 (♀ ZMB); Sumatera Udara, Deli [= Labuhandeli], 3°44′N, 98°40′E — he103/f1 (♀ BMNH); Sumatera Utara, Sibaulangit, 3°19′N, 98°34′E (coll. L Jackhan) — he087/f1 (♀ ZMB); Sumatra, 11 km NW Bukittingi, 0°14′S, 100°18′E, 18.xii.1978 (coll. ES Ross) — he017/f1 (3♀ CAS); Fort de Kock [Bukittinggi], 0°18′S, 100°22′E, 920 m (coll. Jacobson) — he091/f1 (♀ NHMW); xi.1913 (coll. E Jacobson) — he079/f1 (♀ RMNH); ‘W Coast’, Kalung [Kalang], 1°53′N, 98°38′E, x.1913 (coll. E Jacobson) — he080/f1 (♀ RMNH); Kerinci NP, 2°2′S, 101°6′E, 800 m, nr. river, 30.vii.1988 (coll. S Djojosudharmo) — he076/f1 (♀ CD); Gn. Leuser, Ketambe, 3°48′N, 97°32′E, camp, 5.ii.1985 (coll. Suyono) — he071/f1 (♀ CD); trail 11.4; l. litter, 4.v.1986 (coll. Suharto) — he072/f1 (2♀ CD), he072/m1 (2♂ CD); trail 8.1, 8.i.1985 (coll. Sudkro & Sarman) — he075/f1 (♀ CD); ‘Rimba, Panti’ [Panti], 0°21′N, 100°3′E, on rock outcrop, ii.1985 (coll. P Hillyard) — he108/f1 (♀ BMNH), he108/m1 (2♂ BMNH); Sebisi, 26.i.1922 — he132/f1 (♀ AMNH); Si Rambe [Sirambas], 0°48′N, 99°31′E (coll. Ed Reimoser) — he044/f1 (♀ MCZ); [no loc. data], 0°0′N, 101°0′E — he063/f1 (♀ MNHN); Sumatra?, ‘Wai Lima Z. Sum. Lampongs’, xi.1921 (coll. Karny) — he131/f1 (♀ AMNH). **Malaysia:** Frasers Hill [Bukit Fraser], Gap Rest House, 3°42′N, 101°44′E, wall, viii.1983 (coll. RH Kiew) — he106/f1 (2♀ BMNH); 2 mi. E Gopeng, 4°27′N, 101°9′E, 100, 21.vi.1962 (coll. Ross & Cavagnaro) — he013/f1 (♀ CAS); 3 mi. SE Ipoh, 4°34′N, 101°6′E, 50 m (coll. ES Ross) — he003/m1 (♂ CAS); Malakka [= Malayan Pen.] (coll. Jochan) — he085/f1 (♀ ZMB); Penang [P. Island], 5°23′N, 100°15′E (coll.

S Hower) — he095/f1 (♀ BMNH); Perak: Senggong (?) [Lenggong], 5°7′N, 100°49′E, ii.1932 (coll. Burbon) — he068/f1 (♀ MNHN); Penang, Tanjung Bungah, Sungei Siru, 3.xii.1963 (coll. HT Pagden) — he107/f1 (♀ BMNH); 'Malay', Yohore, Mount Austin, 1951 (coll. CW Franck) — he116/f1 (♀ ZMUC); Negeri Johor, Kota Tinggi, 1°43′N, 103°54′E, 19.iii.1948 — he111/f1 (♀ BMNH); Pahang, Beserah, 3°51′N, 103°22′E, tree trunk, 20.x.1901 (coll. Robinson) — he101/f1 (♀ BMNH), he101/m1 (♂ BMNH); Merapoh, Taman Negara, Kuala Juram, 4°38′N, 102°7′E, 75–150 m, on webs over a white wall, 12.iii.1999 (coll. Trilar & al.) — he005/f1 (2♀ PMS), he005/j1 (3 Imm. PMS), he005/m1 (♂ PMS); Sabah, Poring Hotsprings, 5°59′N, 116°14′E, 500, 2.iv.1998 (coll. Deeleman & Zborowski) — he070/m1 (♂ CD). **Myanmar:** Bhamo, 24°15′N, 97°13′E (coll. L Fea) — he120/f1 (♀ ZMUC); 1885–1889 (coll. L Fea) — he081/f1 (♀ ZMH); Kalaw, 20°37′N, 96°34′E, 1308 m, large tree trunk, 11 Nov 1978 (coll. ES Ross) — he016/j1 (5 Imm. CAS), he004/m1 (♂ CAS); Pegu, Burmah, 17°19′N, 96°29′E, xi.1966 (coll. CH Carpenter) — he043/f1 (3♀ MCZ); Tenasserim, 12°5′N, 98°55′E (coll. Oates) — he097/f1 (♀ BMNH); Tharrawaddy, 17°38′N, 95°47′E (coll. EW Oates) — he096/m1 (♂ BMNH). **Nepal:** a few miles W of Beni, on Mayangdi Khola, 28°20′5'N, 83°34′0'E, 914 m, tree trunks, 20.vii.1954 (coll. KH Hyatt) — he100/f1 (2♀ BMNH), he100/m1 (♂ BMNH); Baglung, Along Kali Gandaki River, 28°16′0'N, 83°36′5'E, 914 m, 12.vi.1954 (coll. KH Hyatt) — he099/f1 (♀ BMNH), he099/m1 (♂ BMNH). **Philippines:** Leyte, Near Dulag, 10°57′N, 125°1′E, 30 m, 8.iv. 1945 (coll. LW Saylor) — he130/f1 (♀ AMNH); Philippine Island [no further data] (coll. Ledyard) — he040/f1 (4♀ MCZ), he041/f1 (4♀ MCZ); Philippinen [no exact loc. data] — he105/f1 (♀ BMNH); Luzon, Los Banos, 14°10′N, 121°10′E, vii.1909 (coll. Ledyard) — he027/m1 (♂ MCZ); (coll. Ledyard) — he042/f1 (9♀ MCZ); [Los Banos], Mt. Makiling, 14°8′9'N, 121°11′24'E (coll. Baker) — he028/f1 (♀ MCZ). **Singapore:** Peirce Reservoir, 1°22′N, 103°48′E, tree trunk, edge of secondary forest (coll. Koh) — he006/f1 (♀ WAM); Seletar Reservoir, 1°24′N, 103°47′E, 8 m, forest, 7.xi.1991 (coll. Andersen *et al*.) — he118/f1 (♀ ZMUC), he119/f1 (♀ ZMUC); Singapore, 1°19′N, 103°50′E (coll. HN Ridley) — he110/f1 (2♀ BMNH); Sungei Seletar, 1°24′N, 103°53′E (coll. Koh) — he007/m1 (♂ USNM); Ubin Island, 1°24′N, 103°58′E, 20 m, shrubs along forest edge and fields, 3.xi.1991 (coll. Andersen *et al*.) — he117/f1 (♀ ZMUC). **Sri lanka:** Nähe [near] Aukana Buddha, xii.1981 (coll. Schmidt) — he112/f1 (♀ SMF); [Ceylon], 7°27′N, 80°44′E — he037/f1 (2♀ MCZ); Kandy, 7°17′N, 80°37′E — he069/f1 (25♀ MNHN), he069/m1 (20♂ MNHN); Dec 1925 (coll. G Fairchild) — he039/f1 (2♀ MCZ); Central Prov, Kandy Dist, Kandy; St. Bridget's Guesthouse, 7°17′N, 80°37′E, around the house at night, 20–22.i.1995 (coll. Kuntner & Antauer) — he008/f1 (5♀ USNM); Peradeniya Botanical Gardens, 7°15′N, 80°36′E — he086/f1 (3♀ ZMB); 22 Jan 1995 (coll. M Kuntner) — he010/f1 (♀ USNM); tree trunks, 22 Oct 1982 (coll. Wanless) — he109/f1 (4♀ BMNH); North-Central Prov, Anuradhapura Dist, at Anuradhapura water tank near new bus station, 8°18′N, 80°24′E, taken from a web built against a tree trunk of a bo-tree at night, 18 Jan 1995 (coll. M Kuntner) — he009/f1 (♀ USNM). **Taiwan:** Kankan, Formosa, vii.1909 (coll. Santer) — he088/f1 (♀ ZMB). **Thailand:** 20 mi SE Chantaburi, 12°24′N, 102°19′E, 75 m, 1.viii.1962 (coll. Ross & Cavagnaro) — he015/f1 (♀ CAS); Khao Yai National Park, 14°20′N, 101°30′E, savannah, 10 Nov 1987 (coll. CL & PR Deeleman) — he074/f1 (♀ CD); Sakhon Nakon, King's Palace, 17°9′N, 104°9′E, deciduous forest; on trunk, 7.i.1989 (coll. CL & PR Deeleman) — he073/f1 (2♀ CD), he073/m1 (♂ CD). **Vietnam:** Anam [Annam region], 14°15′N, 107°50′E — he065/f1 (♀ MNHN).

Diagnosis

Females differ from all other *Herennia* species by the epigynal plate with extensive sclerotisation lateral and posterior to the chambers (Figs 2*A–B*, 10*E*, 11*A*, *C*, *E*). Further, they differ from *H. etruscilla*, *H. oz, H. tone, H. deelemanae, H. papuana, H. agnarssoni* and *H. milleri* by the orange to brown carapace with a central yellow V-shaped mark (Figs 1*C*, 14), with sparse and weak warts, each bearing a white long seta (Fig. 5*E–F*), and by the epigynum with round chambers, weak septum and antero-lateral copulatory openings (Figs 2*A–B*, 10*E–F*, 11). They can be further distinguished from *H. papuana*, *H. tone* and *H. deelemanae* by the flat and round abdomen with conspicuous lobes (Figs 1*A*, *C–D*, 8*A–C*, 9*A–B*, *E*, 10*A–D*). Males differ from *H. etruscilla* and *H. papuana* by the short and curved distal embolic conductor with a broad subdistal flap (Figs 4*A–B*, 12–13) and from *H. deelemanae* by the larger size of the pedipalp and by the relatively smaller embolic conductor flap (Figs 4*A–B*, 12–13).

Description

Female (he8/f2, compare with Fig. 1 of he8/f1, both from Kandy, Sri Lanka)

Total length 12.8.

Prosoma (Figs 1*A–D*, 5–6, 14) 4.9 long, 4.6 wide, 2.5 high. Carapace orange and dark red-brown, yellow laterally and posteriorly, and with a median V-shaped yellow pattern. Chelicerae orange. Cheliceral formula 3/4/30. Sternum 1.7 long, 2.1 wide; orange in live animal (white in alcohol). Maxillae and labium orange-brown. Anterior eye row recurved, posterior straight. AME diameter 0.23, ALE 0.13, PME 0.13, PLE 0.13. AME separation 0.22, PME separation 0.32, PME–PLE separation 0.41, AME–ALE separation 0.41, AME–PME separation 0.32, ALE–PLE separation 0.11. Clypeus height 0.38.

Appendages yellow, distal femora and tarsi black. Femoral spines sparse and short. Leg I length 19.1 (Fe 5.4, Pa 1.6, Ti 4.6, Me 6.0, Ta 1.5).

Opisthosoma (Figs 1*A*, *C–D*, 8–10, 14) flattened dorso-ventrally and truncated posteriorly, with four pairs of lateral lobes; 8.7 long, 8.2 wide (maximum width over abdominal lobes), 4.1 high. Dorsum white with numerous red-brown sclerotisations, mostly in depressions, these connected by dark pigment lines. Lateral opisthosoma with longitudinal dorso-ventral brown bands and small sclerotisations. Venter white and yellow, with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets and with a central grey area. Four pairs of central sclerotisations and several rows of lateral smaller sclerotisations present on venter. Book lung covers and the sclerotisation around the spiracles red, as are the epigynum and the sclerotised area anterior to it.

Epigynum as in Figs 2, 10*E–F*, 11 (see also Diagnosis). Circular epigynal chambers divided by a narrow septum. Lateral chamber walls heavily sclerotised, black. Inner epigynum as in Fig. 2*C–D*. Copulatory ducts wide and long, curved.

Male (he14/m1 from Periyar, India, Figs 1E–G, 3–4, 12–13)

Total length 3.5.

Prosoma 2.0 long, 1.6 wide, 1.1 high; dark orange. Sternum 0.8 long, 0.8 wide; orange. AME diameter 0.16, ALE 0.09, PME 0.09, PLE 0.09. AME separation 0.13, PME separation 0.16, PME–PLE separation 0.13, AME–ALE separation 0.06, AME–PME separation 0.16, ALE–PLE separation 0.06. Clypeus height 0.13.

Appendages orange, distal femora and patellae slightly darker. Leg I length 8.0 (Fe 2.1, Pa 0.6, Ti 1.9, Me 2.4, Ta 1.0).

Opisthosoma 2.0 long, 1.8 wide, 1.1 high. Scutum orange-grey, venter light grey. A paired white dot present lateral to the spinnerets.

Pedipalp as in Figs 4, 12–13 (see also Diagnosis). EC sigmoidal. EC proximally wide and mebraneous, distally flat, short and broad, sclerotised, with a ridged edge.

Variation

Females: prosoma length ranges from 3.7 to 6.2; total length from 8.1 to 19.8 (n = 30). The colouration intensity varies, but the general pattern is as described. Yellow legs of some females are strikingly dark brown annulated. Most females have a flattened opisthosoma (Fig. 10*A–B*, but compare with Figs 1*A*, 9*A*, 10*D*). Very often one or both epigynal openings are plugged with male embolic conductors (Figs 2*B*, 10*E–F*, 11). Epigynal shape varies considerably, from round chambers with a thin but conspicuous septum as described, to almost a single chamber with weak septum (Fig. 2*B*, 11*A*, *C*). *Males*: prosoma length ranges from 1.9 to 2.0; total length from 3.3 to 3.5 (n = 5). Male palpal morphology is as diagnosed.

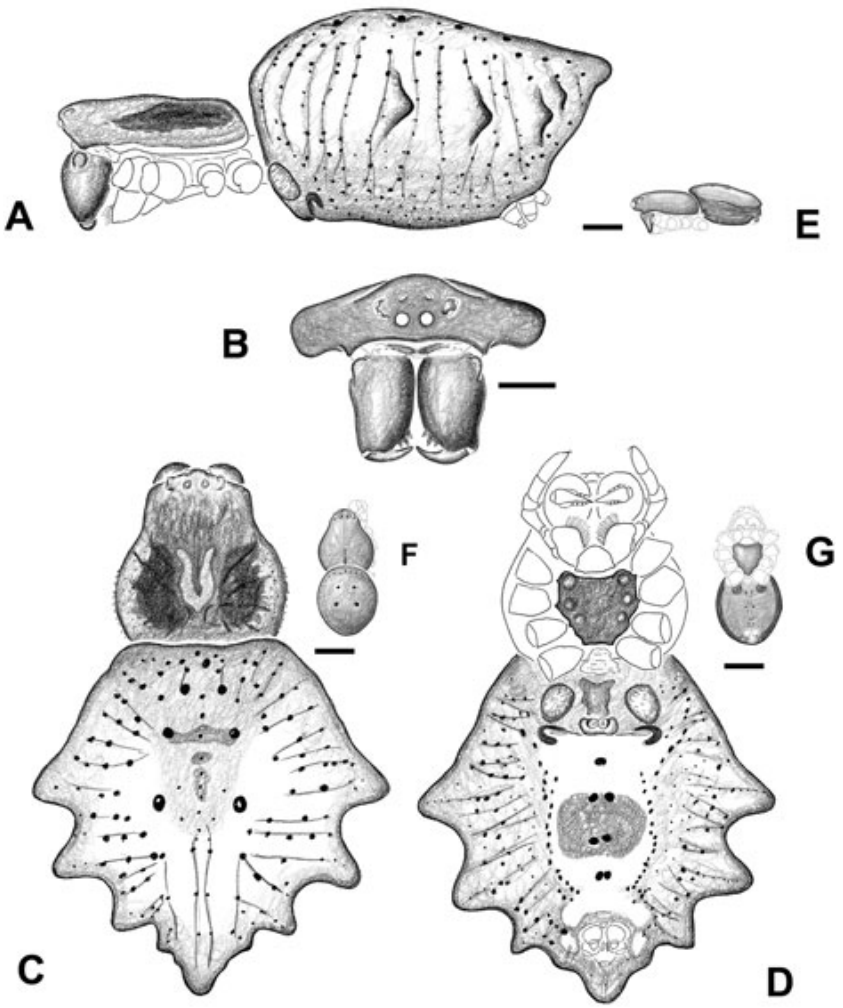

Fig. 1. *Herennia multipuncta* somatic morphology and sexual dimorphism. *A–D*, Female from Sri Lanka (he8/f1): *A*, lateral; *B*, frontal; *C*, dorsal; *D*, ventral; *E–G*, male from India (he14/m1); *E*, lateral; *F*, dorsal; *G*, ventral. Note that corresponding female and male views are in same scale. Scale bars = 1.0 mm.

Distribution

Widespread in South and South-east Asia. Records from Sri Lanka, India, Nepal, Myanmar, Thailand, Malaysia, Singapore, Indonesia (Sumatra, Western Java, Borneo, Sulawesi, Ambon), Philippines, Vietnam, China, Taiwan (Fig. 32).

Natural history

Common on trees and walls close to humans. The species seems to be the most synanthropic in the genus and appears to occupy degraded habitats throughout South and South-east Asia.

Taxonomic history

Doleschall's (1859) 'Second Contribution' to Dutch Indian (Indonesian) arachnology included descriptions of *Epeira (Argyopes) ornatissima* from Amboina (Ambon, Maluku) and *Epeira (Argyopes) multipuncta* from Java. Doleschall's descriptions, both of females, were in Dutch with Latin diagnoses and contained female habitus illustrations of each species. The female syntype of *Epeira ornatissima* from Ambon was found in RMNH and is in a very bad condition. As the description of *E. multipuncta* was based on an illustration (N.K. = 'Natuurkundige Komissie', see Doleschall 1859: 2, 33), the type does not exist. The illustration of *E. multipuncta* depicts a V-shaped mark on the carapace, which is absent in the illustration of *E. ornatissima*, but the Dutch description does mention it and it can be seen in the holotype female. Both Doleschall's descriptions are of the same species (widespread in South and South-east Asia) and thus either of the two names could be used. However, the first reviser's choice (Thorell 1877) was *multipuncta* as the valid name for this species and *ornatissima* as its synonym.

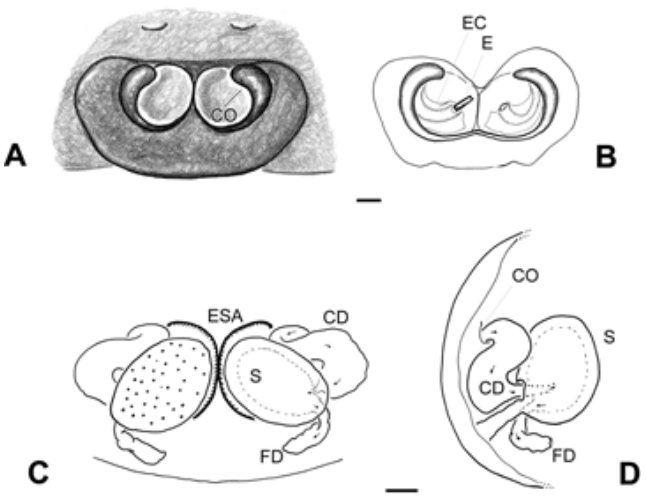

Fig. 2. *Herennia multipuncta*, female epigynum. *A–B*, Ventral: *A*, from Sri Lanka (he8/f1); *B*, from Singapore (he6/f1), note broken embolic conductors and a broken embolus. *C–D*, Cleared epigynum anatomy, from Sri Lanka (he8/f1): *C*, dorsal; *D*, ectal. Scale bars = 0.1 mm.

Stoliczka (1869) described a new species, *Epeira (Argyopes) mammillaris*, from a female collected in Assam. Stoliczka (1869: 204) gave the type depository as 'Indian Museum'. I was unable to locate the type(s) and did not receive replies to my requests from India (Zoological Survey, Kolkatta). The description and figures provide no character that could diagnose the species from the widespread *H. multipuncta* so the species is kept a synonym of *H. multipuncta* as in Thorell (1887).

Karsch (1880: 381) described a female from Borneo (Sampit, Kalimantan) as a new species, *Herennia sampitana*. The holotype was available for examination in ZMB, and the name is here proposed a new synonym of *H. multipuncta*.

Thorell (1887) synonymised *H. mammilaris* with *H. multipuncta*, confirmed his earlier (1877) synonymy of *H. ornatissima* with *H. multipuncta* and described a new species based on a female from Myanmar (then Burma), *Herennia mollis* Thorell, 1887. I failed to locate the type series of *Herennia mollis*, but its depository may be MCSNG. Having examined only *H. multipuncta* from Myanmar, I expect the female holotype of *Herennia mollis* to be conspecific. Thorell's diagnosis mentioned the diagnostic V-shaped mark on the carapace. Bonnet (1957) synonymised *H. mollis* with *H. ornatissima* (= *H. multipuncta*), but the name was listed as valid by Platnick (2005).

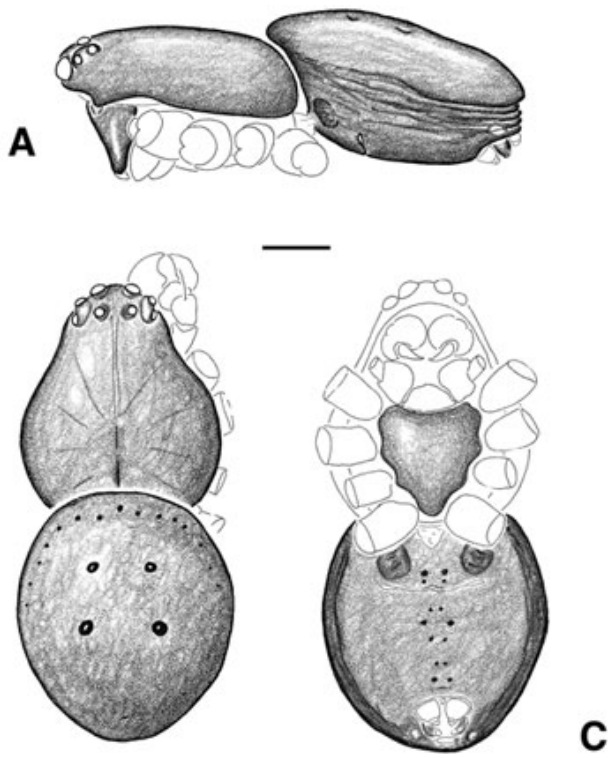

Fig. 3. *Herennia multipuncta*, male from India (he14/m1): *A*, lateral; *B*, dorsal; *C*, ventral. Scale bar = 0.5 mm.

Etymology

The name probably reflects the many dark sclerotised spots on the female abdomen.

Herennia agnarssoni, sp. nov.

(Fig. 16*A–C*)

Material examined

Holotype. Female (he102/f1 BMNH) from Solomon Islands: Mt. Austen, 13.xi.1964, P. Greenslade. The locality lies at 9°28′S 159°58′E on the island Guadalcanal.

Additional material examined. None.

Diagnosis

Females differ from all other *Herennia* species except *H. tone* and *H. gagamba* by a group of long conspicuous spines prolaterally on femur I (Fig. 16*A–B*). The known female can be easily distinguished from *H. tone* and *H. gagamba* by the epigynum with extensive posterior and lateral epigynal chamber sclerotisations (Fig. 16*C*).

Description

Female (holotype, Fig. 16A–C*)*

Total length 13.3.

Prosoma (Fig. 16*A–B*) as described in *H. papuana*, but relatively longer (length to width ratio 1.4; 1.1 in *H. papuana*): 5.5 long, 4.0 wide, 2.9 high. Cheliceral formula 4/4/15. Sternum 2.0 long, 2.1 wide, bright orange. PLE size 0.19, PME 0.16 (PLE larger than PME).

Appendages (Fig. 16*A–B*) as described in *H. papuana* but legs longer (see also Diagnosis). Leg I length 28.8 (Fe 8.4, Pa 1.7, Ti 6.8, Me 9.4, Ta 2.5). Sustentaculum conspicuous.

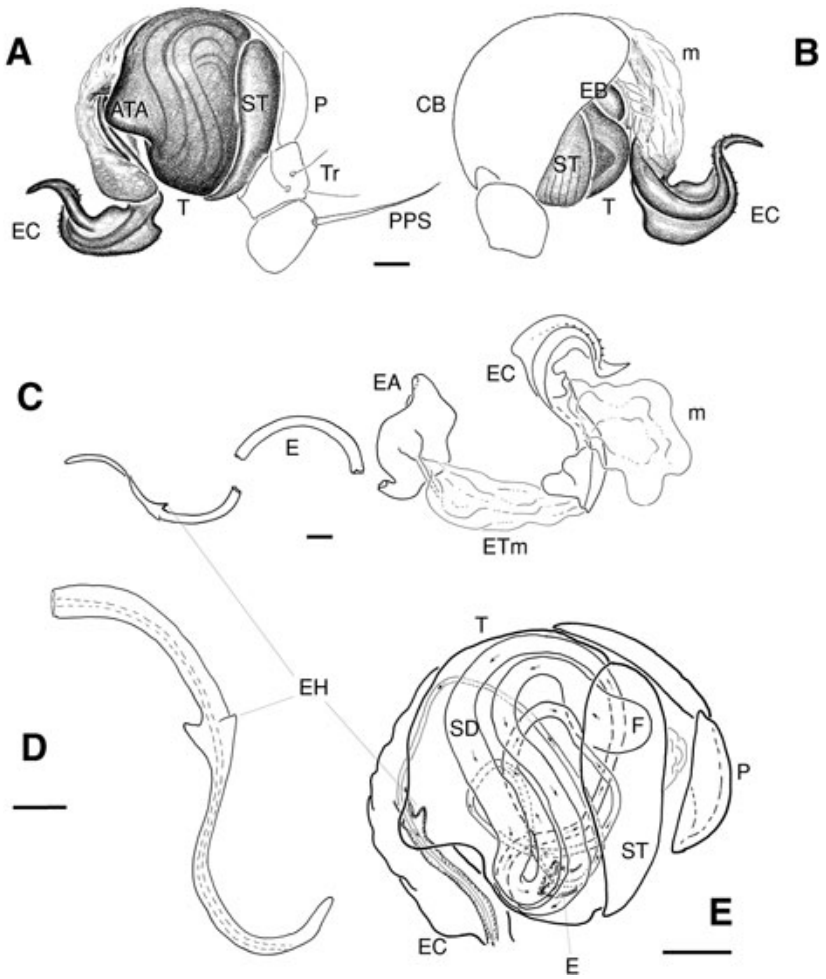

Fig. 4. *Herennia multipuncta*, male pedipalp (*A–B*, *E*, from India, he14/m1; *C*, from Malaysia, he5/m1; *D*, from Java, he20/m1). *A*, Ectal; *B*, mesal; *C*, embolic division, expanded and dissected from tegulum (embolus broken twice), note connection of embolus base and embolic conductor via membrane, ETm (this membrane attaches the embolic division to the tegulum as illustrated in *H. papuana* in Fig. 27*D–E*), and additional membrane on EC; *D*, broken distal embolus, dissected from female epigynum (note embolus hook); *E*, bulb transparent, showing sperm duct, ectal (note position of embolic hook). Scale bars = 0.1 mm.

Opisthosoma (Fig. 16*A–B*) barely flattened dorsoventrally with four pairs of inconspicuous lateral lobes, truncated posteriorly; 7.5 long, 7.4 wide (maximum width over abdominal lobes), 4.9 high. Dorsum white with numerous sigillae. Lateral opisthosoma with small sclerotisations. Venter white with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets. Four pairs of central sclerotisations, and conspicuous lateral sclerotisations in many rows. Book lung covers and the sclerotisation around the spiracles red, as are the epigynum and the sclerotised area anterior to it. Spinnerets of the typical form.

Epigynum (Fig. 16*C*) as diagnosed. Epigynal septum barely present, weak and deep, chambers thus forming a continuous area. Lateral walls heavily sclerotised, black.

Male

Unknown.

Distribution

Known only from the type locality in Solomon Islands (Fig. 32).

Natural history

Unknown.

Etymology

The species epithet is a patronym after my laboratory mate, Ingi Agnarsson.

Herennia deelemanae, sp. nov.

(Fig. 17)

Material examined

Holotype. Male (he115/m1 RMNH) from [Malaysia, Sabah] 'N. Borneo: Mt. Kinabalu N.P., Poring Hot Springs, tree 1+2 night,

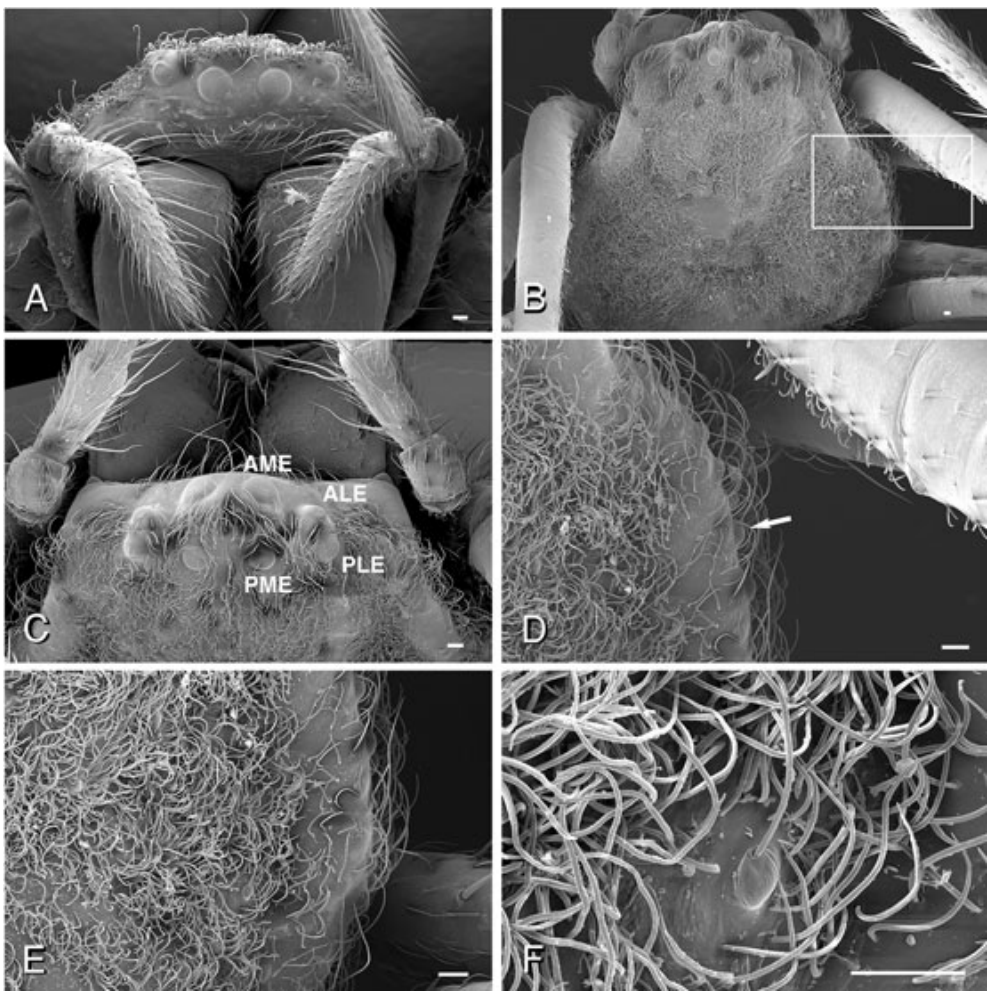

Fig. 5. *Herennia multipuncta*, female prosoma, from Sri Lanka (he8/f5): *A*, frontal; *B*, dorsal, box delimits area of image *D*; *C*, head region, dorsal; *D*, carapace edge, dorsal (note ridged edge, arrow); *E*, same (note extensive hair-like setae); *F*, carapace detail (note warty seta base surrounded by hairs). Scale bars = 100 μm.

6°2′N 116°50′E, primary forest 500–700m, canopy fogging Aglaia sp. (Meliaceae), leg. A. Floren 27.iii.97, ex coll. C.L. Deeleman-Reinhold; 2000-704'; the real date is 1998 (C. L. Deeleman, personal communication).

Paratype. Female (he114/f1 RMNH) from [**Malaysia**] 'S Sabah, Beaufort, 105 km S of: Long Pa Sia area: Payakalaba. 4°25′N 115°44′E. 12 Apr 1987. Van Tol & Huisman; At light. 18.25–21.00h. Somewhat disturbed kerangas vegetation. 1000m'.

Additional material examined. None.

Remarks

The female paratype is hypothesised to be conspecific with the male on the basis of the EC morphology in female copulatory opening (Fig. 17*A*, compare with 17*B–C*) and the relative proximity of the type localities (both in Sabah).

Diagnosis

Females differ from other known species of *Herennia* by the oval epigynum (Fig. 17*A*) with a weak septum, thin lateral sclerotised edge and lateral copulatory openings. Males differ from other known species of *Herennia* by the smaller size (prosoma 1.3, total length 3.0) and by the embolic conductor with an extensive flap (Fig. 17*B–C*).

Description

Female (paratype, Fig. 17A)

Total length 8.2.

Prosoma 3.9 long, 3.0 wide, 2.1 high. Carapace brown-red (no median mark) with conspicuously yellow lateral edge. Carapace distinctly warty. Chelicerae red-brown. Sternum 1.6 long, 1.7 wide; orange, with medially protruding white subcutaneous pigment. Maxillae and labium red-brown. Anterior eye row recurved, posterior straight. PLE size 0.15, PME 0.15.

Appendages. Femora and tibiae yellow, other leg joints brown. Femoral spines fairly sparse, of medium length. Leg

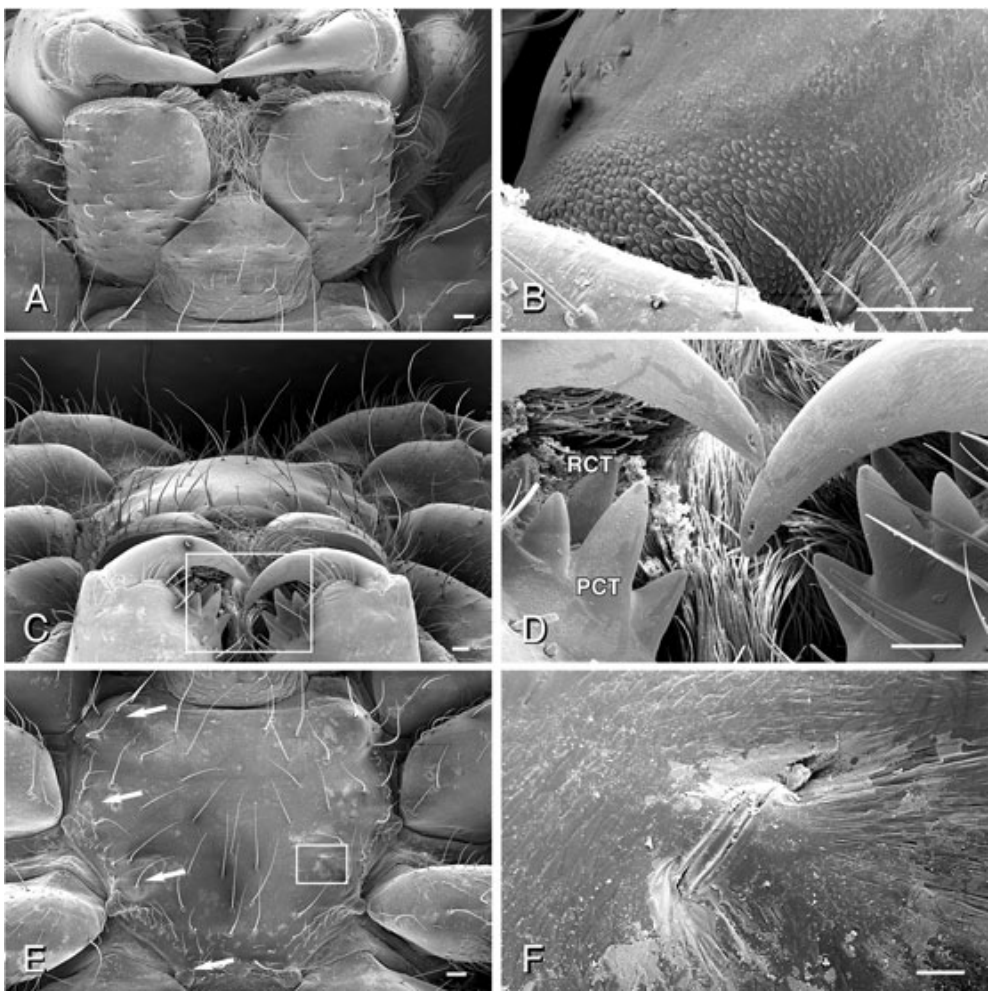

Fig. 6. *Herennia multipuncta*, female prosoma, from Sri Lanka (he8/f5): *A*, mouth parts, ventral; *B*, cheliceral boss, lateral; *C*, ventral prosoma, frontal, box delimits area of image *D*; *D*, cheliceral detail, frontal; *E*, sternum, box delimits area of image *F* (note paired tubercles (arrows) adjacent to each coxa); *F*, sternal slit sensilla. Scale bars = 100 μm, except *F* = 20 μm.

I length 17.0 (Fe 4.9, Pa 1.3, Ti 4.2, Me 5.1, Ta 1.5). Sustentaculum present, hidden among other setae.

Opisthosoma oblong, flattened dorso-ventrally with inconspicuous lateral lobes; 4.5 long, 3.7 wide (maximum width over abdominal lobes), 1.6 high. Dorsum white with numerous sigillae. Lateral opisthosoma with small sclerotisations. Venter white with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets. Four pairs of central sclerotisations, and conspicuous lateral sclerotisations in many rows.

Epigynum (Fig. 17*A*) as diagnosed.

Male (holotype, Fig. 17B–C)

Total length 3.0.

Prosoma 1.3 long, 1.1 wide, 0.9 high; light orange. Sternum 0.6 long, 0.6 wide. AME diameter 0.16, ALE 0.08, PME 0.09, PLE 0.09.

Appendages orange-grey. Leg I length unknown.

Opisthosoma 1.4 long, 1.3 wide, 0.9 high. Scutum brown (in alcohol). Venter and lateral abdomen grey. A paired white dot present lateral to the spinnerets.

Pedipalp as diagnosed (Fig. 17*B–C*).

Distribution

Sabah (Malaysian Borneo) (Fig. 32).

Natural history

The male was collected by canopy fogging *Aglaia* sp. (Meliaceae) in primary forest at 500–700 m. The female was collected in ‘somewhat disturbed kerangas vegetation’ at 1000 m.

Etymology

The species epithet is a patronym after Christa Deeleman-Reinhold, who discovered the species.

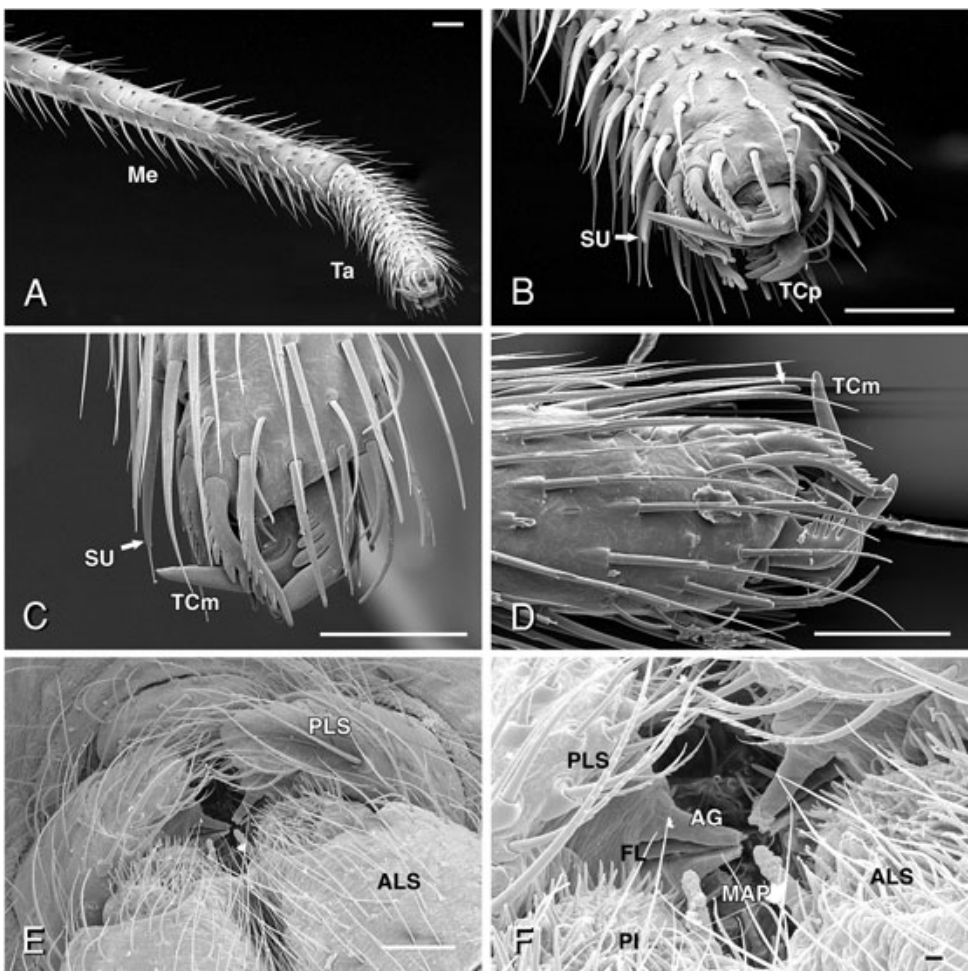

Fig. 7. *Herennia multipuncta*, female from Sri Lanka (*A–C*, he8/f4; *D–F*, he8/f5): *A*, fourth leg distal joints; *B*, fourth tarsus detail, apical (note conspicuous sustentaculum); *C*, same, lateral (note inconspicuous sustentaculum); *D*, fourth tarsus of different female, lateral (note sustentaculum hidden among setae); *E*, presumed natural pose of spinnerets, PMS hidden; *F*, same, detail, showing facing triads (AG and FL spigots). Scale bars = 100 μm, except *F* = 10 μm.

Herennia etruscilla, sp. nov.

(Figs 18–26)

Material examined

Holotype. Male (he58/m1 USNM) from Indonesia: Java, Yogyakarta, Kaliurang village and adjacent forest, 900–1050 m, 16–17 Oct 1996 (coll. Kuntner & Šereg). The locality lies on the slope of Mt. Merapi volcano at ~7°35′S 110°25′E.

Paratypes. Three females (he052/f1 USNM) and two males (he052/m1 USNM) from **Indonesia:** W. Java, Cibodas Botanical Gardens, near Bogor, 1300–1400 m, 24.x.1996 (coll. Kuntner & Šereg). The locality lies in western Javan highlands at ~6°44′S 107°02′E. Two paratype females and a paratype male are also photo vouchers.

Additional material examined. **Indonesia:** Java [no loc. data] — he062/f1 (6♀ MNHN); (coll. H. Jensen) — he121/f1 (♀ ZMUC); Java, Yogyakarta, Kaliurang village, 7°35′S, 110°25′E, 900–1050, 16–17.x.1996 (coll. Kuntner & Šereg) — he058/j1 (Imm. USNM), Forest at night, 18.x.1996 (coll. Kuntner & Šereg) — he051/f1 (♀ USNM); Tjibodas [Cibodas], 6°43′S, 107°2′E, 1907 (coll. T Barbour) — he049/f1 (♀ MCZ); 28.viii.1922 (coll. Th. Mortenssen) — he122/f1 (♀ ZMUC), he122/j1 (Imm. ZMUC); Jawa Barat, Buitenzorg [= Bogor], 6°35′S, 106°47′E, 1909 (coll. Palmer & Bryant) — he053/f1 (♀ MCZ); Jawa Timur, 'O. Java', Tengger Geb. [= Bromo Tengger Semeru NP], 8°0′S, 113°0′E (coll. Fruhstorfer) — he083/f1 (2♀ ZMB); W Java, Cibodas Botanical Gardens, 6°44′S, 107°2′E, 1300–1400 m, web on tree trunk, 24 Oct 1996 (coll. Kuntner & Šereg) —he052/j1 (Imm. USNM).

Diagnosis

Females *Herennia etruscilla* differ from *H. multipuncta*, *H. sonja, H. jernej* and *H. gagamba* by the dark red carapace lacking yellow V-shaped mark (Figs 25–26*A*), with many conspicuous warts, each bearing a short black hook on top (Fig. 19) and by the epigynum with oval chambers, strong septum, and lateral copulatory openings (Figs 18*C*, 22*E–F*). They can be distinguished from *H. tone*, *H. deelemanae, H. papuana,*

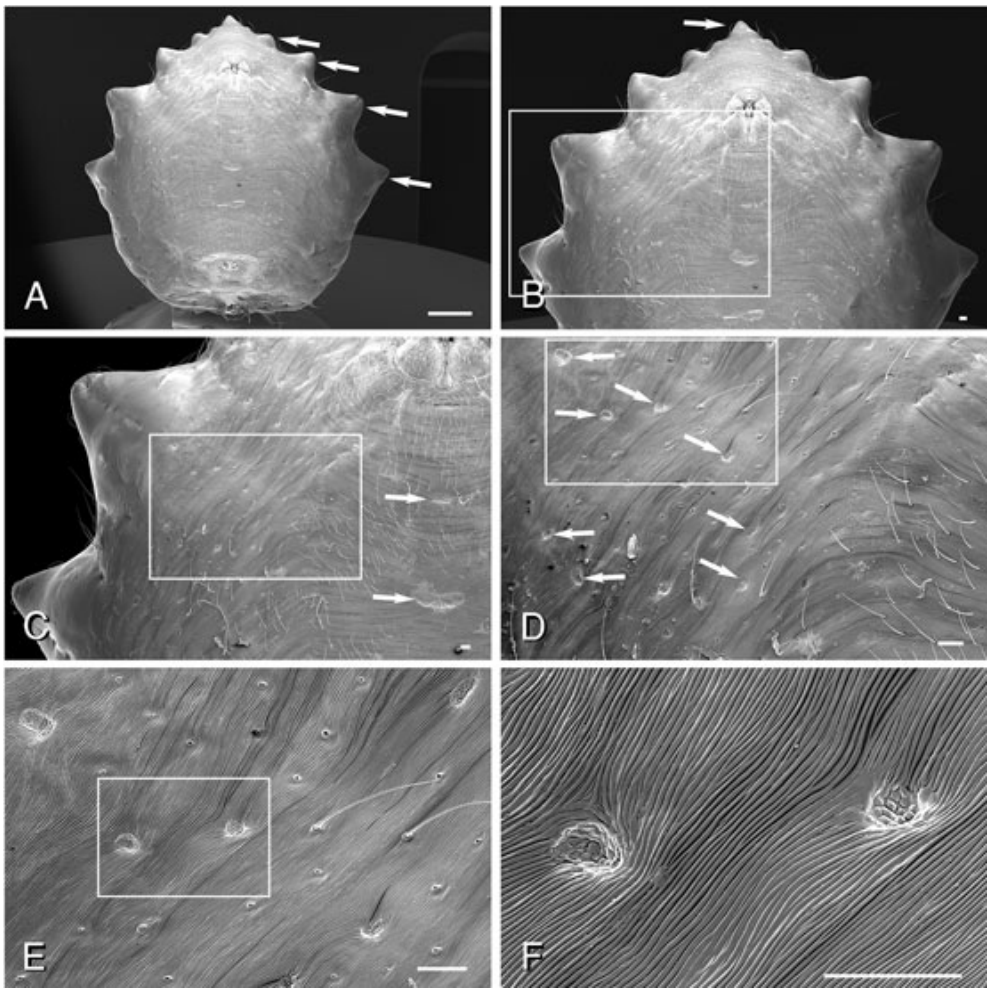

Fig. 8. *Herennia multipuncta*, female opisthosoma, from Sri Lanka (he8/f4), all ventral view: *A*, whole venter, showing four paired opisthosomal lateral lobes (arrows); *B*, posterior venter, showing truncated opisthosomal tip (arrow), box delimits area of image *C*; *C*, venter detail, showing median apodemes (arrows), box delimits area of image *D*; *D*, venter detail, showing numerous lateral sclerotisations (arrows), box delimits area of image *E*; *E*, lateral venter detail with sclerotisations, box delimits area of image *F*; *F*, lateral sclerotisations detail. Scale bars = 100 μm, except *A* = 1 mm.

H. agnarssoni and *H. milleri* by a flat and round abdomen with conspicuous lobes (Figs 22*A–B*, 25–26*A*), and by the lateral epigynal chamber sclerotisation, which reaches about halfway to the anterior epigynal rim (Fig. 18*C*). The epigynum is larger and the lateral sclerotisation thicker (Fig. 18*C*) than in females of *H. oz*, and the posterior lateral eyes are the size of posterior median eyes. Males *Herennia etruscilla* differ from all other *Herennia* species with known males by the extremely long and curved distal embolic conductor with a subdistal flap in the shape of a prong (Fig. 18*A–B*).

Description

Female (paratype he52/f2, Fig. 25, compare with Figs 18C–D, 19–22, 26)

Total length 15.8.

Prosoma (Figs 19–20, 25–26) 5.7 long, 5.6 wide, 2.9 high. Carapace red. Chelicerae red-brown. Cheliceral formula 3/4/23. Sternum 2.2 long, 2.6 wide; bright red in live animal (Fig. 26*B*); in alcohol orange and with medially protruding white subcutaneous pigment. Maxillae and labium red-brown. Anterior eye row recurved, posterior straight. AME diameter 0.32, ALE 0.16, PME 0.19, PLE 0.19. AME separation 0.29, PME separation 0.44, PME–PLE separation 0.49, AME–ALE separation 0.32, AME–PME separation 0.43, ALE–PLE separation 0.18. Clypeus height 0.45.

Appendages (Figs 19*A–B*, 21*A–C*, 25–26). Proximal femora and tibiae yellow, distal femora and tibiae and other leg joints black. Femoral spines normal. Leg I length 27.0 (Fe 7.8, Pa 2.0, Ti 6.2, Me 8.7, Ta 2.3). Sustentaculum present, but may be inconspicuous (e.g. in Fig. 21*C*).

Opisthosoma (Figs 22*A–D*, 25–26) circular, flattened dorso-ventrally, with four pairs of conspicuous lateral lobes, truncated posteriorly; 9.6 long, 10.1 wide (maximum width over abdominal lobes), 6.8 high. Dorsum with numerous

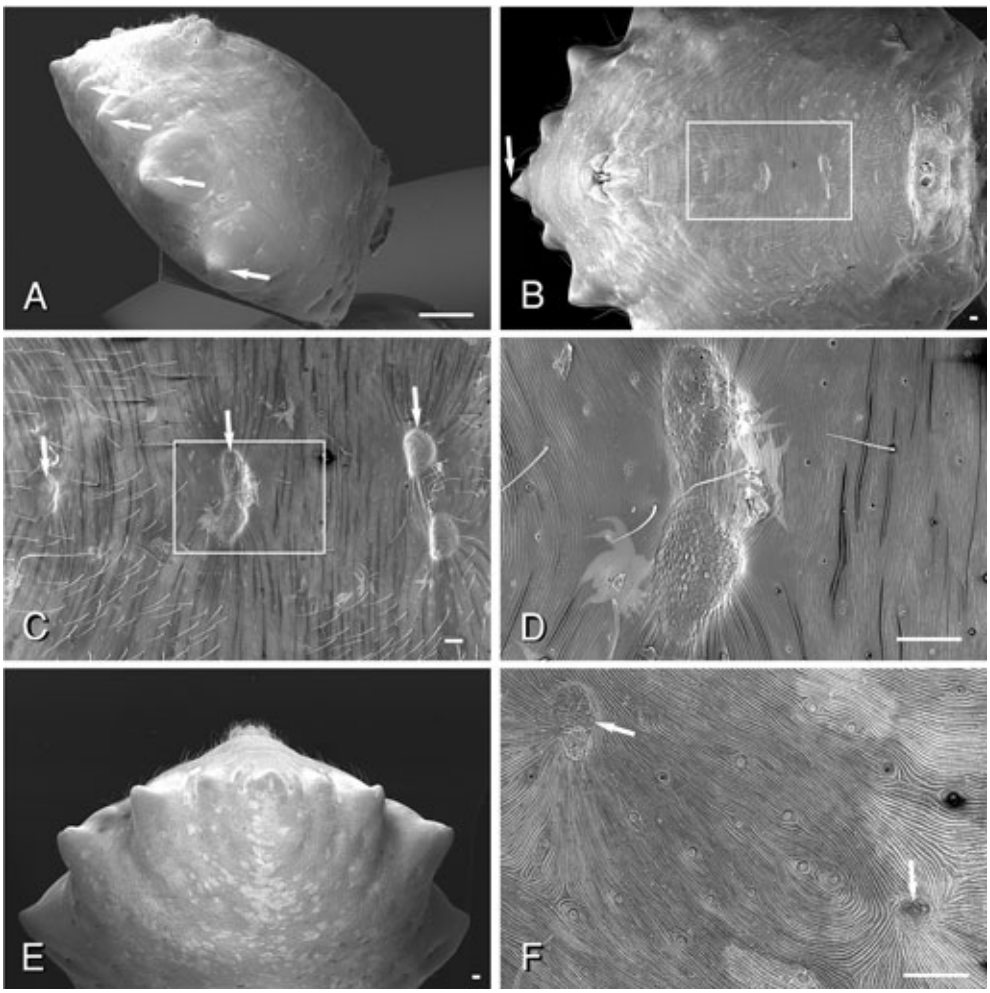

Fig. 9. *Herennia multipuncta*, female opisthosoma, from Sri Lanka (he8/f4): *A*, lateral, showing four paired opisthosomal lateral lobes (arrows); *B*, ventral, showing truncated opisthosomal tip (arrow), box delimits area of image *C*; *C*, venter detail, showing median apodemes (arrows), box delimits area of image *D*; *D*, venter detail, showing (medially fused) paired apodeme; *E*, posterior dorsum; *F*, dorsum detail, with two sigillae (arrows). Scale bars = 100 μm, except *A* = 1 mm.

apodemes and sigillae (Fig. 22*B–D*). Folium with numerous orange-brown fields on white (Figs 25–26*A*). Lateral opisthosoma with dorso-ventral longitudinal brown bands and small sclerotisations. Venter in live animal bright orange with a central black spot (Fig. 26*B*); venter in alcohol white and grey, with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets, and with a central grey area. Five pairs of central sclerotisations, and numerous rows of lateral sclerotisations present on venter. Book lung covers and the sclerotisation around the spiracles red, as are the epigynum and the sclerotised area anterior to it.

Epigynum as diagnosed (Figs 18*C–D*, 22*E–F*). Oval epigynal chambers divided by a strong septum. Lateral chamber walls heavily sclerotised, thick, black. Inner epigynum as in Fig. 18*D*. Copulatory ducts wide and short, curved, fertilisation ducts thin.

Male (holotype, Fig. 18A–B, compare with Figs 23–24, 25A)

Total length 4.7.

Prosoma (Fig. 23, 25*A*) 2.5 long, 1.9 wide, 1.4 high; light orange (bright orange in live animal, Fig. 25*A*). Sternum 1.0 long, 1.0 wide. AME diameter 0.19, ALE 0.09, PME 0.09, PLE 0.11.

Appendages (Figs 23*C–D*, *F*, 25*A*) dark orange. Leg I length unknown.

Opisthosoma (Figs 24, 25*A*) 2.6 long, 2.0 wide, 1.1 high. Scutum whitish (but, orange in live animal, Fig. 25*A*). Venter grey, lateral abdomen dark grey. Two paired white dots present lateral to the spinnerets.

Pedipalp as diagnosed (Fig. 18*A–B*). Conspicuous tegular apophysis and large embolic conductor present. Embolic conductor proximally wide and membranous, distally thin, sclerotised, with a ridged edge and a conspicuous subdistal prong.

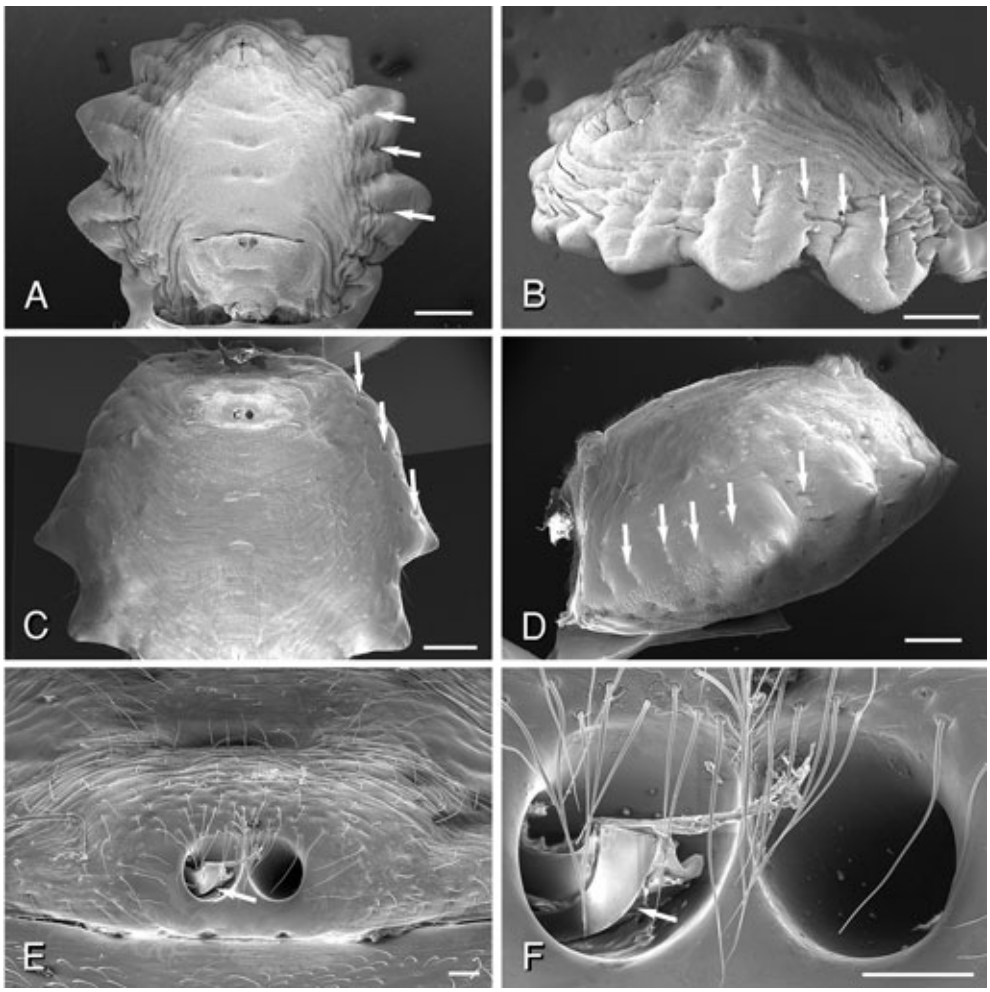

Fig. 10. *Herennia multipuncta*, female opisthosoma, from Sri Lanka (*A–B*, he8/f5; *C–F*, he8/f4): *A–B*, flat opisthosoma (he8/f5) showing extensive rows of lateral sclerotisations (arrows); *A*, ventral; *B*, lateral; *C–D*, round opisthosoma (he8/f4) showing less conspicuous rows of lateral sclerotisations (arrows); *C*, ventral; *D*, lateral; *E–F*, epigynum, ventral, with embolic conductor (arrow) stuck in copulatory opening. Scale bars *A–D* = 1 mm, *E–F* = 100 μm.

Variation

Females: prosoma length ranges from 4.9 to 6.1; total length from 12.4 to 15.8 (n = 10). Cheliceral formula 3/4/23 or 3/5/30 (n = 2). *Males*: prosoma length ranges from 2.0 to 2.5; total length from 3.7 to 4.7 (n = 2). Live males are bright orange (Fig. 25*A*), whereas preserved ones in alcohol are yellow to grey.

Distribution

Java (Indonesia) (Fig 32).

Natural history

Found on trees in primary forest (Kaliurang) as well as parks (Cibodas and Bogor). See Biology.

Etymology

Named after Herennia Etruscilla (3rd century AD), wife of the Roman emperor Trajan Decius, and mother of Roman emperors Herennius Etruscus and Hostilian. Old Roman coins with the portrait of Herennia Etruscilla may have been the source of the generic name derivation (see Etymology of *Herennia*). The species epithet is a noun in apposition.

Herennia gagamba, sp. nov.

(Fig. 27*C–D*)

Herennia sp. Hormiga *et al*., 1995: 334, fig. 11G–J (female genitalic illustrations).

Material examined

Holotype. Female (he54/f2 USNM) from Philippines: Luzon; Nueva Vizcaya. Imugan. Sta. Fe, Smooth-barked tree, farmland. 31.v.1987 (coll. CK Starr). The approximate coordinates of the type locality are 16°12′N 120°51′E.

Paratypes. 25 females (he54/f1, USNM) from the same sample as above.

Additional material examined. **Philippines:** Luzon, Laguna Prov., Los Banos, 14°11′N, 121°10′E, 18.ii.1945 (coll. B Malkin) — he127/f1

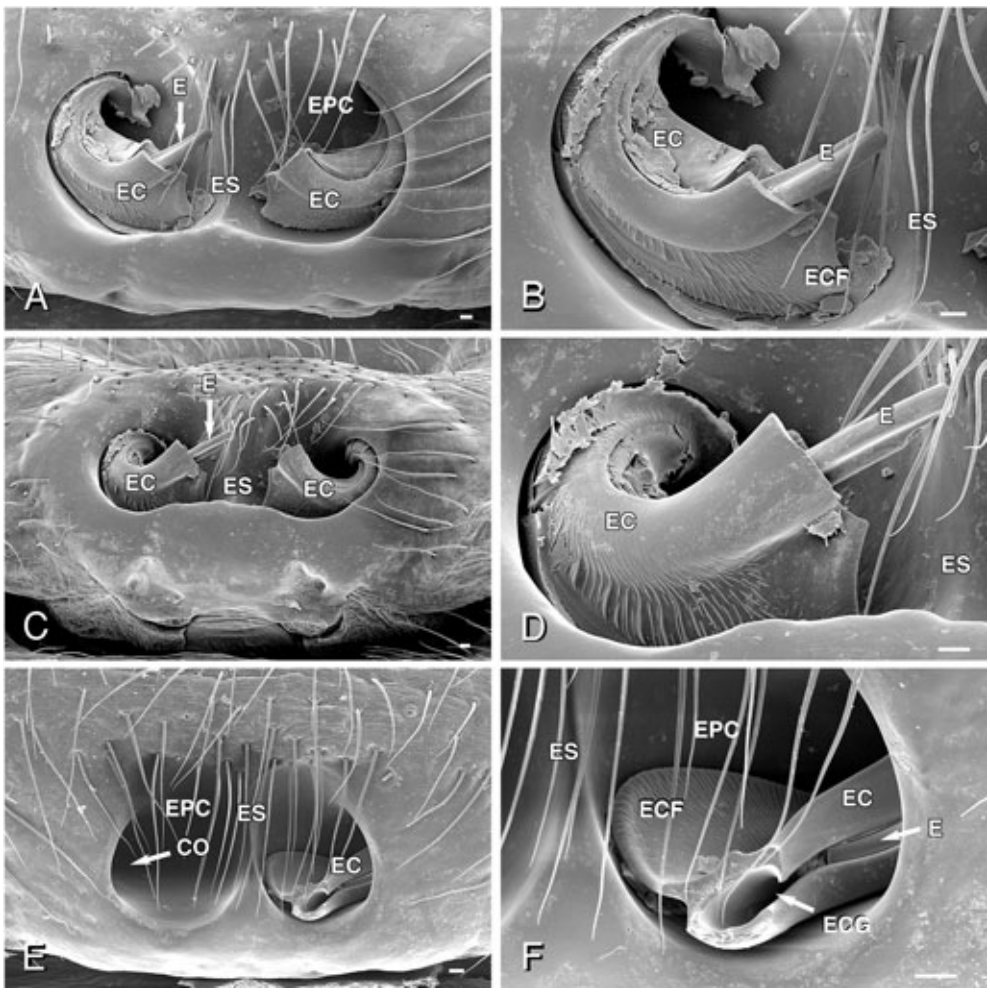

Fig. 11. *Herennia multipuncta*, female epigyna and male EC plugs: *A–D*, from Singapore (he6/f1); *A*, ventral; *B*, same, right epigynal chamber detail; *C*, posterior; *D*, same, right epigynal chamber detail; *E–F*, from Sri Lanka (he8/f5); *E*, ventral; *F*, same, left epigynal chamber detail. Scale bars = 20 μm.

(♀ AMNH), he127/m1 (♂ AMNH); Nueva Vizcaya. Imugan. Sta. Fe, 16°12′N, 120°51′E, smooth barked tree, farmland, 31.v.1987 (coll. CK Starr) —he055/f1 (♀ USNM); [Luzon], Laguna [de Bay], Mt. Makiling, above Los Banos, 14°8′9’N, 121°11′24’E, 1984 (coll. CK Starr) — he128/f1 (♀ AMNH); 10.iii.1985 (coll. CK Starr) — he129/f1 (♀ AMNH).

Diagnosis

Females differ from all other *Herennia* species by the longer than wide sternum and from all species, except *H. tone* and *H. agnarssoni*, by a group of long conspicuous spines prolaterally on femur I (Fig. 27*C*). They can be easily distinguished from *H. tone* and *H. agnarssoni* by the epigynum shape (Fig. 27*D*), which is round, has a strong septum and medially positioned copulatory openings. Although the epigynum shape of *Herennia gagamba* (Fig. 27*D*) resembles that of *H. deelemanae*, the copulatory openings are positioned medially and not laterally, and the septum is very pronounced, in the shape of an inverted letter ‘T’.

Description

Female (paratype, he54/f1)

Total length 13.6.

Prosoma as in *H. multipuncta*, but relatively longer and narrower (Fig. 27*C*): 5.6 long, 4.4 wide, 2.5 high. Sternum 2.1 long, 2.0 wide; orange, with medially protruding white subcutaneous pigment. Maxillae and labium red-brown. Cheliceral formula 3/3/18 and 3/4/15. Anterior eye row recurved, posterior straight. PLE size 0.16, PME 0.16.

Appendages (Fig. 27*C*). femora and tibiae yellow, other leg joints brown. Femoral spines short, except the diagnostic prolateral group of long spines on first femur. Leg I length 21.3 (Fe 6.4, Pa 1.6, Ti 4.9, Me 6.5, Ta 1.9). Sustentaculum present, hidden among other setae.

Opisthosoma (Fig. 27*C*) oblong, slightly flattened dorsoventrally with inconspicuous lateral lobes; 9.3 long, 6.8 wide (maximum width over abdominal lobes), 5.6 high. Dorsum white with numerous sigillae, covered with sparse but strong spines, especially posteriorly. Lateral opisthosoma with

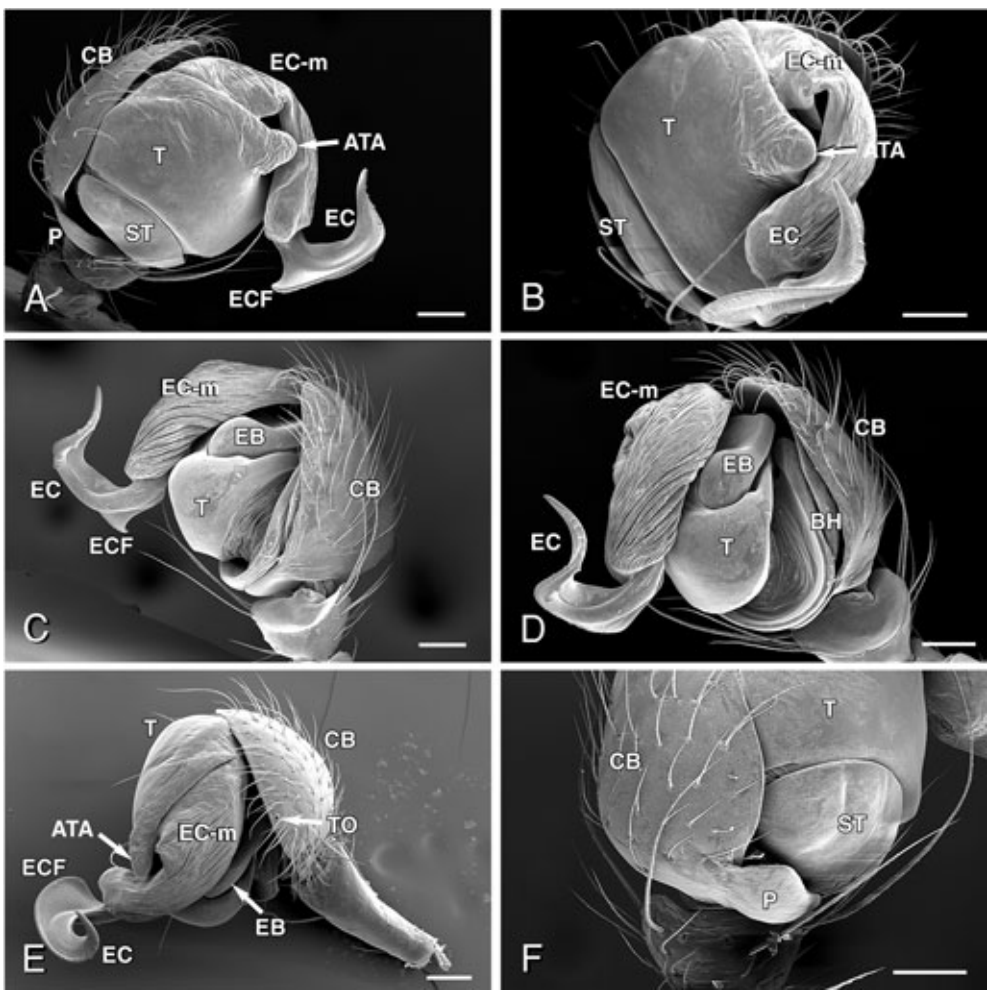

Fig. 12. *Herennia multipuncta*, male right pedipalp, from India (he14/m1): *A*, ectal; *B*, ecto-apical; *C*, mesal; *D*, meso-apical; *E*, dorso-apical; *F*, bulb detail, dorso-ectal. Scale bars = 100 μm.

small sclerotisations. Venter white with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets. Four pairs of central sclerotisations and conspicuous lateral sclerotisations in many rows. Spinnerets of the typical nephiline condition.

Epigynum (Fig. 27*D*) as diagnosed.

Male

The only known male (he127/m1) lacks both pedipalps. Male pedipalp known only by epigynal plugs consisting of EC and embolus, found stuck in female copulatory openings (Fig. 27*D*); this also illustrated in Hormiga *et al*. (1995: fig. 11G–J). EC is distally massive with a subdistal flap resembling that of *H. deelemanae*.

Variation

Females: prosoma length ranges from 5.1 to 5.8; total length from 10.4 to 15.5 (n = 26). Cheliceral formula varies within the same individual (see above). Opisthosoma almost unlobed (Fig. 27*C*) to lobed. Spines on dorsum are very pronounced in some females, and less in others, but are consistently present.

Distribution

Luzon (Philippines) (Fig. 32).

Natural history

Unknown. The collection label (see above) implies the spiders were collected from tree bark.

Etymology

The species epithet, a noun in apposition, is a Tagalog word for a spider.

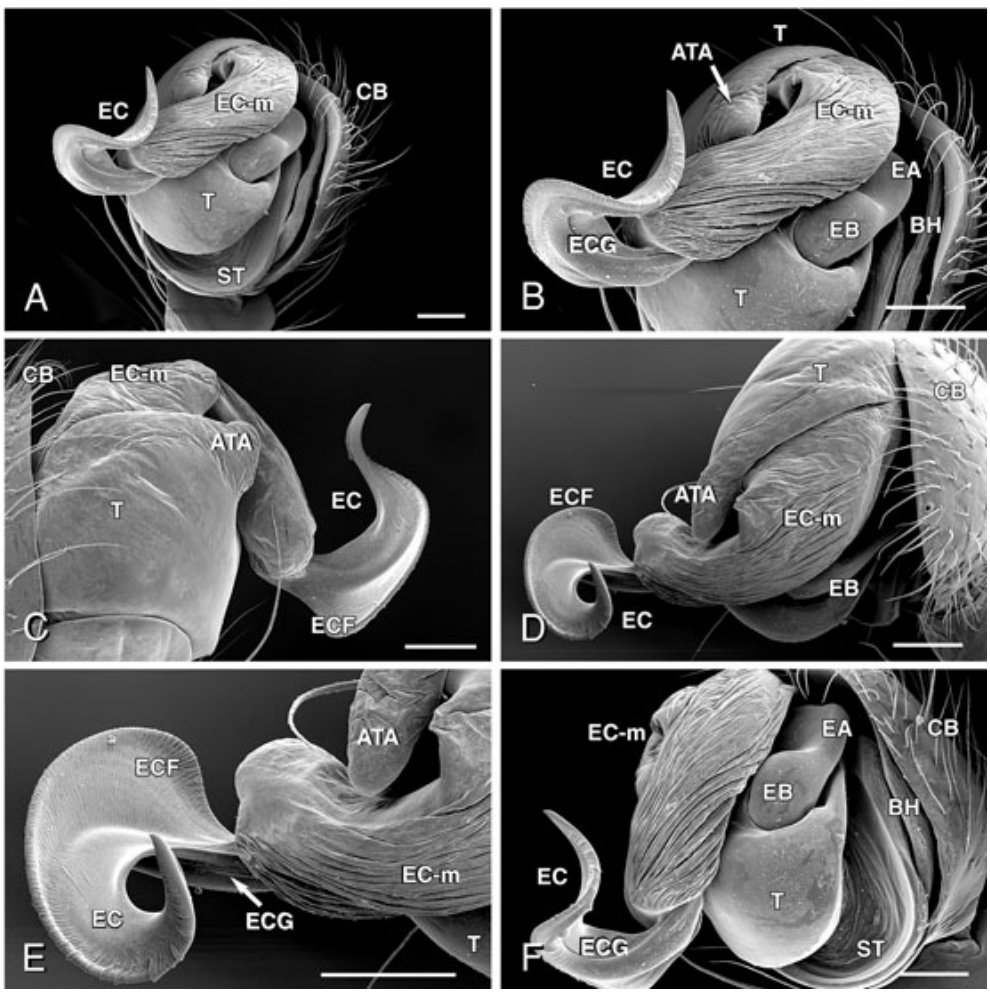

Fig. 13. *Herennia multipuncta*, male right pedipalp distal sclerites, from India (he14/m1): *A–B*, apical; *C*, ectal; *D–E*, dorso-apical; *F*, meso-apical. Membranous part of embolic conductor (EC-m) is continuous with the sclerotised part (EC), both attached to embolus base (EB) and tegulum (T) via membrane (compare with Fig. 4*C*). Scale bars = 100 μm.

Herennia jernej, sp. nov.

(Fig. 27*E*)

Material examined

Holotype. Female (he19/f1 CAS) from Indonesia: 'Sumatera Barat; Mangani, mine near Kota Tinggi. 700m. 20 July 1983 Edward S. Ross'. The approximate coordinates of the type locality on Sumatra are 00°02′S 100°20′E.

Paratypes. Two immature specimens (he20–21 CAS) from the same sample as above.

Additional material examined. None.

Diagnosis

Holotype differs from all *Herennia* species but *H. multipuncta, H. gagamba* and *H. sonja* by the carapace with a central yellow V-shaped mark. Epigynum (Fig. 27*E*) differs from *H. multipuncta, H. gagamba* and *H. sonja* by the oval chambers, strong septum, and a fairly thin posterior sclerotised edge. Leg formula (1, 2 = 4, 3) appears to be unique in *Herennia*. Male unknown.

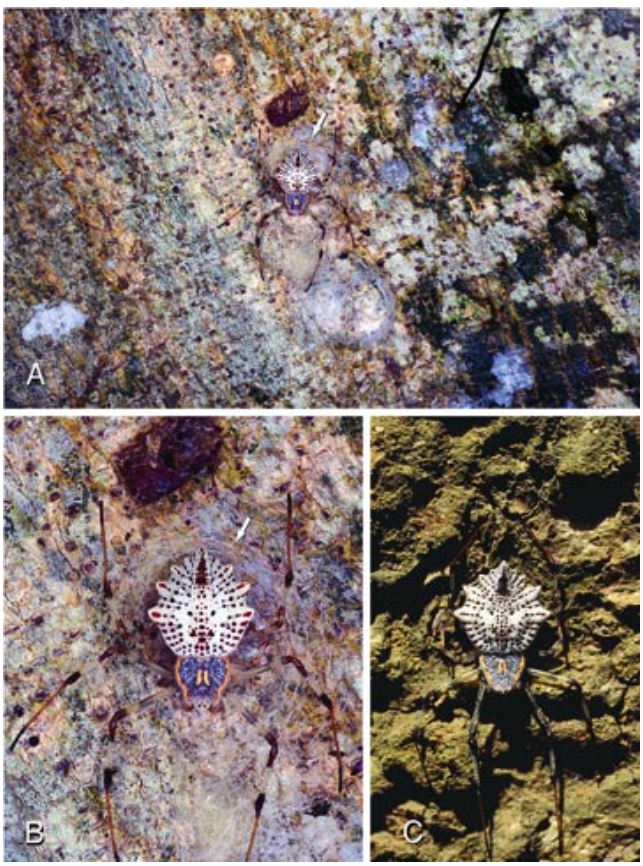

Fig. 14. *Herennia multipuncta*, photographs of live spiders from Sri Lanka: *A–B*, female in her web built tightly against tree trunk, resting at hub in the shape of a depression ('hub-cup', arrow); *C*, female on a mud wall. Note diagnostic yellow V-shaped mark on carapace and white and spotted dorsum.

Description

Female (holotype, Fig. 27E)

Total length 10.3.

Prosoma 5.2 long, 4.8 wide, 2.8 high. Sternum 2.0 long, 2.4 wide. Prosoma as described in *H. multipuncta* except pale colouration (almost white). Cheliceral formula 3/4/30. AME diameter 0.23, ALE 0.16, PME 0.14, PLE 0.13. AME separation 0.32, PME separation 0.38, PME–PLE separation 0.45, AME–ALE separation 0.28, AME–PME separation 0.38, ALE–PLE separation 0.19. Clypeus height 0.40.

Appendages. Leg I length 21.3 (Fe 6.2, Pa 1.4, Ti 4.9, Me 6.9, Ta 1.9). Femora with long spines.

Opisthosoma as described in *H. multipuncta*, but longer than wide and white, 6.2 long, 5.1 wide (maximum width over abdominal lobes), 3.5 high.

Epigynum as diagnosed (Fig. 27*E*).

Male

Unknown.

Distribution

Only known from the type locality on the Indonesian island of Sumatra (Fig. 32).

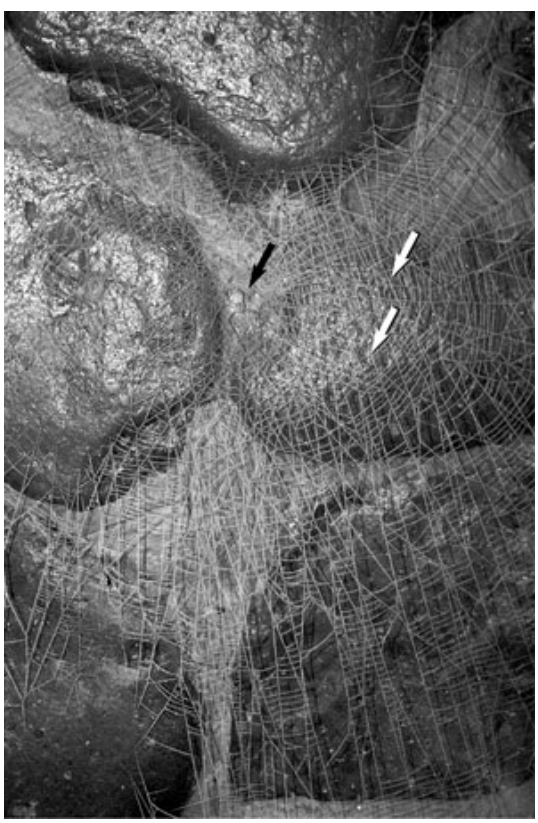

Fig. 15. *Herennia multipuncta*, photograph of a female in her web, from Thailand (by G. Hormiga). Note 'pseudoradii' (white arrows), which do not pass the hub (black arrow).

Natural history

Unknown.

Etymology

The species epithet (pronounced 'yer-ney'), a noun in apposition, is a patronym after my brother, Jernej Kuntner.

Herennia milleri, sp. nov.

(Fig. 16*D–G*)

Material examined

Holotype. Female (he113/f1 ZMUC) from Papua New Guinea: Bismarck Isl., New Britain, Yalom 1000 m, 10 May 1962, Noona Dan Exp. 61–62. The locality is approximately at 4°25′S 151°44′E.

Paratype. Female (he126/f1 AMNH) from **Papua New Guinea:** Louisiade Arch., Rossel Island, Abaleti, SSW of Mt. Rossel, 11°21′S, 154°10′E, 0–50, Camp #12 (Fifth Archbold Exped. to New Guinea: Papau [sic], 1956 (coll. LJ Brass).

Additional material examined. None.

Diagnosis

Females diagnosed as *H. papuana* except in having posterior lateral eyes larger than posterior median eyes. Male embolic conductor (known only from the broken organ in holotype epigynum, Fig. 16*G*) has a subdistal prong (unlike *H. papuana*), which is longer than in *H. etruscilla* and *H. oz*.

Description

Female (holotype, Fig. 16D–G)

Total length 12.4. Somatic and external genital morphology as described in *H. papuana* but opisthosoma flatter.

Prosoma (Fig. 16*D–E*) 5.6 long, 4.7 wide, 3.1 high. Cheliceral formula 3/4/30. Sternum 2.1 long, 2.3 wide, bright orange. PLE size 0.16, PME 0.13 (PLE larger than PME).

Appendages (Fig. 16*F*) as in *H. papuana*. Leg I length 23.9 (Fe 6.9, Pa 1.7, Ti 5.6, Me 7.8, Ta 1.9). Sustentaculum apparently absent.

Opisthosoma (Fig. 16*D–E*) flattened dorso-ventrally with four pairs of inconspicuous lateral lobes, truncated posteriorly; 7.4 long, 5.5 wide (maximum width over abdominal lobes), 3.7 high.

Epigynum (Fig. 16*G*) as in *H. papuana*.

Male

Unknown, except for EC (see Diagnosis).

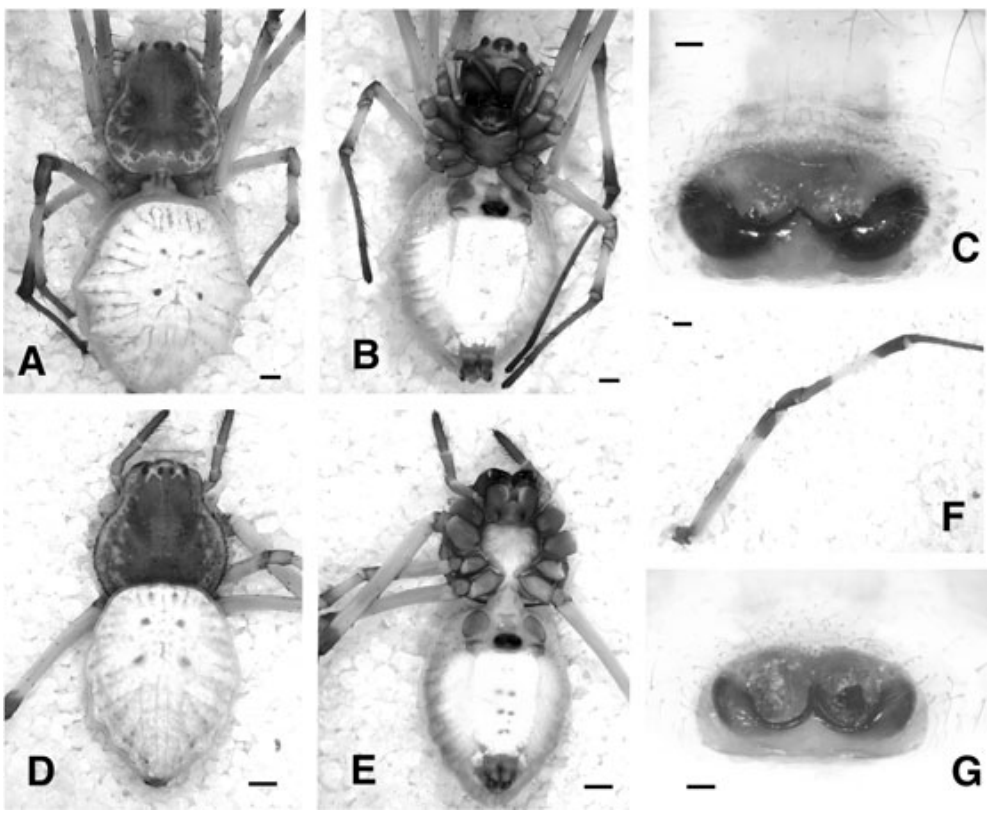

Fig. 16. *Herennia agnarssoni*, sp. nov., female holotype from Solomon Islands (*A–C*) and *Herennia milleri*, sp. nov., female holotype from New Britain (*D–G*): *A*, dorsal, note diagnostic long spines on first femur; *B*, ventral; *C*, epigynum, ventral; *D*, dorsal; *E*, ventral; *F*, first femur prolateral (note absence of long spines); *G*, epigynum, ventral. Scale bars *A–B*, *D–F* = 1.0 mm, *C*, *G* = 0.1 mm.

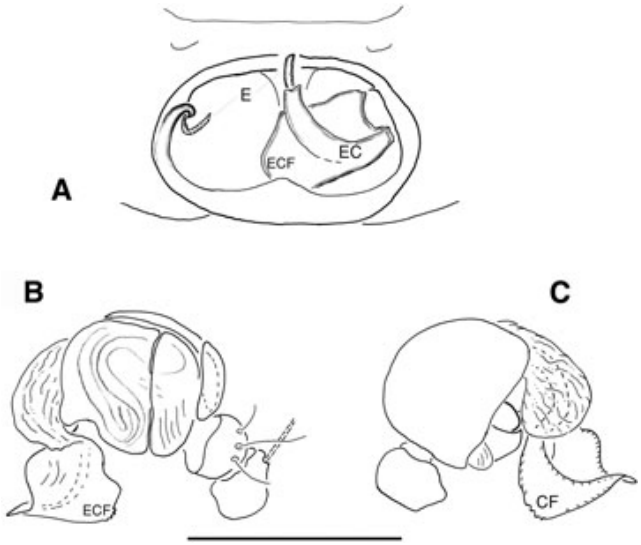

Fig. 17. *Herennia deelemanae*, sp. nov., female paratype and male holotype, from Sabah, Malaysian Borneo: *A*, epigynum, ventral (note EC with extensive flap in one copulatory opening and only embolus in the other); *B*, male left pedipalp, ectal; *C*, same, mesal (note extensive EC flap used as evidence for conspecificity of sexes, each known from one individual). Scale bar = 0.5 mm.

Distribution

New Britain and Rossel Island (Papua New Guinea) (Fig. 32).

Natural history

Unknown.

Etymology

The species epithet is a patronym after my laboratory mate, Jeremy Miller.

Herennia oz, sp. nov.

(Fig. 28)

H. sp. Davies, 1988: fig. 18 (in part), illustration of female habitus and epigynum.

Material examined

Holotype. Female (he22/f1 QM) from Australia: Northern Territory: East Alligator River, 12°25′S, 132°58′E, 16–18 July 1979 '(RF), G. Monteith & D. Cook' with additional label 'Drawn 1985 SR. Monteith'.

Paratype. Female (he23/f1 QM) from **Australia:** Northern Territory: West Alligator River, mouth, 12°12′S, 132°13′E, 'WA1, 22–24 July 1979 (OF), G. Monteith & D. Cook'.

Additional material examined. **Australia:** Northern Territory: Edge Arhemland Res., Ben Hole Billabong, 120 mi SE Darwin, 13°57′S, 131°57′E, ii.1972 (coll. J Anderson) — ne123/f1 (♀ AMNH), ne124/f1 (♀ AMNH), ne125/f1 (♀ AMNH).

Diagnosis

Females diagnosed as *H. etruscilla*, but differ from it by the smaller epigynum with narrower lateral sclerotisation (Fig. 28*B–C*) and by the more oblong opisthosoma. Males unknown, except an embolic conductor in epigynum (Fig. 28*B*), which has a flap in the shape of a prong (compare *H. etruscilla*).

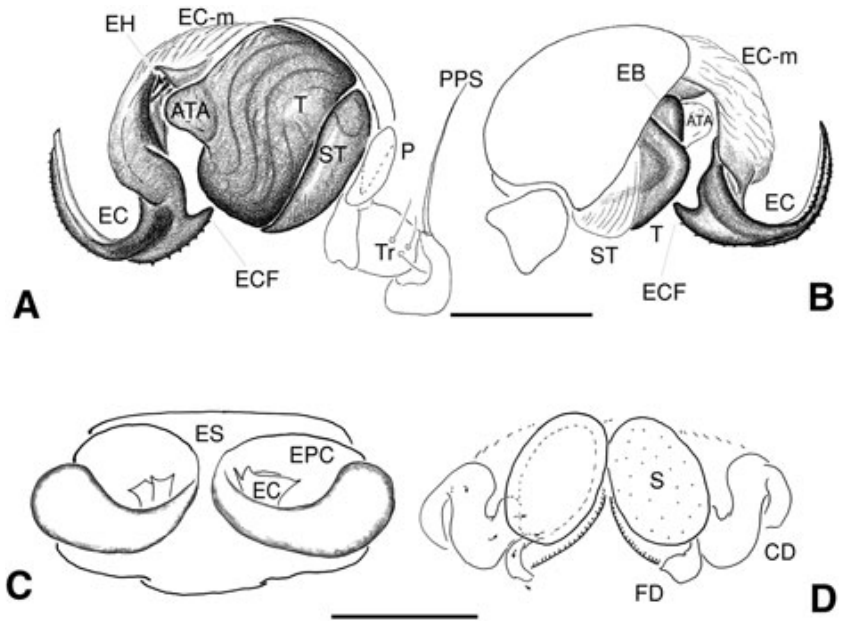

Fig. 18. *Herennia etruscilla*, sp. nov. *A*, *B*, Male pedipalp, from Java (holotype): *A*, ectal; *B*, mesal. *C*, *D*, Female epigynum, from Java (he53): *C*, ventral; *D*, dorsal, cleared. Scale bars = 0.5 mm.

Description

Female (holotype, Fig. 28A–B, compare with 28C)

Total length 11.6.

Prosoma (Fig. 28*A*) as described in *H. etruscilla*, but with less warty carapace and with less rounded edges, 5.6 long, 4.6 wide, 2.1 high. Cheliceral formula 3/4/13. Sternum 2.0 long, 2.3 wide, orange with protruding white pigment. PLE size 0.18, PME 0.16 (PLE larger than PME).

Appendages yellow, tarsi brown. Femora with numerous short spines. Leg I length 22.0 (Fe 6.2, Pa 1.6, Ti 5.6, Me 6.6, Ta 2.0). Sustentaculum conspicuous.

Opisthosoma (Fig. 28*A*) flattened dorso-ventrally with four pairs of conspicuous lateral lobes, truncated posteriorly; 7.1 long, 6.5 wide (maximum width over abdominal lobes), 2.6 high. Dorsum white with numerous sigillae. Venter white with a distinct broad median band of white pigment connecting with white pigment patches around spinnerets. Four pairs of central sclerotisations and inconspicuous lateral sclerotisations.

Epigynum (Fig. 28*B*, compare with 28*C*) as diagnosed. Epigynal septum strong, chambers oval, copulatory openings lateral. Inner epigynal anatomy as in *H. etruscilla*.

Male

Unknown, except the EC (see Diagnosis).

Variation

Females: prosoma length ranges from 5.6 to 5.8; total length from 11.6 to 13.6 (n = 2). Cheliceral formula 3/3/12 (paratype) or 3/4/13 (holotype).

Distribution

Australia's Northern Territory (Fig. 32).

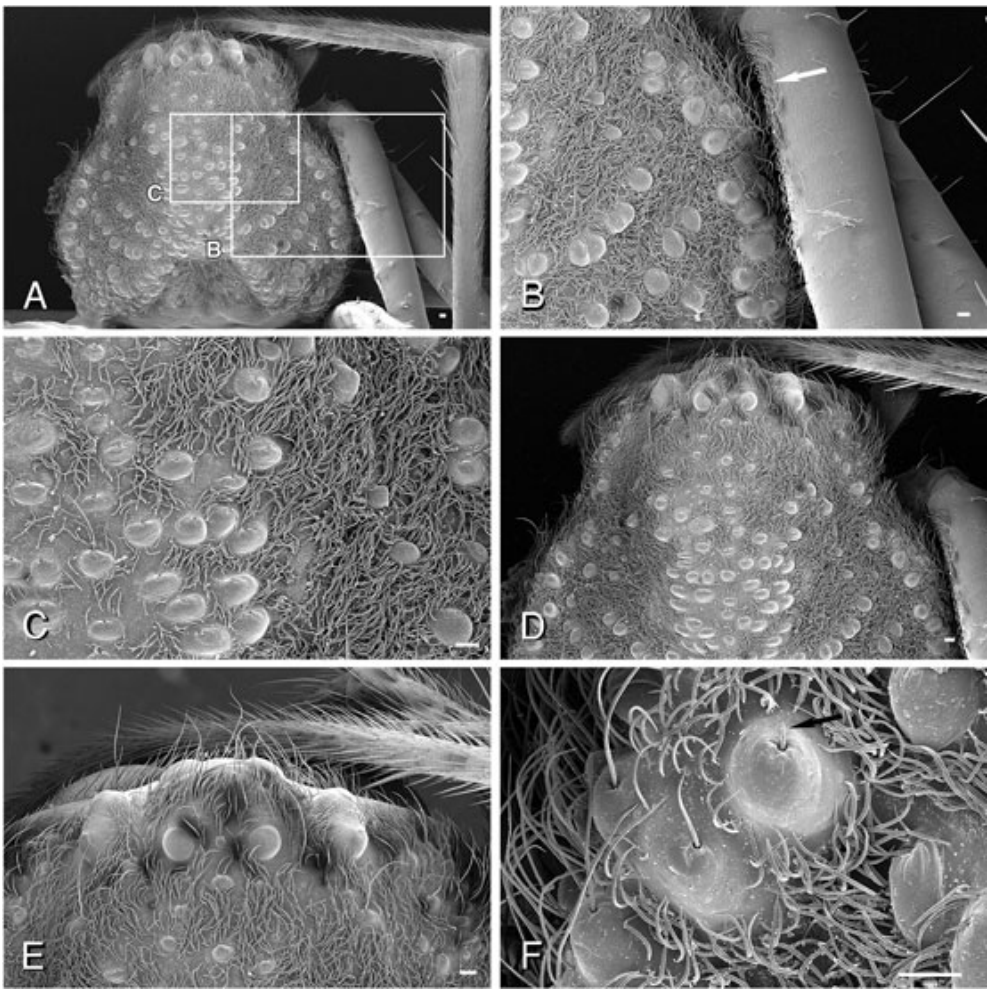

Fig. 19. *Herennia etruscilla*, sp. nov., female prosoma, from Java (paratype he52/f1): *A*, dorsal, boxes delimiting areas of images *B* and *C*; *B*, lateral carapace detail, note warty cuticle, dense and thin setae prolaterally on first femur (arrow); *C*, head region detail with warts and hair-like setae; *D*, head region; *E*, eye region; *F*, thoracic region detail (note seta (arrow) on top of wart surrounded by hair-like setae). Scale bars = 100 μm.

Natural history

Unknown.

Etymology

Named after a nickname for Australia, Oz; the species epithet is a noun in apposition.

Herennia papuana Thorell

(Figs 29–30)

Herennia papuana Thorell, 1881: 77, description of female (from New Guinea).

H. ornatissima Chrysanthus, 1971: 41, figs 85–86, description of female, **misidentification**.

H. sp. Davies, 1988: fig. 18 (in part), illustration of damaged male pedipalp, also in Hormiga *et al*., 1995: fig. 5J.

Material examined

Type material. Not found.

Additional material examined. **Papua New Guinea:** 'Pindiu, Territory New Guinea', 6°26′S, 147°30′E, 18.vi.1964 (coll. R Zweifel) — he135/f1 (2♀ AMNH); New Guinea, Regensberg, 12.v.1919 (coll. Buergers) — he082/f1 (♀ ZMB); Morobe Prov, Wau Ecology Institute grounds, 7°20′S, 146°43′E, tree trunks, shrubs, litter, 2.xi.1980 (coll. WA Shear) — he133/f1 (♀ AMNH); 11.xi.1980 (coll. WA Shear) — he134/f1 (♀ AMNH), he134/m1 (♂ AMNH); Morobe Province, Wau, 7°20′S, 146°43′E, 6.iii.1979 (coll. Levi, Lubin, Robinson) — he025/f1 (2♀ MCZ); Jul 1979 (coll. M Robinson) — he024/m1 (5♂ MCZ); roadside, 19.iii.1979 (coll. H. Levi) — he050/f1 (♀ MCZ), he050/m1 (♂ MCZ).

Diagnosis

Females differ from *H. multipuncta*, *H. sonja, H. jernej* and *H. gagamba* by the dark red carapace lacking yellow V-shaped mark (Fig. 29*A*), with many conspicuous warts, each bearing a short black hook on top and by the epigynum (Fig. 29*C*) with oval chambers, strong septum, and lateral

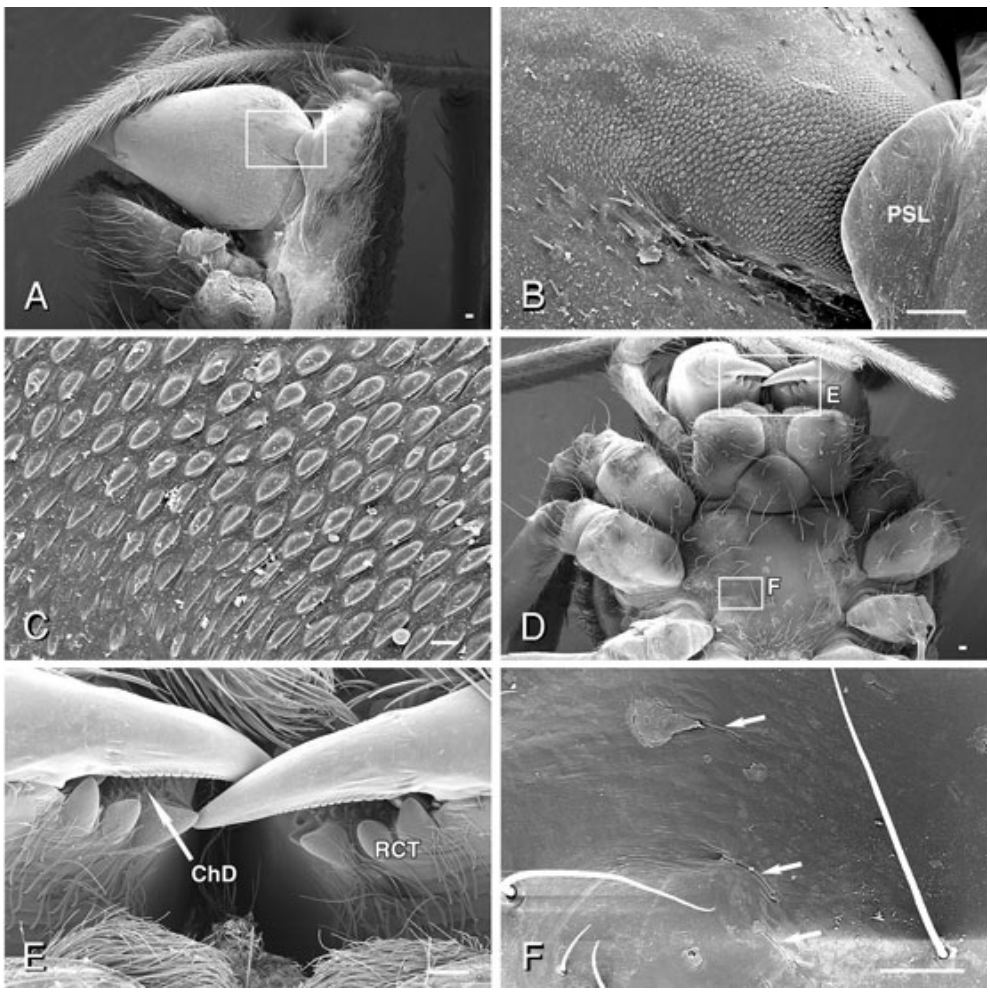

Fig. 20. *Herennia etruscilla*, sp. nov., female prosoma, from Java (paratype he52/f1): *A*, lateral, box delimits area of image *B*; *B*, cheliceral boss; *C*, cheliceral boss detail; *D*, ventral, boxes delimiting areas of images *E* and *F*; *E*, chelicerae, ventral; *F*, detail of sternum with slit sensilla (arrows). Scale bars = 100 μm, except *C* = 10 μm.

copulatory openings. They can be distinguished from *H. etruscilla*, *H. oz, H. tone* and *H. deelemanae* by an oblong abdomen with inconspicuous lobes (Fig. 29*A–B*), and by the lateral epigynal chamber sclerotisation, which reaches high to the anterior epigynal rim (Fig. 29*C*). They differ from *H. agnarssoni* and *H. milleri* by the stronger epigynal septum (Fig. 29*C*). Males differ from all other *Herennia* species with known males by the long and thin distal EC, which lacks a flap or prong (Fig. 30*A–B*).

Description

Female (he25/f1 from Papua New Guinea, Fig. 29)

Total length 13.6.

Prosoma (Fig. 29*A*) 4.9 long, 4.4 wide, 2.5 high. Carapace red medially and orange laterally. Chelicerae red-brown. Cheliceral formula 3/3/25. Sternum 2.0 long, 2.2 wide; orange, with medially protruding white subcutaneous pigment. Maxillae and labium red-brown. Anterior eye row recurved, posterior straight. AME diameter 0.28, ALE 0.17, PME 0.14, PLE 0.14. AME separation 0.22, PME separation 0.35, PME–PLE separation 0.47, AME–ALE separation 0.25, AME–PME separation 0.25, ALE–PLE separation 0.13. Clypeus height 0.28.

Appendages. Femora and tibiae yellow, other leg joints brown. Femoral spines fairly sparse and short. Leg I length 20.4 (Fe 5.7, Pa 1.5, Ti 4.9, Me 6.4, Ta 1.9). Sustentaculum apparently absent.

Opisthosoma (Fig. 29*A–B*) barely flattened dorso-ventrally with three pairs of inconspicuous lateral lobes, truncated posteriorly; 8.1 long, 5.7 wide (maximum width over abdominal lobes), 4.8 high. Dorsum white with numerous little sclerotised brown dots. Lateral opisthosoma with longitudinal dorso-ventral brown bands and small sclerotisations. Venter white and grey, with a distinct broad median band of white pigment connecting with white pigment

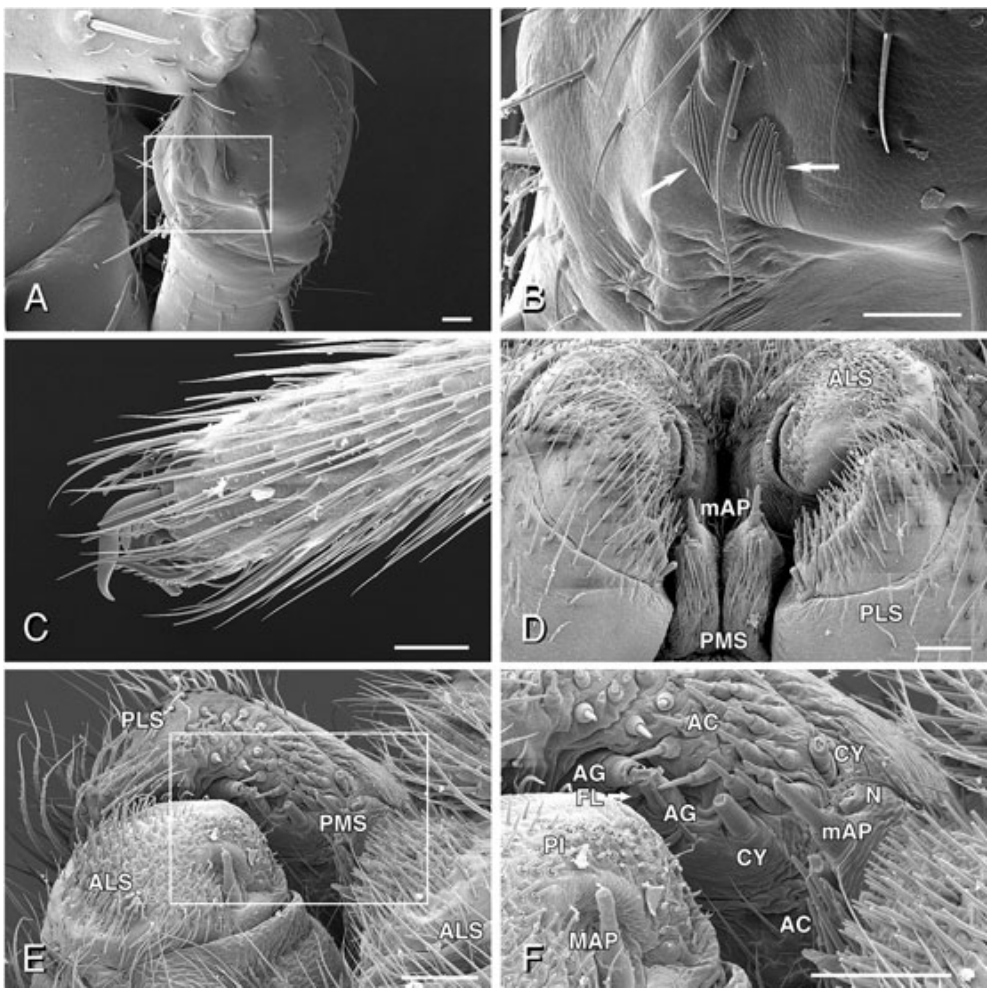

Fig. 21. *Herennia etruscilla*, sp. nov., female, from Java (paratype he52/f1): *A*, fourth tibia, prolateral, box delimits area of image *B*; *B*, same, detail, arrows pointing to paired lyriform organ; *C*, fourth tarsus, with apparent absence of sustentaculum; *D*, spinnerets, apical; *E*, same, lateral, box delimits area of image *F*; *F*, detail of spinnerets. Scale bars = 100 μm.

patches around spinnerets and with a central grey area. Four pairs of central sclerotisations, and a single row of inconspicuous lateral sclerotisations present on venter. Book lung covers and the sclerotisation around the spiracles red, as are the epigynum and the sclerotised area anterior to it.

Epigynum as diagnosed (Fig. 29*C*). Oval epigynal chambers divided by a strong septum. Lateral chamber walls heavily sclerotised, black.

Male (he24/m1 from Papua New Guinea, Fig. 30)

Total length 3.5.

Prosoma 2.0 long, 1.6 wide, 1.1 high; dark orange. Sternum 0.9 long, 0.8 wide; orange, with wide dark lateral edges. AME diameter 0.15, ALE 0.09, PME 0.08, PLE 0.09. AME separation 0.11, PME separation 0.16, PME–PLE separation 0.13, AME–ALE separation 0.07, AME–PME separation 0.16, ALE–PLE separation 0.03. Clypeus height 0.13.

Appendages dark orange. Leg I length 8.0 (Fe 2.2, Pa 0.6, Ti 1.9, Me 2.3, Ta 1.0).

Opisthosoma 2.1 long, 1.6 wide, 1.0 high. Scutum light orange, caudally black. Venter grey, lateral abdomen yellow and dark grey. Two paired white dots present lateral to the spinnerets.

Pedipalp as in Fig. 30 (see also Diagnosis). EC proximally wide and membranous, distally thin, sclerotised, and with a ridged edge, lacking a flap.

Variation

Females: prosoma length ranges from 4.9 to 5.6; total length from 11.5 to 13.6 ($n = 3$). *Males*: prosoma length ranges from 1.6 to 2.0; total length from 3.1 to 3.5 ($n = 5$). The intensity of colouration varies. Abdomen colour (in alcohol) ranges from whitish through orange to dark grey. Distal leg joints of some males are dark grey.

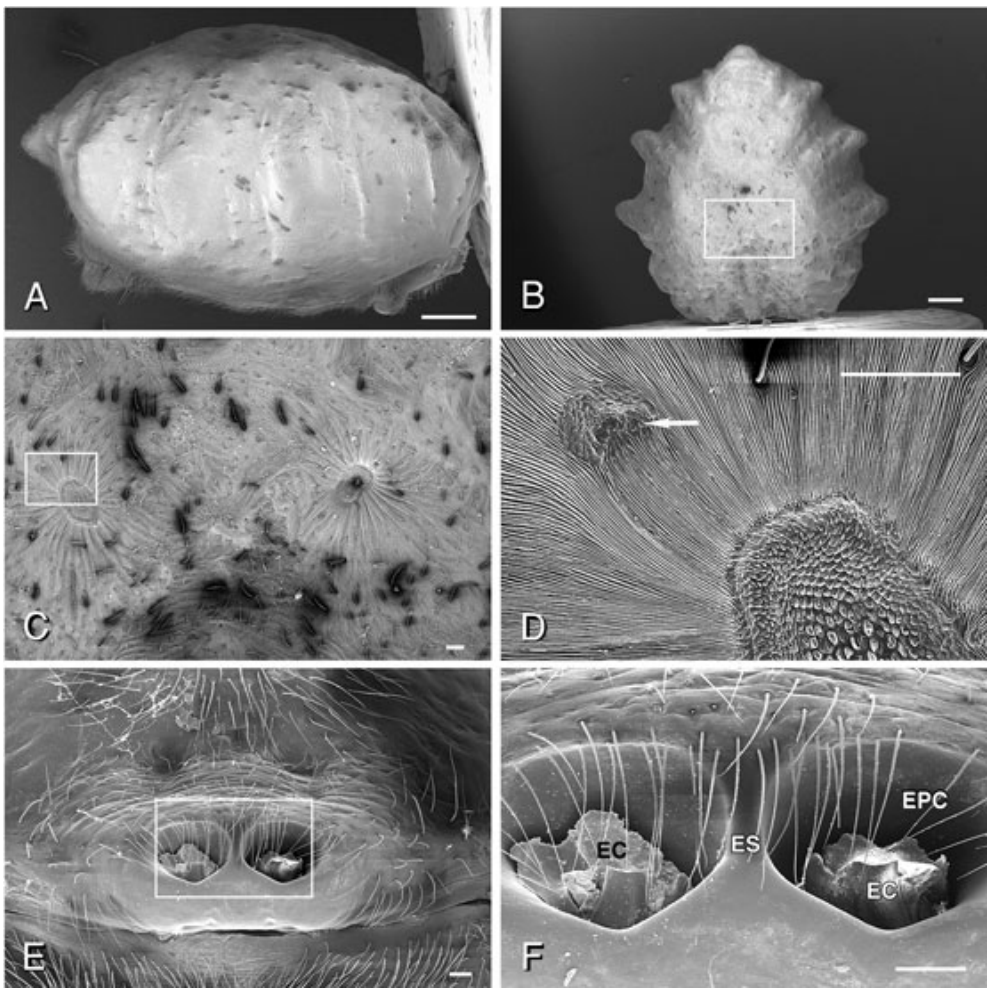

Fig. 22. *Herennia etruscilla*, sp. nov., female opisthosoma, from Java (paratype he52/f1): *A*, lateral; *B*, dorsal, box delimits area of image *C*; *C*, dorsum detail, box delimits area of image *D* (note large paired apodemes); *D*, detail of dorsal apodeme and another sclerotisation posterio-lateral to it (arrow); *E*, epigynum, ventral, box delimits area of image *F*; *F*, epigynum detail, note embolic conductors plugging copulatory openings. Scale bars = *A–B* = 1 mm, *C–F* = 100 μm.

Distribution

Papua New Guinea (Fig. 32).

Natural history

Summarised in Biology.

Taxonomic history

Based on a female from New Guinea, Thorell (1881: 77) described a new species, *Herennia papuana*. Thorell's three-page Latin description treats only two diagnostic characters; the warty prosoma and the epigynum, which is of a different form to *H. multipuncta*. I believe the type depository to be MCSNG, but the type has remained unavailable for my examination. As I only know of one species occurring in New Guinea, I fix the name *papuana* to that species.

Herennia sonja, sp. nov.

(Fig. 27*A–B*)

Material examined

Holotype. Female (he47/f1 USNM), from Indonesia: South Kalimantan, Loksado-Malaris villages, E of Kandagan. 250m Elev. 18 Nov 1996 (coll. Kuntner & Šereg). The approximate coordinates are 02°05′S 115°25′E.

Paratype. Female (he57/f1 USNM), from **Indonesia:** Propinsi Kalimantan Selatan, Aranio Dist., Belangian village and surroundings. 100m elev. 10–15 Nov 1996 (coll. Kuntner & Šereg). The approximate coordinates are 3°36′S, 115°4′E.

Additional material examined. **Indonesia:** Celebes [Sulawesi], Minahassa [peninsular], 1°0′N, 124°4′E (coll. Kunenethae) — he104/f1 (♀ BMNH).

Diagnosis

Females differ from all *Herennia* species but *H. multipuncta, H. gagamba* and *H. jernej* by the carapace with a central yellow V-shaped mark (Fig. 27*A*). Epigynum (Fig. 27*B*) differs from

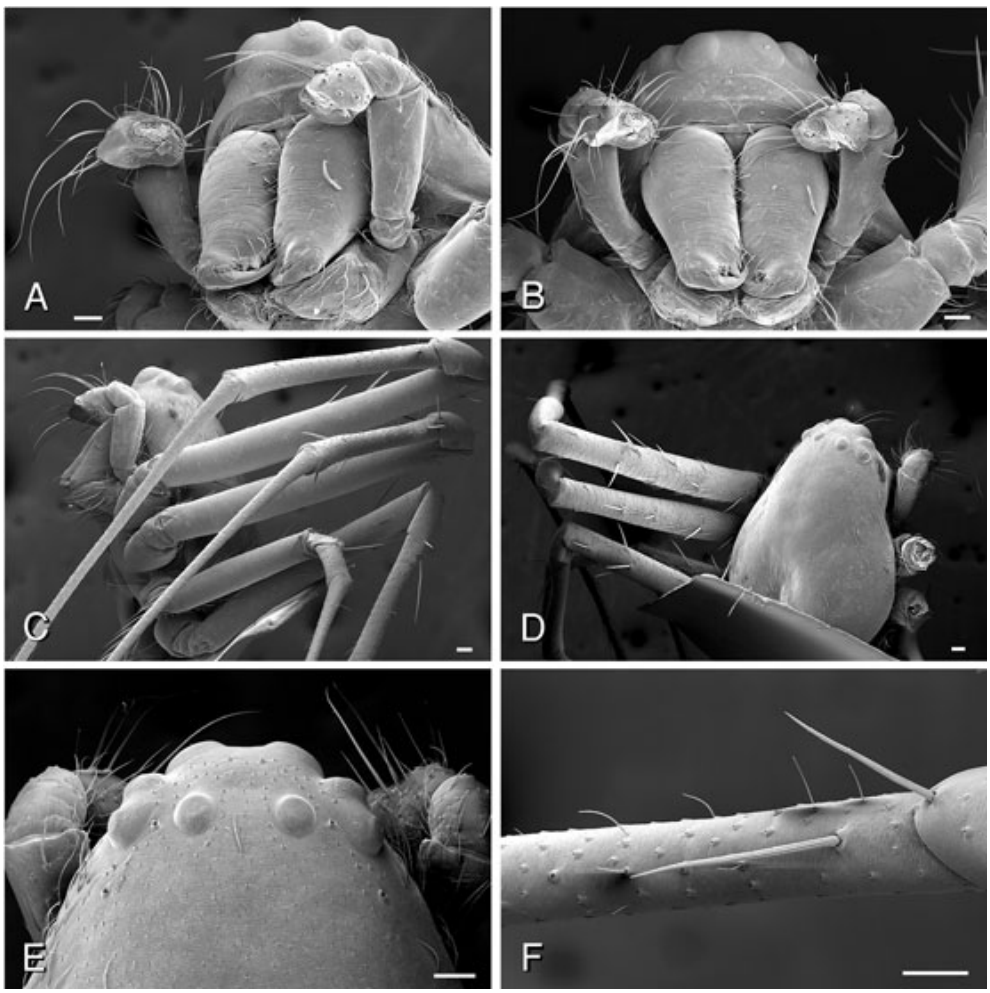

Fig. 23. *Herennia etruscilla*, sp. nov., male 'eunuch' prosoma (note both palpal bulbs lacking), from Java (he52/m1): *A*, prolateral; *B*, ventroapical; *C*, lateral; *D*, dorsolateral; E, head region, dorsal; *F*, second tibia, detail, ectal. Scale bars = 100 μm.

H. multipuncta, H. gagamba and *H. jernej* by the elongate chambers, thin septum and a thin posterior sclerotised edge.

Description

Female (holotype, Fig. 27A–B)

Total length 10.2. Prosoma, opisthosoma, and legs as described in *H. multipuncta*.

Prosoma (Fig. 27*A*) 4.4 long, 3.5 wide, 2.3 high. Sternum 1.4 long, 1.9 wide. AME diameter 0.25, ALE 0.16, PME 0.14, PLE 0.13. AME separation 0.22, PME separation 0.30, PME–PLE separation 0.38, AME–ALE separation 0.26, AME–PME separation 0.28, ALE–PLE separation 0.10. Clypeus height 0.32.

Appendages. Leg I length 19.5 (Fe 5.3, Pa 1.4, Ti 4.4, Me 6.5, Ta 1.9).

Opisthosoma (Fig. 27*A*) 5.8 long, 5.8 wide (maximum width over abdominal lobes), 2.9 high.

Epigynum as diagnosed (Fig. 27*B*).

Male

Unknown.

Distribution

Indonesia: Southern Kalimantan, Sulawesi (Fig. 32).

Natural history

Unknown.

Etymology

The species epithet (pronounced ‘son-ya’), a noun in apposition, is a patronym after my mother, Sonja Kuntner.

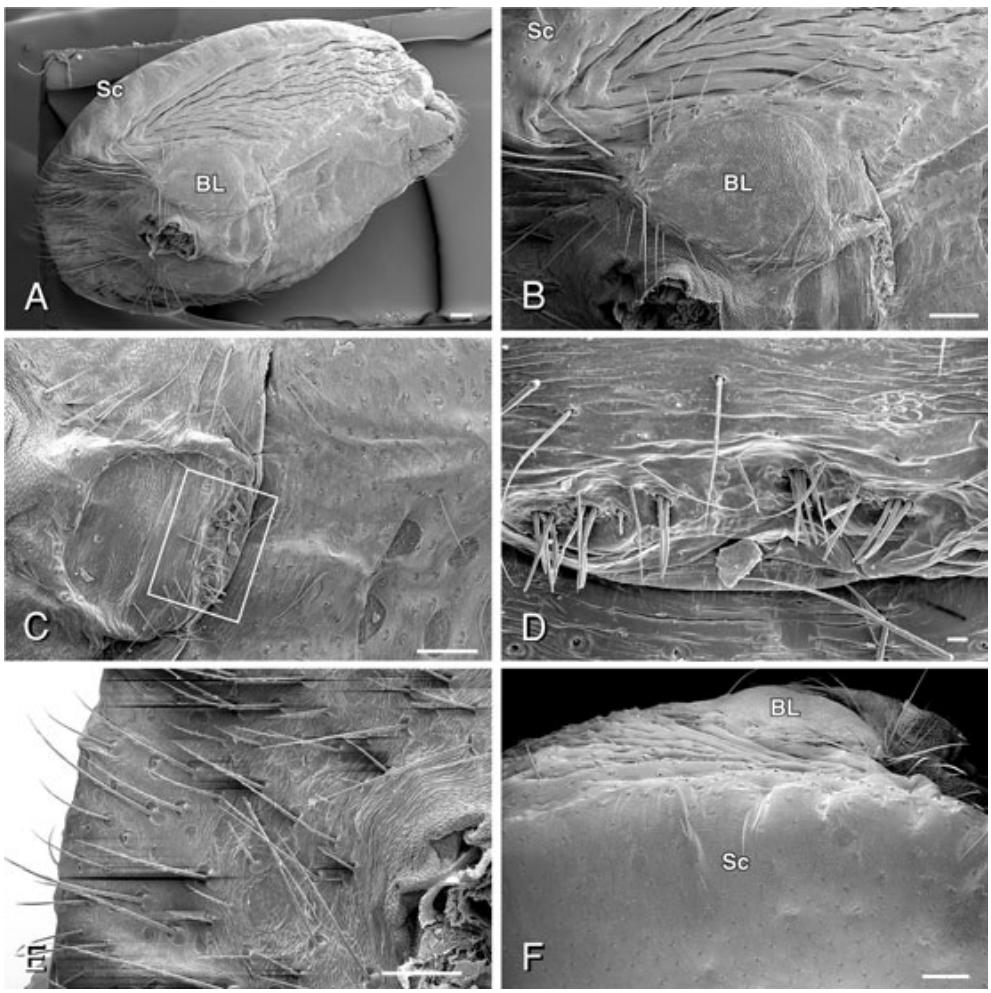

Fig. 24. *Herennia etruscilla*, sp. nov., male opisthosoma, from Java (he52/m1): *A*, ventrolateral; *B*, book lung, detail (note ridged surface); *C*, venter, box delimits area of image *D*; *D*, epigastral area with epiandrous gland spigots; *E*, anterior venter; *F*, dorsum and lateral opisthosoma (note numerous scleriotisations on scutum). Scale bars = 100 μm, except *D* = 10 μm.

Herennia tone, sp. nov.

(Fig. 31)

Material examined

Holotype. Female (he26/f1 MCZ) from Philippines: Dumaquete Negros 1500' 6–3-1949 (coll. BB Brues). The approximate coordinates of the type locality are 09°18′N 123°18′E. In the same vial a male of *Nephilengys malabarensis* was stored, which is now labelled as such.

Paratype. Female (he32/f1 MCZ) from **Philippines:** Dumaguete, Negros Or. 3600Ft. x.1942 (coll. JW Chapman). The approximate coordinates are 09°19′N 123°08′E.

Additional material examined. **Philippines:** Luzon, Beguios [= Baguio], 16°24′N, 120°35′E, 1933 (coll. JW Chapman) — he031/f1 (♀ MCZ); Negros, Dumaguete, Cuernos Mts. 9°19′N, 123°8′E, 1097 m, 18.x.1942 (coll. JW Chapman) — he029/f1 (♀ MCZ), he030/f1 (2♀ MCZ); Samar Island, [no exact loc. data], 12°0′N, 125°0′E (coll. Whitehead) — he098/f1 (♀ BMNH).

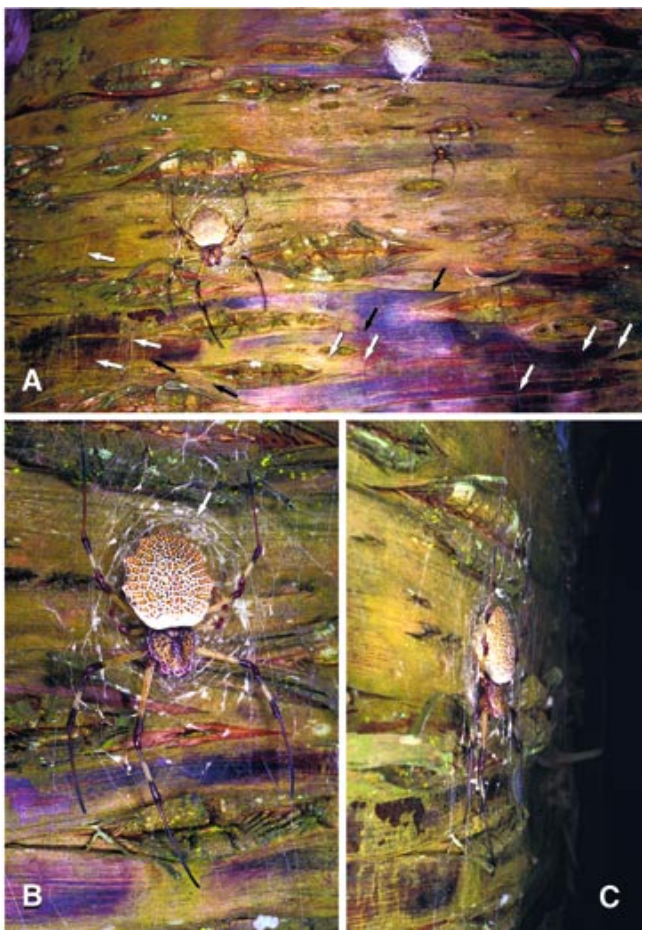

Fig. 25. *Herennia etruscilla*, sp. nov., photographs of live spiders from Java (paratype female he52/f2 and male he52/m1): *A*, female at hub of orb web built tightly against tree trunk and tiny orange 'eunuch' male (above, right, see Figs 21–22) cohabiting; note 'pseudoradii' (white arrows), which do not pass the hub unlike true radii (black arrows); *B*, close up of female resting at hub in the shape of a depression ('hub-cup', arrow); *C*, same, lateral view (note two-dimensionality of spider and its web, tightly following tree shape). Note female cryptic colouration matching tree bark and absence of V-shaped mark on carapace.

Diagnosis

Females differ from all other *Herennia* species except *H. gagamba* and *H. agnarssoni* by a group of long conspicuous spines prolaterally on femur I (Fig. 31*B*). They can be easily distinguished from *H. agnarssoni* and *H. gagamba* by the shape of epigynum (Fig. 31*C–D*), which is wide with lateral copulatory openings, a weak septum and thin sclerotised edge.

Description

Female (holotype, Fig. 31)

Total length 9.5.

Prosoma (Fig. 31*A–B*) 3.9 long, 3.2 wide, 2.0 high. Carapace orange-red medially, yellow laterally and frontally, with few weak warts. Chelicerae orange. Cheliceral formula 3/3/10. Sternum 1.6 long, 1.6 wide; transparent (in alcohol), with medially protruding white subcutaneous pigment. Maxillae and labium orange. Anterior eye row recurved, posterior straight. AME diameter 0.22, ALE 0.18, PME 0.13, PLE 0.16. [PLE larger than PME] AME separation 0.22, PME separation 0.30, PME–PLE separation 0.35, AME–ALE separation 0.19, AME–PME separation 0.25, ALE–PLE separation 0.13. Clypeus height 0.25.

Appendages (Fig. 31*A–B*). Femora and tibiae yellow, other leg joints brown. Femoral spines fairly sparse and short, except for the prolateral group of long spines on femur I. Leg I length 18.6 (Fe 5.2, Pa 1.3, Ti 4.4, Me 5.8, Ta 1.9).

Opisthosoma (Fig. 31*A–B*) slightly flattened dorsoventrally with four pairs of inconspicuous lateral lobes, barely truncated posteriorly; 6.0 long, 5.4 wide (maximum width over abdominal lobes), 2.8 high. Dorsum white with

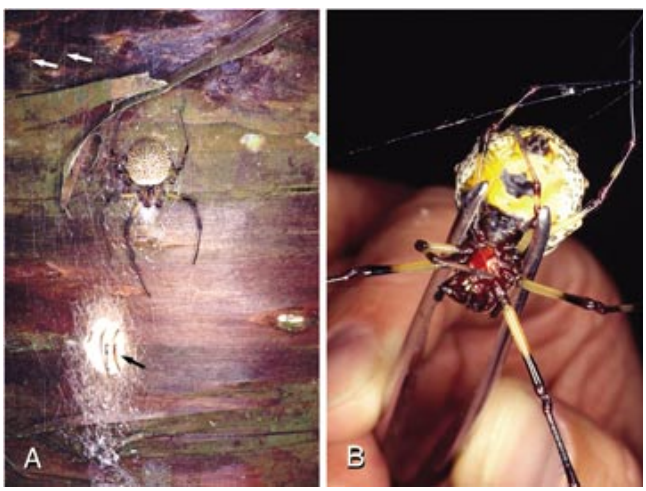

Fig. 26. *Herennia etruscilla*, sp. nov., photographs of live female from Java (paratype he52/f3): *A*, female at hub of her web; note spider cryptic dorsal colouration, 'pseudoradii' in web (white arrows), and egg sac in web (black arrow); *B*, close up of female ventral side after removing her from the web; note bright ventral colouration (blood-red sternum and orange venter) in striking contrast with cryptic dorsal side (*A*).

numerous sclerotised brown dots. Lateral opisthosoma with longitudinal dorso-ventral brown bands and small sclerotisations. Venter white, with a central grey area, and with white pigment patches around spinnerets. Four pairs of central sclerotisations, and a single row of inconspicuous lateral sclerotisations present on venter. Book lung covers and the sclerotisation around the spiracles red, as are the epigynum and the sclerotised area anterior to it.

Epigynum (Fig. 31*C–E*) wide, with narrow lateral sclerotisation and thin black sclerotised edge. Oval epigynal chambers almost connected medially, barely separated with weak septum. Lateral sclerotised chamber walls thin, posterior sclerotised chamber wall conspicuously 'tongued'. Inner epigynum as in Fig. 31*E*. Oval spermathecae juxtaposed medially, copulatory ducts long and massive, connected to the integument by enveloping the lateral sclerotisation.

Male

Unknown, except for epigynal plugs consisting of embolic conductors and emboli, found stuck in copulatory openings of four females (Fig. 31*D*). The distal EC is massive and different to the ones described, but seems to have the subdistal flap.

Variation

Females: prosoma length ranges from 3.9 to 4.6; total length from 9.3 to 11.5 ($n = 6$). Carapace colour ranges from orange to dark red-brown, almost black. Carapace lacks a yellow

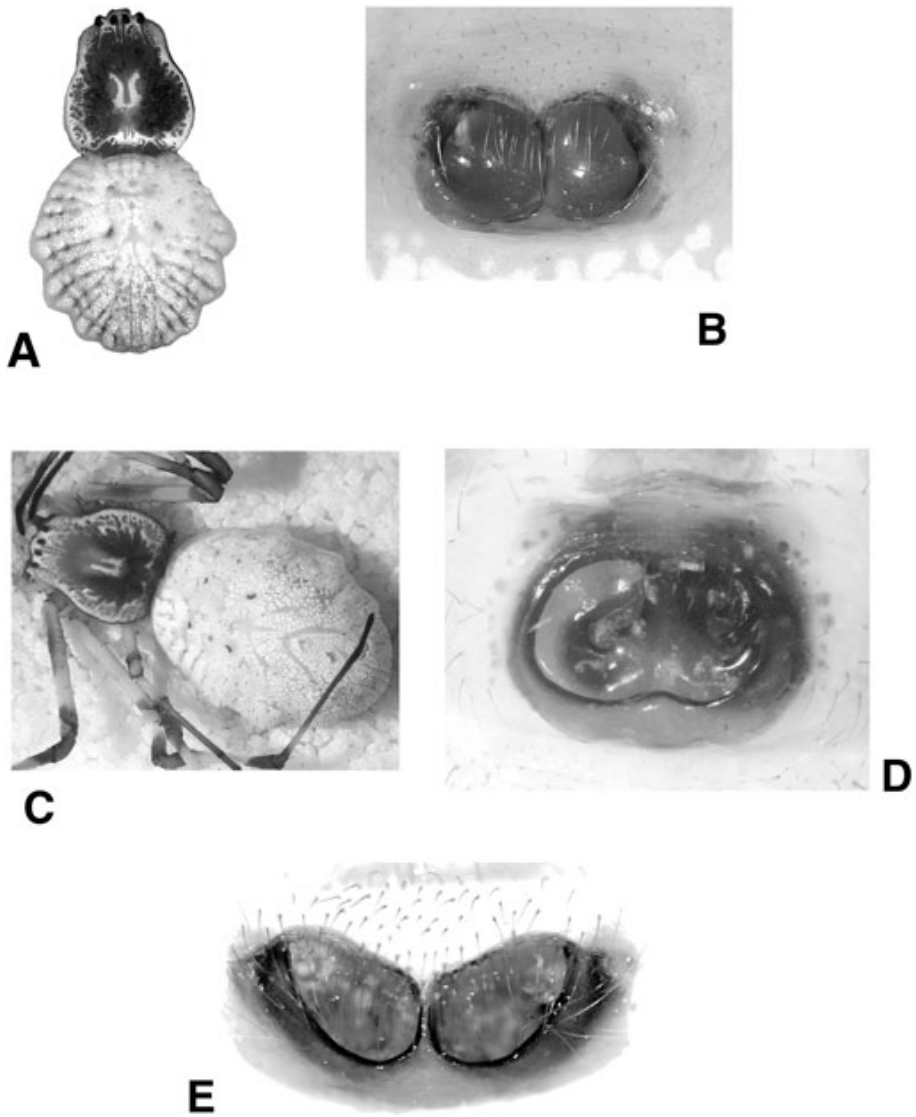

Fig. 27. *A–B*, *Herennia sonja*, sp. nov., female holotype from Kalimantan: *A*, habitus, dorsal; *B*, epigynum, ventral. *C–D*, *Herennia gagamba*, sp. nov., female paratype (he54/f1) from Luzon: *C*, habitus, dorsal (note prolateral long spines on first femur); *D*, epigynum, ventral. *E*, *Herennia jernej*, sp. nov., epigynum of female holotype from Sumatra, ventral.

V-shaped mark entirely (Fig. 31*A*) or the mark inconspoicuously present (Fig. 31*B*). Warts on carapace can carry dark macrosetae. Sternum can be wider than long (he31) or as wide as long (holotype). Opisthosoma almost unlobed (Fig. 31*A*) to lobed (Fig. 31*B*).

Distribution

Philippine Island Negros (Fig. 32). An additional, questionable locality is that of the female sample he31, the MCZ locality label reading: 'Philippines: Beguio_s 1933; J.W. Chapman.' The closest name to Beguios, which does not seem to exist, is Baguio on the island of Luzon (see above for coordinates of Baguio).

Natural history

Unknown.

Etymology

The species epithet (pronounced 'to-ne'), a noun in apposition, is a patronym after my father, Tone Kuntner.

Phylogeny

Equally weighted analyses resulted in ten most parsimonious trees (tree length = 490 steps, *CI* = 40, *RI* = 70). In the strict consensus, four nodes collapse and the length increases to 506 steps (Fig. 33*A*). Nephilid monophyly (*Clitaetra, (Herennia, (Nephilengys, Nephila*))) and the monophyly of all nephilid genera, *Herennia* included, is confirmed. As in previous analysis (Kuntner, in press) the sister-group to nephilids remains ambiguous. Equally parsimonious trees group nephilids with: (*1*) the clade containing all other araneoids; (*2*) araneids; (*3*) the clade containing tetragnathids + reduced piriform clade (here represented by Theridiosomatidae, Linyphiidae, Pimoidae, Theridiidae and Nesticidae); (*4*) *Phonognatha*, nephilids + *Phonognatha*, in turn, are sister to *Deliochus*, and this clade groups with the clade containing tetragnathids + reduced piriform clade; and (*5*) the clade ((*Deliochus* + *Phonognatha*) + (tetragnathids + reduced piriform clade)).

Successive weighting analysis stabilised after the second iteration and resulted in a single tree (Fig. 33*B*) identical to one of the fundamental cladograms described above as '*4*'. This tree differs from the successively weighted trees derived from datasets focusing on Clitaetrinae (Kuntner, in press) and *Nephilengys* (M. Kuntner, unpublished data) in the sister-group relationship of nephilids with *Phonognatha*. Such grouping, though very poorly supported (Fig. 33*B*), corroborates Hormiga *et al*.'s (1995) nephiline placement of *Phonognatha*, though not within tetragnathids. The unambiguous synapomorphies of *Phonognatha* + Nephilidae are sternum colouration (character 24/state 3), absence of conductor (133/1), absence of hub bite-out (166/1), presence of tertiary radii (173/1) and persistence of a non-sticky spiral in the finished web (176/1). Hormiga *et al*. (1995) did not include *Deliochus*; its grouping with the *Phonognatha* + nephilid clade also receives meagre support in the present study, it is supported by two unambiguous synapomorphies (chambered epigynum 76/1, presence of the embolic con-

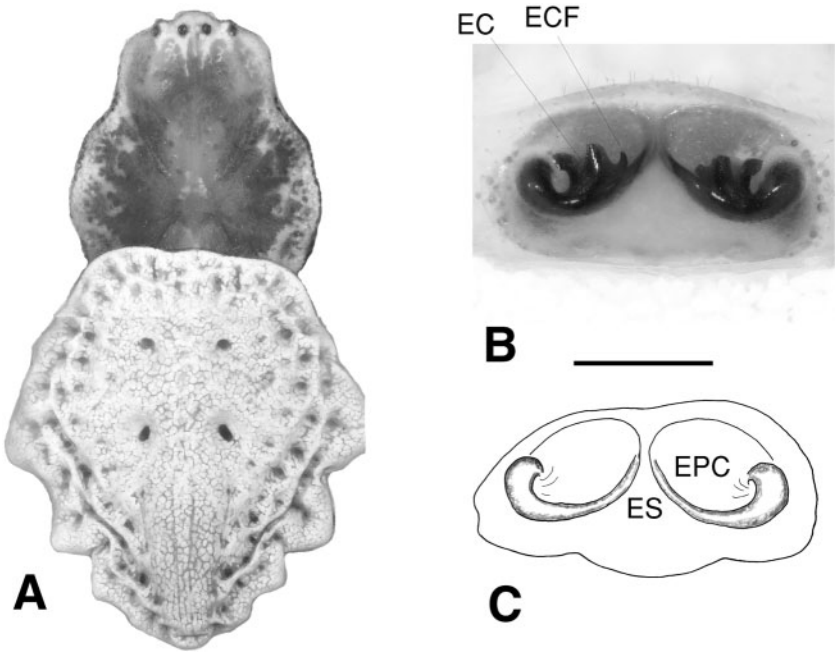

Fig. 28. *Herennia oz*, sp. nov., female from Australia. *A–B*, Holotype (he22); *A*, habitus, dorsal; *B*, epigynum, ventral (note EC in each copulatory opening). *C*, Paratype (he23), epigynum, ventral. Scale bar (*B–C*) = 0.5 mm.

ductor 136/1), but like the clade *Phonognatha* + nephilids, collapses in the strict consensus (Fig. 33*A*).

Nephilid monophyly *sensu* Kuntner (in press) is well supported (23 unambiguous synapomorphies, bootstrap 97/Bremer > 10), and so is the monophyly of Clitaetrinae (represented by *Clitaetra*, 99/6), Nephilinae (with *Herennia*, *Nephila* and *Nephilengys*, 73/4), *Nephilengys* (90/5), *Nephila* (87/4) and *Herennia* (100/7). The support for *Nephila* + *Nephilengys* is relatively low (50/3). Within *Herennia, H. papuana* is sister to all other species (47/1) and within the latter clade, the group *H. multipuncta* + *H. etruscilla* (56/1) is sister to the clade with the newly described species. Among these, all but *H. deelemanae* are known from a single sex, which may be the reason for shaky branches (Fig. 33*B*).

Discussion

Classification

The successively weighted tree (Fig. 33*B*) is the basis for the proposed taxonomy of *Herennia,* but it cannot offer a strong hypothesis for the position of the enigmatic Australian *Phonognatha* and *Deliochus*. Along with the exact position of Nephilidae within Araneoidea, the relationships of these two genera will be tested with a broader taxon sample elsewhere. However, the results imply that nephilines are not tetragnathids (*contra* Hormiga *et al*. 1995), and their araneid placement (Wunderlich 1986, 2004; Kuntner 2003; Pan *et al*. 2004) is supported only by a subset of trees and is thus questionable. Thus, treating the clade Nephilidae at family level (as in Kuntner, in press) seems appropriate and such classification will be retested in future analyses.

Biogeography

Biogeographic lines delimiting regional biotas are usually derived for one taxon at a time but some well known boundaries, like Wallace's line marking the boundary between the Oriental and Australian regions, often coincide with geological or climatic barriers of the past, which have prevented organism dispersal (Brown and Lomolino 1998). Wallace's line corresponds well to the outer limit of the Sunda Shelf, which is believed to have been part of continental South-east Asia during the Pleistocene (Brown and Lomolino 1998). Wallace's and Huxley's lines (Fig. 34) run between Bali and Lombok and between Borneo and Sulawesi, but differ in the inclusion of the Philippine islands; Wallace's line marks them as Oriental and Huxley's as Australasian (from Brown and Lomolino 1998). Other lines marking biotic boundaries have been proposed (see Brown and Lomolino 1998: fig. 10.10) to accommodate specific taxa, but they mostly run between the islands of eastern

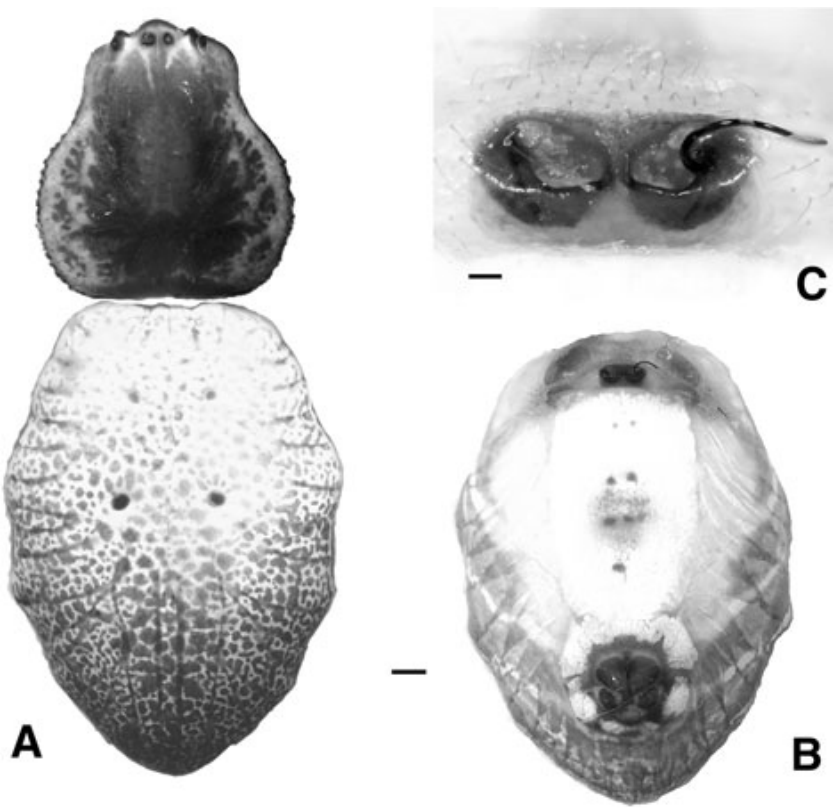

Fig. 29. *Herennia papuana*, female, from Papua New Guinea (he25): *A*, habitus, dorsal; *B*, opisthosoma, ventral; *C*, epigynum, ventral (note embolus in copulatory opening). Scale bars *A–B* = 1 mm, *C* = 0.1 mm.

Indonesia, in the so called Wallacea region. Those eastern lines may not be relevant for *Herennia*. The currently understood *Herennia* phylogeny is plotted on the geographic distribution of the species included in the analysis (Fig. 34). The 'basalmost' species is *H. papuana* from New Guinea, and the most 'derived' species are *H. agnarssoni* from Solomon Islands and *H. tone* from the Philippines. Kuntner (in press) roughly estimates the nephiline clade (with *Herennia, Nephila* and *Nephilengys*) to be at least 160 million years old and of Gondwanan origin. The currently understood *Herennia* phylogeography does not dispute the above, but calls for an explanation of speciation/colonisation of the Laurasian landmasses: mainland Asia, islands of Indonesia and the Philippines.

Assuming an Australasian origin of *Herennia*, four dispersal events could be postulated over Wallace's line (Fig. 34): the clade (*H. etruscilla* + *H. multipuncta*), *H. deelemanae*, and two dispersals to the Philippines (*H. gagamba*, *H. tone*). The alternative, and more parsimonious, explanation may be one dispersal event in the common ancestor to all species excluding *H. papuana* and one to Solomon Islands (*H. agnarssoni*). Over Huxley's line (Fig. 34), at least two dispersal events could be postulated, the clade (*H. etruscilla* + *H. multipuncta*) and *H. deelemanae* or, alternatively, one dispersal in the common ancestor to all species excluding *H. papuana* and a reversal in the common ancestor to *H. gagamba, H. tone* and *H. agnarssoni*. However, the newly drawn '*Herennia* line' (Fig. 34), joining only Sumatra and Taiwan with SE Asia, is crossed by a single species, *H. multipuncta*, suggesting all Australasian speciation events in *Herennia*.

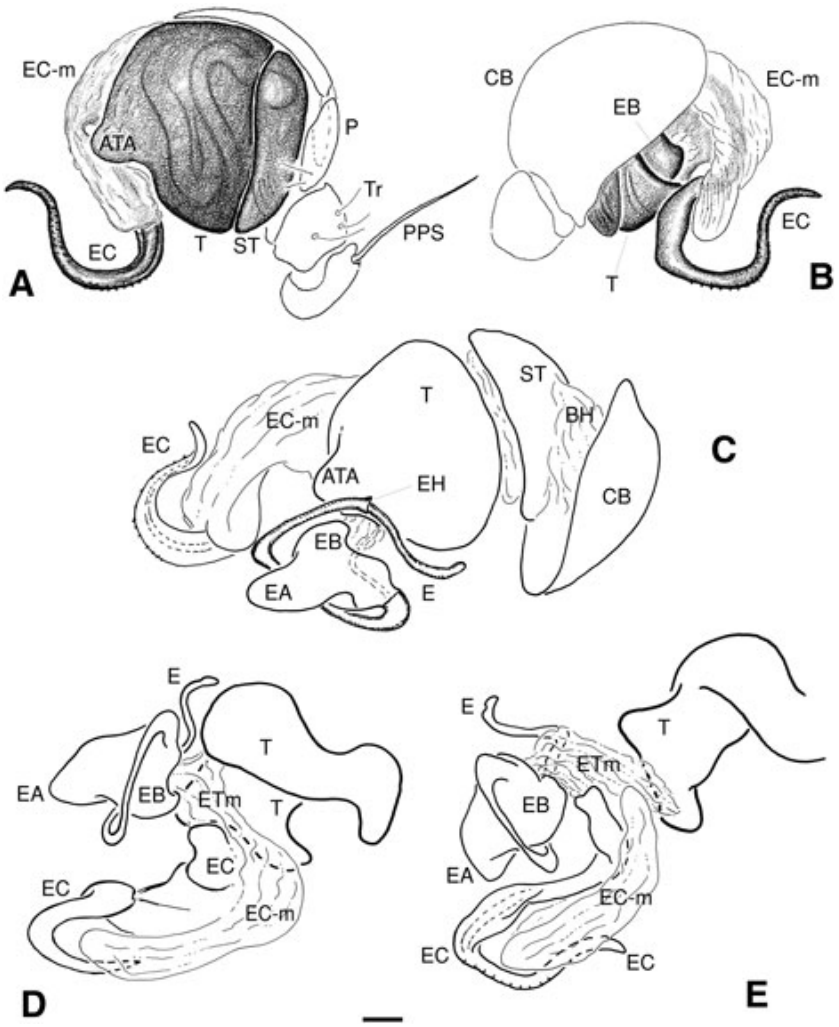

Fig. 30. *Herennia papuana*, male left pedipalp, from Papua New Guinea (*A–B*, he24/m1; *C–E*, he24/m2): *A*, ectal; *B*, mesal; *C*, expanded, embolus pulled out of EC, dorsal; *D*, distal sclerites dissected from remaining sclerites; *E*, further dissection of embolic division. Scale bar = 0.1 mm. Note that embolus base (EB) and embolic conductor (EC) are attached to tegulum (T) via joint membrane (ETm) and together form the nephilid embolic division. Embolic conductor has a sclerotised (EC) and a membranous part (EC-m).

Such hypothesis of Australasian speciation in *Herennia* is consistent with the currently understood ecology of *Herennia*, where most species appear to be narrow island endemics, likely confined to pristine forests, whereas the widespread *H. multipuncta*, ranging from India and Sri Lanka to eastern Indonesia, appears to expand its range easily with human influence (forest degradation). Indeed, *H. multipuncta* appears to be synanthropic and invasive. Thus, I believe coin spiders have a potential in Australasian conservation efforts.

Biology

The most well known (ecologically and behaviourally) species is *H. papuana*, owing to the research of Robinson and colleagues (Robinson and Robinson 1978, 1980; Robinson 1975, 1982; Robinson and Lubin 1979) conducted at Wau, Papua New Guinea in the 1970s (MCZ vouchers examined), briefly summarised below.

Habitat preferences

The species is obligately arboricolous. Although the webs were seen on larger trees of coffee plantations, they were not documented on rock faces, in contrast to *H. multipuncta*.

Web architecture

The web is adpressed to the tree surface, is eccentric (hub in the upper portion) and is generally described as a 'ladder web', meaning it is elongate with parallel sides and more or less horizontal radii. The so-called 'hub-cup' is a retreat of dense silk that touches the substrate, where the female rests head-down (compare Figs 14–15, 25–26). Barrier webs and stabilimenta are absent. The authors explained the side-to-side curvature of the web plane with the so called pseudoradii (Fig. 2), which are structurally similar to radii, but differ in running parallel from top to bottom frame and thus offer support for the sticky spiral, which follows the basic curvature

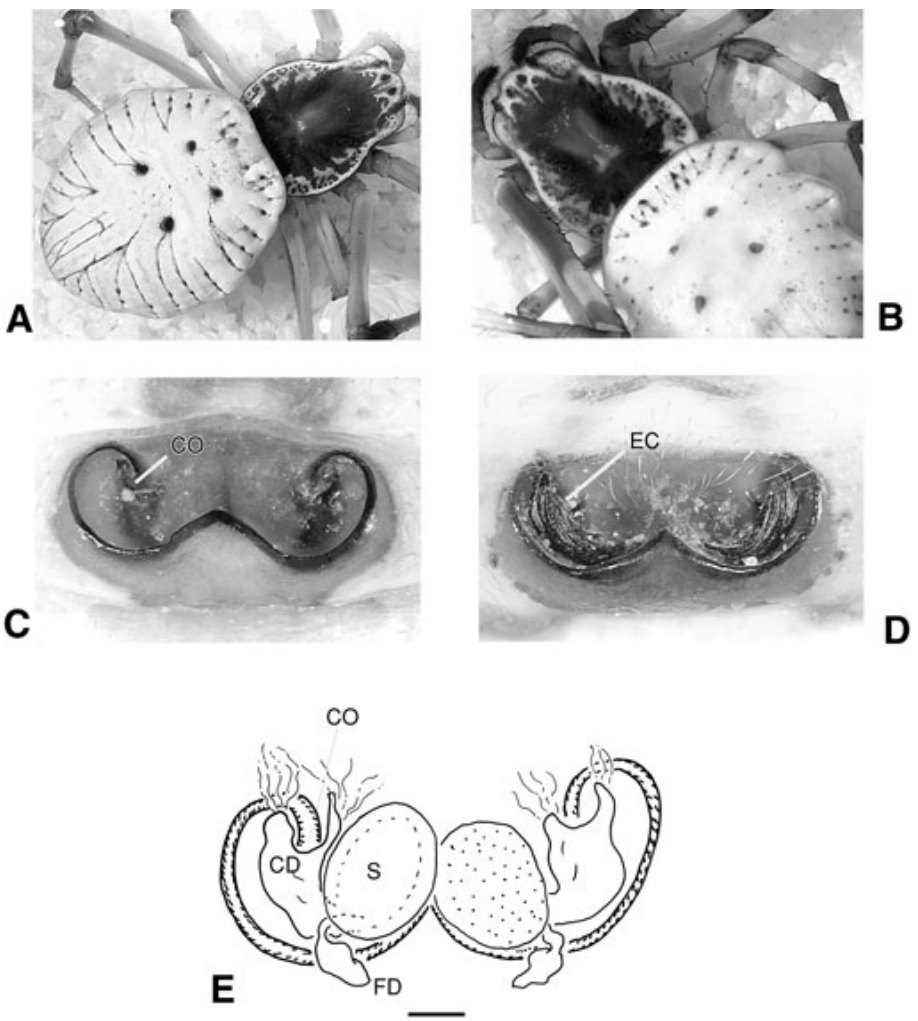

Fig. 31. *Herennia tone*, sp. nov., female from Philippines: *A*, habitus, dorsal (holotype, he26); *B*, same (he31), note prolateral long spines on first femur; *C*, epigynum, ventral (paratype, he32); *D*, same (he31); *E*, epigynum, cleared, dorsal (paratype, he32). Scale bar *E* = 0.1 mm.

of the trunk. Like the ribs of an umbrella, the authors noted, the pseudoradii give a curvature to the covering. This architecture is typical of adult females in their natural environment, but juvenile spiders and captive adults build a more or less circular orb web, not necessarily against substrate.

Behaviour

Robinson and coauthors (Robinson and Robinson 1978, 1980; Robinson 1975, 1982; Robinson and Lubin 1979) documented partial web renewal in *H. papuana*, a behaviour typical of all nephilid genera. Web renewal was always done at night. Egg sacs were attached to the bark of the tree, not in the web (compare with *H. multipuncta*). Defence responses involved raising and flexing of legs and jumping off the web. The authors discussed the nocturnal habits of *Herennia* (the spiders more readily attacked prey at night) as well as their highly cryptic stance. The female dorsal colour is such that it blends with the tree bark (and the web does not stand out). Curiously, the spider's ventral side is bright red (as for *H. multipuncta* and *H. etruscilla*, which also have bright red sterna, see Fig. 26*B*). The authors considered such colouration function problematical, especially since cage-raised specimens were yellow (see below for a possible explanation). Small reddish males cohabited in female webs, sometimes as eunuchs (lacking palpal bulbs, see below).

Predation

The authors found no preference for a particular prey taxon or ecotype (the spiders generally avoided ants). The predatory repertoire resembled that of *Nephila*, attacking all prey with a bite (never attack wrapping). After a biting attack, the spider either wrapped the prey *in situ* or pulled it from the web at capture site. This was followed by the transportation and attachment of prey (either in chelicerae or suspended on silk) to the hub. The spiders sometimes attacked by shuttling through the web at the hub-cup and approaching the prey on the inner side of the web, with the dorsal side facing the bark. Although the frequency or significance of such 'backside attack' was not discussed, it may protect the spider from predators. A similar 'side flip' as predator avoidance is known in *Clitaetra* (Kuntner, in press), some *Nephila* (M. Kuntner, unpublished data) and some *Argiope* (M. Kuntner, unpublished data). In female *Herennia*, the brightly coloured ventral side, which during backside attack has to be exposed, could be interpreted as aposomatic.

Mating

Courtship and mating take place on the female web (Robinson and Robinson 1978, 1980), the behaviour fitting in a 'group A' type, which, in addition to *Herennia*, included *Nephila, Nephilengys* and certain *Argiope* species (Robinson

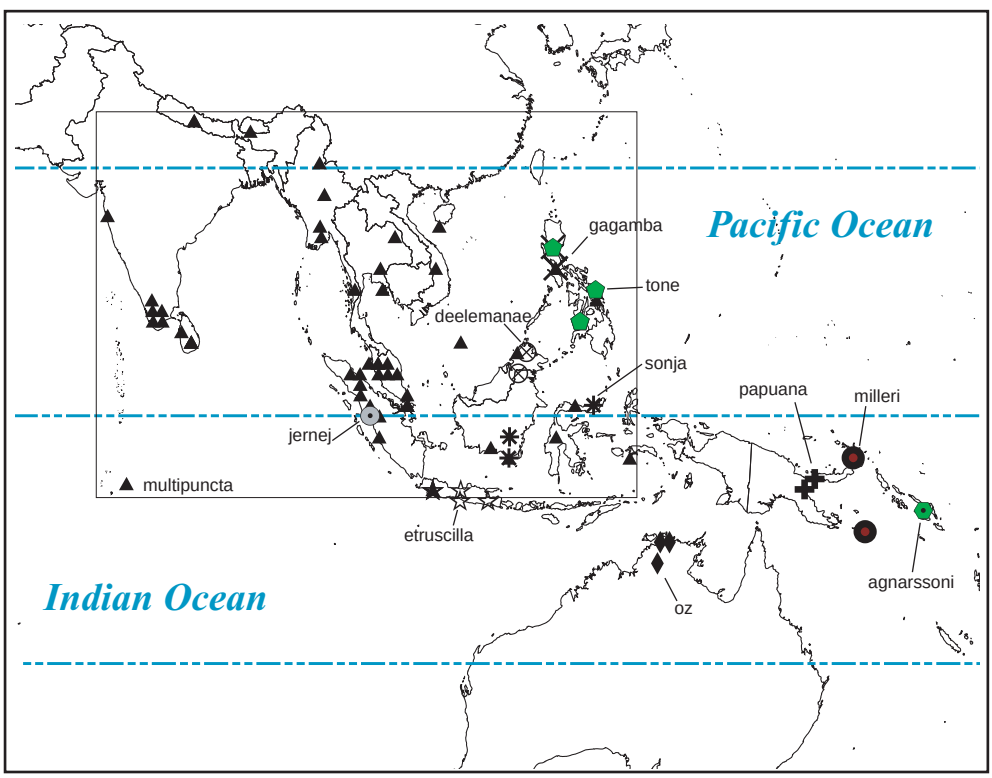

Fig. 32. *Herennia* species distribution map. The widespread, synanthropic and possibly invasive *H. multipuncta* ranges from India and Sri Lanka to eastern Indonesia, but other species appear to be narrow island endemics, likely confined to pristine forests.

and Robinson 1978, 1980). *Herennia papuana* exhibits the 'suitor phenomenon' (male cohabiting with immature female) and 'eunuchs'. Up to seven males cohabit in the female web. The only seemingly different behaviour from other nephilids (e.g. *Nephila*) is the female access posture, where a receptive female responds to male stimuli by raising her body partly out of the hub-cup, thus allowing male access to her venter.

Other species

Web architecture of *H. multipuncta* (Figs 14–15) and *H. etruscilla* (Figs 25, 26*A*) seems identical to *H. papuana*: eccentric ladder webs closely following the transverse curvature of tree trunks (or other substrates), with hub-cups (Fig. 14*A–B*, 25–26) and pseudoradii (Fig. 25*A*; the latter are only known in *Herennia*). Both *H. multipuncta* (Fig. 14) and *H. etruscilla* (Figs 25, 26*A*) commonly inhabit disturbed habitats in addition to forests. The web and its varied location in Sri Lanka were first described by Simon (1894: 758); *Herennia multipuncta* webs can be on walls (Figs 14*C*, 15), rock faces (Robinson and Lubin 1979; Murphy and Murphy 2000) as well as on trees (Fig. 14*A–B*). Masumoto and Okuma (1995) reported a tendency of *H. multipuncta* to build on *Eucalyptus* trees in Malaysia, which supports the interpretation that the species benefits from primary habitat destruction. In Java *H. etruscilla* webs were found on trees in rain forest (Kaliurang) and on (likely non-native) trees in Cibodas botanical gardens (Figs 25–26*A*). According to available data, both species are sympatric in Bogor, Java. Egg sacs of *H. etruscilla* seem to be attached to the web (Fig. 26*A*; compare with *H. papuana*).

Mating plugs and eunuchs

In most *Herennia* species, broken-off male embolic conductors were commonly found stuck in female copulatory openings (Figs 10*E–F*, 11, 17*A*, 18*C*, 22*E–F*, 28*B*, 31*D*). Despite this, only one male with broken embolic conductors was found in collections. Instead, the so-called eunuch males are common, which lack entire palpal bulbs (Fig. 23*A–E*). Eunuch males are also found in *Nephilengys*. Although the function (if any) and frequency of severed bulbs are unknown, it seems that male embolic conductor mutilation and bulb amputation are correlated. In fact, Robinson and Robinson (1980) found the evidence that *Nephilengys* males deliberately lose the bulb after mating.

With its peculiar sexual biology, *Herennia* calls for attention. The apparently consistent mutilation of male sexual organs, which plug female genitals, and the bulb severance (eunuch phenomenon), known in *Herennia* and *Nephilengys*, require explanations. A possible, though at this point speculative, explanation of these behaviours is presented as three hypotheses consistent with the currently available morphological and behavioural data: (*1*) the broken embolic conductor may function as a mating plug preventing future (successful) copulation attempts by other males; (*2*) losing/removing the bulb after initial mutilation of the embolic conductor is advantageous for the (sterile) male in stopping hemolymph leakage; and (*3*) a eunuch may protect his parental investment by fighting off rival males in search of the female. These hypotheses could be tested with a variety of approaches: morphological, molecular,

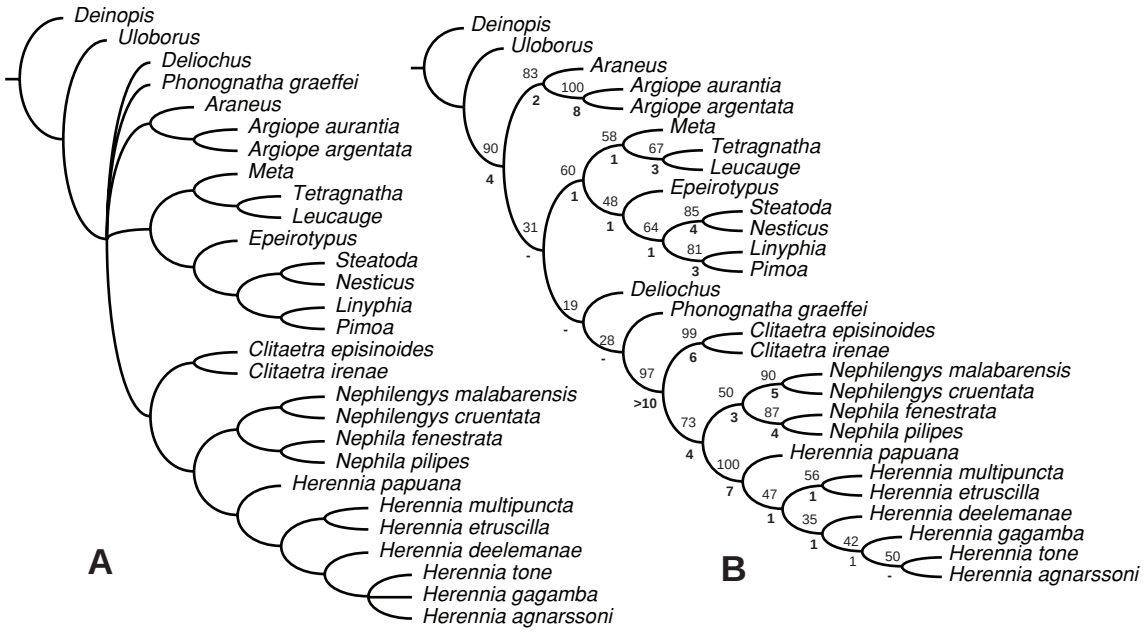

Fig. 33. Phylogeny of the Nephilidae, with particular reference to *Herennia*. A, Strict consensus of ten shortest cladograms ($L = 490$, $CI = 40$, $RI = 70$) collapsing four nodes. *B*, Successively weighted tree identical to one of the fundamental cladograms. Branch supports given as bootstrap (above, regular type) and Bremer (below, bold).

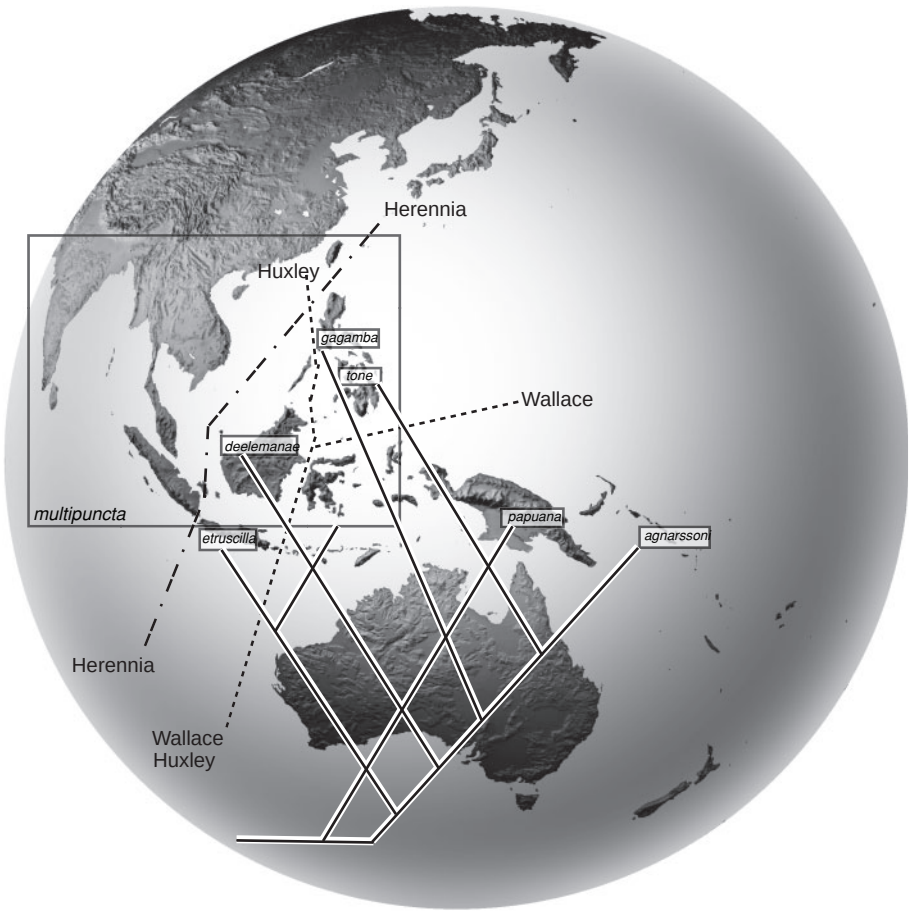

Fig. 34. *Herennia* phylogeography. At least two dispersal events have to be postulated over Wallace's and Huxley's line, respectively, whereas the newly drawn '*Herennia* line', dividing Australasia from the core Oriental region, is only crossed by a single species, *H. multipuncta*. See text for details.

behavioural, experimental and phylogenetic. In this analysis, the eunuch phenomenon is ambiguously optimised: under fast optimisation it is a synapomorphy for the clade *Herennia* + *(Nephila* + *Nephilengys)* with a reversal in *Nephila*, whereas under slow optimisation the feature is hypothesised to have evolved separately in *Nephilengys* and *Herennia*.

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Appendix 1. List of characters and character states used in the phylogenetic analysis, with description of characters relevant for *Herennia*

A rigorous homology test of these and additional characters relevant for nephilids will be presented elsewhere (Kuntner, Hormiga and Coddington, unpublished data)

(*1*) *Female cephalic region:* 0, low (Fig. 1*A*); 1, conspicuously high.
(*2*) *Female carapace:* 0, piriform (Fig. 1*C*); 1, oval with wide head region.
(*3*) *Female carapace edge:* 0, smooth; 1, ridged (Figs 1*C*, 5*B*, *D*).
(*4*) *Female carapace edge:* 0, glabrous or with few hair-like setae; 1, with an extensive row of hair-like setae (Fig. 5*B–E*).
(*5*) *Female median pair of prosomal tubercles:* 0, absent (Figs 1*A–C*, 5*B*); 1, present.
(*6*) *Fovea (female carapace):* 0, inconspicuous (Figs 1*A*, *C*, 5*B*, 19*A*); 1, pronounced.
(*7*) *Female carapace macrospines:* 0, absent; 1, present.
Note: in all *Nephilengys* species stout erect macrospines aer present on carapace.
(*8*) *Female carapace warts:* 0, absent; 1, present (Figs 5*F*, 19*A–F*).
Note: the carapace cuticle is warty (enlarged functional and non-functional setal bases) in all *Herennia* species, especially pronounced in *H. etruscilla* (Fig. 19).
(*9*) *Female carapace V-mark:* 0, absent; 1, present (Figs 1*C*, 14, 27*A*, *C*).
(*10*) *Female carapace hair-like setae:* 0, present (Figs 5, 19); 1, absent.
Note: apart from regular setae nephilids (and certain outgroups) have thin short white hair-like setae.
(*11*) *Female median eye region:* 0, rounded; 1, median eyes on a tubercle (Figs 1*B–C*, 5*C*, 19*E*).
(*12*) *Female lateral eye region:* 0, lateral eyes on separate tubercles; 1, lateral eyes on a single tubercle (Figs 1*B–C*, 5*C*, 19*E*); 2, rounded.
(*13*) *Female LE separation from ME:* 0, not widely separated (Figs 1*B–C*, 5*C*, 19*E*); 1, widely separated.
Note: ratio of the distance between the PLE and PME (at its widest point) divided by the width of the PME ocular area (at the widest point). If the ratio is less than 1, the separation is normal; if the ratio is more than 1, the separation is wide.
(*14*) *Posterior eye row (dorsal view):* 0, straight to recurved (Figs 1*C*, 5*B–C*, 19*A*, *D*, *E*); 1, procurved.
Note: the character is from Scharff and Coddington (1997: character 54).
(*15*) *Female PME:* 0, less than one PME diameter apart; 1, one PME diameter or more apart (Figs 1*C*, 5*B–C*, 19*A*, *D*, *E*).
(*16*) *Female PLE size:* 0, equal or less than PME (Fig. 19*E*); 1, larger than PME.
(*17*) *PME canoe tapetum:* 0, absent; 1, full; 2, narrow.
Note: corresponds to character 4 in Hormiga *et al*. (1995), characters 51 and 52 in Scharff and Coddington (1997) and characters 28 and 29 in Griswold *et al*. (1998). *Herennia* lacks eye tapeta.
(*18*) *PLE canoe tapetum:* 0, absent; 1, full; 2, narrow.
Note: as above.
(*19*) *Female clypeus height:* 0, low (less than three AME diameters); 1, equal or more than three AME diameters.
(*20*) *Endites:* 0, very long (> 2 × width); 1, short (length < 2 × width).
(*21*) *Labium and sternum:* 0, separate; 1, fused.
(*22*) *Female sternum:* 0, longer than wide; 1, as wide as or wider than long.
(*23*) *Sternal slit sensilla:* 0, present (Figs 6*E–F*, 20*F*); 1, absent.
(*24*) *Female sternum colour pattern:* 0, inconspicuously coloured; 1, uniformly orange/red (Fig. 26*B*); 2, medially dark, laterally pale; 3, medially light, laterally dark; 4, with yellow spots corresponding to tubercles.
(*25*) *Sternal white pigment:* 0, absent; 1, present.
(*26*) *Female sternal tubercle I:* 0, absent; 1, present.
Note: paired elevations of the female sternum adjacent to coxae I-IV are termed sternal tubercles (Fig. 6*E* – arrows).
(*27*) *Female sternal tubercle II:* 0, absent; 1, present (Fig. 6*E* – arrows).
(*28*) *Female sternal tubercle III:* 0, absent; 1, present (Fig. 6*E* – arrows).
(*29*) *Female sternal tubercle IV:* 0, absent; 1, present (Fig. 6*E* – arrows).
(*30*) *Female frontal sternal tubercle:* 0, absent; 1, present.
(*31*) *Female chilum:* 0, absent; 1, present.
Note: The chilum is present as a paired sclerite (Fig. 1*B*) at the base of chelicerae, just under the clypeus in most nephilids (not in certain *Clitaetra* species).
(*32*) *Female chelicerae:* 0, massive (width > 1/2 length); 1, slender (width < 1/2 length).
Note: nephilids have massive chelicerae with the width from profile more than 1/2 length (Figs 1*A*, 20*A*).
(*33*) *Cheliceral ectal margins:* 0, smooth; 1, with stridulatory striae.
(*34*) *Cheliceral boss:* 0, present (Figs 6*B*, 20*A–C*); 1, absent.
(*35*) *Cheliceral boss surface:* 0, smooth; 1, striated (Figs 6*B*, 20*A–C*).
(*36*) *Prosomal supracheliceral lobe (PSL):* 0, present (Fig. 20*B*); 1, absent.
(*37*) *Cheliceral furrow:* 0, denticulated (Fig. 20*E*); 1, smooth.
(*38*) *Female first femur:* 0, more/less straight; 1, sigmoidal.
(*39*) *Femoral macrosetae:* 0, present (Figs 5*B*, *D*, 19*B*); 1, absent.
(*40*) *Femoral (I, II) macrosetae length:* 0, long (Fig. 19*B*); 1, short, stout (Fig. 5*D*).
(*41*) *Female femur 1 group of prolateral long spines:* 0, absent; 1, present (Figs 16*A–B*, 31*B*).
(*42*) *Dorsal femoral trichobothria:* 0, absent; 1, present.
(*43*) *Female tibia I tufts:* 0, absent; 1, present.
Note: all *Nephila* species at some stage possess dense tibial setae on legs I, II, IV.

(*continued next page*)

Appendix 1. (continued)

(*44*) *Female tibia II tufts:* 0, absent; 1, present.
(*45*) *Female tibia IV tufts:* 0, absent; 1, present.
(*46*) *Patella-tibia autospasy:* 0, absent; 1, present.
(*47*) *Ventral tarsus IV setae:* 0, irregular; 1, comb-like.
(*48*) *Tarsus IV median claw:* 0, long (as long or longer than the main claw; Fig. 7*A–D*); 1, short (shorter than the paired main claw).
(*49*) *Sustentaculum:* 0, present (Fig. 7*B–D*); 1, absent.
(*50*) *Sustentaculum angle:* 0, wide, diverging from other setae; 1, narrow, parallel to other setae (Fig. 7*B–D*).
(*51*) *Female abdomen length:* 0, very long (> 2 × width); 1, long (longer than wide, but < 2 × width); 2, short (as wide as long or wider).
(*52*) *Female abdomen width:* 0, elliptical; 1, widest anteriorly; 2, widest posteriorly; 3, pentagonal.
(53) *Female lateral abdominal margin:* 0, smooth; 1, with 3–4 pairs of lobes (Figs *1A–D*, 8*A–C*, 9*A–B*, *E*, 10*A–D*).
(*54*) *Female anterior abdominal humps:* 0, absent; 1, present.
(*55*) *Female abdomen tip:* 0, rounded; 1, truncated (Fig. 9*B* – arrow).
(*56*) *Female ventro-median sclerotisations:* 0, absent; 1, paired sclerotisations (Figs 1*D*, 8*A–C*, 9*B–D*, 10*A*).
Note: all nephilids possess a row of conspicuous sclerotized apodemes medially on venter and one to several rows of sclerotisations laterally on venter.
(*57*) *Female ventro-median sclerotisations:* 0, 1–5 pairs; 1, 6–11 pairs.
(*58*) *Female ventro-lateral abdominal sclerotisations:* 0, present (Figs 1*D*, 8, 10*A–D*); 1, absent.
(*59*) *Ventro-lateral abdominal sclerotisations:* 0, one paired line of small dots; 1, sclerotisations in several lines (Figs 1*D*, 8, 10*A–D*).
(*60*) *Female dorso-median abdominal apodemes:* 0, absent; 1, 3–5 prominent pairs (Figs 1*A*, *C*, 16*A*, *D*, 22*B–D*, 27*A*, 28*A*, 29*A*, 31*A–B*).
(61) *Female dorso-lateral abdominal sclerotisations:* 0, present (Figs 1*A*, *C*, 16*A*, *D*, 22*B–D*, 27*A*, 28*A*, 29*A*, 31*A–B*); 1, absent.
(*62*) *Female dorso-central abdominal sclerotisations:* 0, absent; 1, present (Figs 1*C*, 22*C*, 31*A*).
(*63*) *Female abdominal sigillae:* 0, absent; 1, present (Figs 14, 23, 24*A*).
(*64*) *Female anterior abdomen:* 0, without; 1, with a broad light-pigmented band.
(*65*) *Female abdominal dorsal pattern:* 0, inconspicuous; 1, conspicuous.
(*66*) *Female dorsum dark spots:* 0, absent; 1, present (Figs 14, 25, 26*A*).
(*67*) *Female dorsum 'butterfly' pattern:* 0, absent; 1, present.
(*68*) *Female abdomen tip color:* 0, no different to the subapical abdomen; 1, paired white dots around spinnerets.
(*69*) *Female abdomen silver pigment spots:* 0, absent; 1, present.
(*70*) *Female venter light pigmented pattern:* 0, absent; 1, present (Fig. 1*D*, 29*B*).
(71) *Female venter light pigmented pattern form:* 0, one central light area; 1, transverse line(s); 2, four large spots; 3, numerous spots; 4, longitudinal lines.
(*72*) *Book lung cover:* 0, grooved (Figs 1*D*, 10*A–C*); 1, smooth.
(*73*) *Area around female book lung spiracle:* 0, little sclerotised; 1, strongly sclerotised (Fig. 1*D*).
(*74*) *Posterior epigynal plate:* 0, round; 1, grooved.
Note: in some species of *Nephila* and *Nephilengys* the epigynal plate posterior edge is grooved and leads to lateral copulatory openings.
(*75*) *Epigynal ventral area:* 0, low; 1, swollen.
(*76*) *Epigynal openings:* 0, simple; 1, in chambers (Fig. 11).
Note: copulatory openings are within larger chambers in *Nephilengys*, *Herennia*, some *Nephila* species and in some outgroups.
(*77*) *Chamber opening position:* 0, medial (Fig. 27*D*); 1, lateral (Figs 2*A–B*, 10*E–F*, 11).
(*78*) *Epigynal septum:* 0, absent; 1, present (Figs 11, 18*C*, 28*C*).
(*79*) *Epigynal septum shape:* 0, simple border between chambers (Figs 11, 18*C*, 28*C*); 1, extensive, broader posteriorly (Fig. 27*D*); 2, extensive, broader anteriorly.
(*80*) *Epigynal paired sclerotised pocket:* 0, absent; 1, present.
(*81*) *Anterior epigynal area:* 0, with a pair of apodemes; 1, round.
(*82*) *Cuticle anterior to the epigynal area:* 0, rounded; 1, depressed.
(*83*) *Copulatory opening position:* 0, caudal; 1, ventral.
(*84*) *Caudal copulatory openings:* 0, on the posterior sclerotised epigynal margin; 1, anterior to the posterior margin.
(*85*) *Copulatory opening form:* 0, elongated slit openings; 1, rounded openings (Fig. 11).
(*86*) *Copulatory duct morphology:* 0, flattened duct (longer than wide, flat); 1, tube (longer than wide, cylindrical); 2, broad attachment to body wall (wider than long).
(*87*) *Spermathecae:* 0, lobed; 1, spherical; 2, oval.
Note: in *Herennia* spermathecae are adjacent, oval, with gland pores over their entire surface (Figs 2*C–D*, 18*D*, 31*E*).
(*88*) *Spermathecae separation:* 0, wide (separated more than two widths); 1, small or none (separated less than two widths).
(*89*) *Epigynal sclerotised arch:* 0, absent; 1, present (Figs 2*C*, 18*D*, 31*E*).
(*90*) *Female copulatory aperture:* 0, never plugged; 1, sometimes plugged with emboli a/o conductors (Fig. 11). See Discussion.
(*91*) *Female copulatory plugs:* 0, emboli; 1, emboli plus (embolic) conductors (Fig. 11).
(*92*) *Cribellum:* 0, present; 1, absent.
(*93*) *ALS piriform gland spigot bases:* 0, normal; 1, reduced.
Note: the spinneret spigot characters (93–99) are from Hormiga *et al*. (1995), characters 54–60, and follow the homology assessments of Coddington (1989). An almost uniform nephilid spinneret morphology is: ALS with 'normal PI field' where the PI spigot base is nearly as long or longer than the shaft (Griswold *et al*., 1998: character 69, fig. 48*B*), the major ampullate spigot and a nubbin, PMS with a sparse aciniform field, and a nubbin, PLS with the aggregate spigots embracing the flagelliform, and with the two cylindrical spigots of normal size, the mesal being peripheral (compare with Figs 7*E–F*, 21*D–F*).
(*94*) *PMS nubbin:* 0, absent; 1, present.

(*continued next page*)

Appendix 1. (continued)

(*95*) *PMS aciniform field:* 0, extensive; 1, sparse.
(*96*) *PLS mesal cylindrical gland spigot base:* 0, subequal to other PLS cylindrical spigot; 1, larger.
(*97*) *PLS mesal cylindrical gland spigot position:* 0, central; 1, peripheral.
(*98*) *PLS aggregate-flagelliform relation:* 0, aggregates apart from flagelliform; 1, distal aggregate spigots embrace flagelliform.
(*99*) *PLS aggregate gland spigot:* 0, normal; 1, large.
(*100*) *Male size:* 0, more than half the size of female; 1, less than 0.4 female.
Note: corresponds to character 14 in Hormiga *et al*. (1995) arbitrarily quantifying the extreme sexual size dimorphism, within nephilids typical of *Nephila*, *Nephilengys* and *Herennia* (Fig. 1).
(*101*) *Male dorsal abdomen:* 0, cuticle soft; 1, with scutum (Figs 3*A–C*, 24*A–B*, *F*).
(*102*) *Male lateral eyes:* 0, separate (Figs 3*A–B*, 23*A–E*); 1, juxtaposed.
(*103*) *Male cephalic region:* 0, narrower than in female (Fig. 1*C*, *F*); 1, same proportion to cephalothorax as in female.
(*104*) *Male clypeus:* 0, as in female; 1, more horizontal (Fig. 1*A*, *E*).
(*105*) *Male v. female cheliceral size:* 0, same; 1, larger; 2, smaller (Fig. 1*A*, *E*).
(*106*) *Male paturon posteriorly:* 0, smooth; 1, with a tubercle.
(*107*) *Male leg II tibial macrosetae:* 0, similar to those on tibia I; 1, stronger and more robust; 2, absent.
(*108*) *Male endite depression:* 0, absent; 1, present.
(*109*) *Male palpal trochanter:* 0, short (twice the width or less); 1, long (more than twice the width).
(*110*) *Male palpal femoral tubercle:* 0, absent; 1, present.
Note: see character 3 of Scharff and Coddington (1997: Fig. 4).
(*111*) *Male palpal patella macrosetae:* 0, none; 1, one (Figs 4*A*, 18*A*, 30*A*); 2, two.
Note: modified from character 19 in Hormiga *et al*. (1995).
(*112*) *Male palpal tibia length:* 0, short (not exceeding 1.5 times its width); 1, long (exceeding 1.5 times its width).
(*113*) *Cymbium length:* 0, short (less than 2 × width); 1, long (more than 2 × width).
(*114*) *Cymbial ectal margin:* 0, sclerotised as cymbium; 1, transparent.
(*115*) *Paracymbium (P):* 0, absent; 1, present.
(*116*) *Paracymbial base sclerotisation:* 0, like cymbium; 1, less sclerotised.
(*117*) *Paracymbium morphology:* 0, short basal structure, more or less hook-shaped; 1, longer than wide and finger-like; 2, flat and roughly rectangular; 3, U-shaped; 4, flat and roughly triangular; 5, *Phonognatha* condition.
(*118*) *Paracymbium edge:* 0, glabrous; 1, with setae.
(*119*) *Anterior paracymbial apophysis (APA):* 0, absent; 1, present.
(*120*) *Paracymbial margin fold:* 0, absent; 1, present.
(*121*) *Paracymbium apically:* 0, rounded; 1, with a prong.
(*122*) *Tegulum in ectal view:* 0, same size as or larger than subtegulum (Fig. 4*A*); 1, smaller than subtegulum.
(*123*) *Reservoir course:* 0, spiralled; 1, with a switchback (Fig. 4*E*).
(*124*) *Ventral tegular switchback:* 0, single; 1, double.
(*125*) *Ejaculatory duct:* 0, within the entire length of embolus; 1, joins distal embolus.
(*126*) *Median apophysis (MA):* 0, absent; 1, present.
(*127*) *Median apophysis:* 0, without sperm duct; 1, with a loop of the sperm duct.
(*128*) *Median apophysis thread-like spur:* 0, absent; 1, present.
(*129*) *Apical tegular apophysis (ATA):* 0, absent; 1, present (Figs 4*A*, 12*A–B*, *E*, 13*B–E*, 18*A–B*, 30*A*, *C*).
(*130*) *Ventral tegular apophysis (VTA):* 0, absent; 1, present.
(*131*) *Mesal tegular apophysis (MTA):* 0, absent; 1, present.
(*132*) *Theridiid tegular apophysis (TTA):* 0, absent; 1, present.
(*133*) *Conductor (C):* 0, present; 1, absent.
(134) *Conductor size:* 0, small (less than half bulb volume); 1, large (more than half bulb volume).
(*135*) *Conductor form:* 0, rounded; 1, grooved for embolus.
(*136*) *Embolic conductor (EC):* 0, absent; 1, present.
Note: Nephila, Nephilengys, Herennia, Clitaetra, Phonognatha and *Deliochus* possess one or more sclerites of the embolic division, connected to EB and T via membrane. The sclerite(s) function(s) as conductor, enclosing the embolus. In *Nephila* and *Clitaetra* (Kuntner, in press) the sclerite is simple, long and finger-like, with a groove in which the embolus sits fully wrapped. In *Nephilengys* and *Herennia* (Figs 4*A–C*, 12–13, 18*A–B*, 30, 17*B–C*) the sclerite is complex, wide and sigmoidal, with membranous and sclerotised parts (distally with ridged edges), though functioning as one large sclerite.
(*137*) *EC membrane:* 0, absent; 1, present.
(*138*) *EC shape:* 0, complex; 1, finger-like.
(*139*) *Finger EC:* 0, short; 1, long.
(*140*) *EC (division):* 0, not subdivided; 1, subdivided into more sclerites.
(*141*) *Distal EC flap:* 0, absent; 1, present.
(*142*) *EC edge:* 0, smooth; 1, ridged.
(*143*) *EC curvature:* 0, more or less straight; 1, sigmoidal; 2, bent distally.
(*144*) *EC tip:* 0, straight; 1, with a hook.
(*145*) *Embolus (E) length:* 0, long (> 2 × CB); 1, medium (0.5–1.5 CB length); 2, short (< 1/2 cymbium).

(*continued next page*)

Appendix 1. (continued)

(*146*) *Embolus form:* 0, thin (Figs 4*C–E*, 30*C–E*); 1, thick; 2, filiform.
(*147*) *Embolus–tegulum orientation:* 0, parallel; 1, 90 degrees.
(*148*) *Embolus–tegulum membrane:* 0, absent; 1, present.
(*149*) *Embolus base:* 0, thin; 1, enlarged (= radix) (Figs 4*B–C*, 12*C–D*, 13*B*, *F*, 18*B*, 30*B–E*).
(*150*) *Embolus base distal part:* 0, smooth; 1, denticulated.
(*151*) *Embolic apophysis:* 0, absent; 1, present.
(*152*) *Radical membrane:* 0, absent; 1, present.
(*153*) *Stipes:* 0, absent; 1, present.
(*154*) *Embolus constriction:* 0, absent; 1, present.
(*155*) *Embolus:* 0, smooth; 1, hooked.
Note: embolus has a single hook in *Argiope* and *Herennia* (Figs 4*C–E*, 30*C–E*) and a row of hooks in *Deliochus*.
(*156*) *Embolus distal apophysis:* 0, present; 1, absent.
(*157*) *Embolus tip:* 0, flat (Fig. 30*C–E*); 1, cylindrical (Fig. 4*C–D*).
(*158*) *Web architecture:* 0, orb; 1, sheet; 2, gum foot.
Note: *Herennia* web architecture and known behaviours are summarised in text, see also Figs 14–15, 25–26.
(*159*) *Orb–web angle:* 0, horizontal (0–45 degrees); 1, vertical (46–90 degrees).
(*160*) *Orb shape:* 0, round; 1, rectangular.
(*161*) *Silk color:* 0, white; 1, golden.
(*162*) *Stabilimentum:* 0, absent; 1, present.
(*163*) *Barrier (3D) web:* 0, absent; 1, present.
(*164*) *Hub position:* 0, aerial; 1, against substrate.
(*165*) *Hub relative position:* 0, central; 1, displaced up; 2, displaced down.
(*166*) *Hub bite-out:* 0, present; 1, absent.
Note: *Nephila, Nephilengys, Herennia, Clitaetra, Phonognatha* and *Uloborus* leave the hub intact after completing the orb web, whereas araneids and tetragnathids remove it by biting it out. The character corresponds to character 45 in Hormiga *et al*. (1995), which was modified from the states G1 (hub left intact), G2 (hub centre removed) and G4 (entire hub removed) in Eberhard (1982).
(*167*) *Hub:* 0, closed; 1, open.
(*168*) *Hub-cup:* 0, absent; 1, present (Figs 14*A–B* – arrow, 25*B* – arrow).
Note: the hub of *Herennia* orbs is in the shape of a depression of dense silk, coming in touch with the substrate. Robinson and Lubin (1979) referred to the structure as the hub-cup.
(*169*) *Hub loop – non-sticky spiral transition:* 0, gradual; 1, abrupt.
(*170*) *Radius construction:* 0, cut and reeled; 1, doubled.
Note: corresponds to the characters 49 in Hormiga *et al*. (1995) and in part to 76 in Scharff and Coddington (1997), all modified from Eberhard's (1982) character F (states F1, F2, F4). In araneids and tetragnathids the trip from hub to frame on a pre-existing radius attaches a new 'temporary radius', which is then cut and reeled on the way back to hub, while laying a new one behind (see Eberhard, 1982: fig. 5*A–D*, character state F1). Uloborids and nephilids do not cut and reel but spin a double radius (Eberhard 1982: figs 6, 8).
(*171*) *Radius attachment on frame:* 0, attached singly; 1, attached twice.
(*172*) *Secondary (split) radii:* 0, absent; 1, present.
(*173*) *Tertiary (split) radii:* 0, absent; 1, present.
(*174*) *Pseudoradii:* 0, absent; 1, present (Figs 15, 25*A*).
Note: a unique feature in *Herennia* webs (where known) are perpendicular 'radii' (which do not run through the hub) described and termed pseudoradii by Robinson and Lubin (1979: Fig. 2).
(*175*) *Sticky spiral:* 0, spiralling; 1, parallel.
(*176*) *Non-sticky spiral (NSS):* 0, removed; 1, persists in web.
(*177*) *NSS form:* 0, linear; 1, zig-zag *Nephila* form.
(*178*) *First sticky spiral (SS) spiral–NSS contact:* 0, NSS contacted; 1, no contact.
(*179*) *Sticky spiral localisation:* 0, oL1; 1, iL1; 2, oL4.
(*180*) *Web posture:* 0, flexed legs I, II; 1, extended legs I, II.
(*181*) Argiope *posture:* 0, absent; 1, present.
Note: a typical web pose of *Argiope* species is with first two and last two leg pairs close together, thus forming a 'leg-cross'.
(*182*) *Attack behaviour:* 0, wrap-bite; 1, bite-wrap.
(*183*) *Wrap-bite silk:* 0, dry; 1, sticky.
(*184*) *Cheliceral clasp:* 0, absent; 1, present.
(*185*) *Bulbus detachment (eunuchs):* 0, absent; 1, present.
(*186*) *Body shake:* 0, absent; 1, present.
Note: in *Clitaetra, Nephilengys* and some *Nephila* a body shake is a common behavioural ritual in response to threat. A similar behaviour is known in *Argiope*.
(*187*) *Side change:* 0, absent; 1, when in danger, rushing on other side of orb.
(*188*) *Partial web renewal:* 0, absent; 1, present.
(*189*) *Retreat:* 0, absent; 1, off-web; 2, in web.
(*190*) *Retreat form:* 0, silken tube; 1, utilisation of a leaf.

Appendix 2. Phylogenetic matrix

Taxa	Characters									
	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000001
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Deinopis	0000000000	0000000000	0000000000	0000000000	0000000000	000000-000	0000---000	-00000-0-0	0000000000	-0000----0
Uloborus	0001000000	0200100001	0000000000	0000000000	0110000000	100100-000	1000---000	-10000-0-0	1000111100	-000000-00
Araneus	0000000000	0110001101	0000011101	1000000000	0000000000	11010101-1	1000---101	400000-0-1	111-1?11?1	0101000100
Argiope aurantia	0001000000	1101112201	0003111100	1000000000	0000000000	A001110001	0100---101	401000-0-0	1101122111	0101000101
Argiope argentata	0001000000	1101112201	0103111100	1000000000	0000100000	1011110001	0100---101	4010010120	111-122101	0101000101
Linyphia	0000010001	0200101111	1000000000	0010-11000	000001011-	100000-1-1	1000---000	-100010100	101-112000	-110111000
Pimoa	0000010001	0200001111	0010000000	0011-11000	000001011-	100000-1-1	1000---000	-01000-0-0	001-111100	-110111000
Steatoda	0000000001	0200101111	0010000000	0101-1101-	-00000111-	10000101-1	1000---000	-10000-0-0	101-111100	-110101010
Nesticus	0000010001	0201101111	1010000000	0101-1001-	-00000111-	100000-1-0	1000---000	-10000-0-0	1000111100	-111101010
Epeirotypus	1000000001	0201101101	0000000000	0001-10000	000000001-	10000101-1	1100---010	-10000-0-0	1000011100	-111101000
Tetragnatha	0000010001	0200100000	0000000000	0100001000	010000001-	01000101-1	1000---111	410-0-----	000?1-0000	-101101000
Meta	0000010001	0200001101	1000011101	0100001000	000000001-	1000010001	1000---001	400010-0-0	101-112000	-101101000
Leucauge	0000010001	0200101101	1100010100	0000001000	010000001-	100000-1-1	1000---111	010000-0-0	101-012101	0101101100
Deliochus	0000000001	0210101101	0000010000	1000000100	000000011-	10000A0A01	1000---000	-100010110	101-110101	010110100A
Phonognatha graeffei	1100000001	1210101101	0003010100	1000000100	000000011-	1000010001	1000---000	-001010A00	101-120100	-10110100A
Clitaetra episinoides	0000000000	0200110001	0103100010	0000100000	0000000001	1300011001	1000101101	010000-0-0	1000111100	-101101100
Clitaetra irenae	0001000000	0200110001	0003100000	0000100000	0000000001	1300111001	1000101101	000010-0-0	1001111100	-10110110A
Nephila fenestrata	1111100000	1110101101	0002011111	1000100000	0011100001	AA00010011	0100100001	1010110111	011-111111	1101101101
Nephila pilipes	1100A00000	1110101101	0000011101	1000100001	0011100001	0100010011	0100100001	301110-0-0	0100011101	1101101101
Nephilengys malabarensis	1100001000	1110100001	0001111100	1000100000	0000000001	1000010001	01010--101	2010010110	111-111110	-101101101
Nephilengys cruentata	1101001000	1110100001	0001111110	1000100000	0000000001	1000010001	01010--101	20110110-1	011-121101	1101101101
Herennia multipuncta	0011000110	1100100001	0101111110	1000100001	0000000001	2010110011	0110110101	0010011100	011-112111	1101101101
Herennia etruscilla	0011000100	1100100001	0101111110	1000100000	0000000001	2010110011	0110110101	0010011100	011-112111	1101101101
Herennia deelemanae	0011000100	1100100001	0101111110	1000100000	0000000001	1010010011	01100--101	0010011100	011-1???? 1	11???????1
Herennia papuana	0011000100	1100100001	0101111110	1000100001	0000000001	1010110001	0110110101	0010011100	011-1???? 1	1101101101
Herennia tone	00110001A0	1100110001	0101111110	1000100001	1000000001	1010110011	01100--101	0010011100	011-112111	11????????
Herennia gagamba	0011000110	1100100001	0001111110	1000100001	1000000001	1010110011	01100--101	0010010110	011-1121?1	1101101102
Herennia agnarssoni	0011000100	1100110001	0101111110	1000100000	1000000001	1010110011	01100--101	0010011100	011-1???? 1	1101101102

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Appendix 2. (continued)

Taxa	Characters								
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Deinopis	0000000000	00000-----	-00-00--00	000000----	----000000	00000A00A0	000000---0	000000--00	00--00000-
Uloborus	0001000001	10000-----	-00-010000	000000----	----100000	0000001000	010001-001	010000-001	00-?00010-
Araneus	0101201001	2001100000	010-010000	000000----	----210110	0110011010	0000000000	0?0000-000	000000000-
Argiope aurantia	0111000100	1001100000	010-010100	000100----	----110110	0111110010	0100000000	0??000-000	100001?00-
Argiope argentata	1101200000	1001100000	010-110100	000110----	----110110	0111111010	01A0000000	010000-?00	100001100-
Linyphia	0110100000	10011-3100	000-00--00	001--0----	----100110	00000111--	001-------	---------0	01-?00-10-
Pimoa	0110000000	1001104100	010010000	000000----	----100000	00000111--	001-------	---------0	01-?0?-10-
Steatoda	0110002000	00000-----	-00-011000	010110----	----100110	00000112--	001-------	---------0	001?00-00-
Nesticus	0110012000	1001103110	0010011000	011--0----	----100000	00000112--	001-------	---------0	001000-00-
Epeirotypus	0110000000	0000100000	001?010000	000100----	----110000	0000010010	0000001010	000000-110	01-?00000-
Tetragnatha	0010A10110	11101-1110	000-10--00	000110----	----100110	0000011000	0000001010	000000-111	01-100000-
Meta	0110000000	0000101100	011000--00	000110----	----210111	1000000010	0000001010	000000-110	000000000-
Leucauge	0110000010	1100101100	001000--00	000110----	----100110	00000110A0	00A0001010	000000-110	000100000-
Deliochus	0110000000	1001A--0--	-10-10--00	00000110-1	0000100110	0000111010	000020100?	?10000-?00	01-?100011
Phonognatha graeffei	0110110100	1111105000	000-00--00	001--110-1	0001120110	0100011010	001011-00?	0110010000	01-?000021
Clitaetra episinoides	10102?0?00	100?112101	101000--01	001--10110	0000001111	000001101?	0001??????	?????????0	????0???0-
Clitaetra irenae	10102?0?00	100?112101	101000--01	001--10100	0000001110	000001?011	000111-101	1110110120	01-?01110-
Nephila fenestrata	1101200000	1001112101	101100--00	001--11100	0011001110	1000011010	101011-00?	?110011?20	01-0010?0-
Nephila pilipes	1101200000	1000112101	101100--00	001--10110	0000021110	1000011010	111011-001	0110011120	01-001110-
Nephilengys malabarensis	1001200000	2001112101	101100--00	101--110-0	0110001110	1001011010	00111??10?	?11001?1?0	01-01???10
Nephilengys cruentata	1001200000	2001112101	101100--00	101--110-0	0110001110	1000010010	001111-101	1110011120	01-0110110
Herennia multipuncta	1001200000	1001112001	001000--10	001--110-0	1110001110	100011?011	0001???1??	?????????0	0???1???0-
Herennia etruscilla	1001200000	1001112001	0010?0--10	001--110-0	1110001110	???011?011	0001???10?	???1?????0	0???1???0-
Herennia deelemanae	1001200000	1001112?01	0010?0--10	001--110-0	1110001110	?????1????	??????????	??????????	??????????
Herennia papuana	1001200000	1001112101	001000--10	001--110-0	0110001110	1000110011	000111-101	1??111??20	01-010010-
Herennia tone	??????????	??????????	??????????	?????1?0-?	111000????	??????????	??????????	??????????	??????????
Herennia gagamba	??????????	??????????	??????????	?????1?0-?	111000????	??????????	??????????	??????????	??????????
Herennia agnarssoni	??????????	??????????	??????????	?????1?0-?	??????????	??????????	??????????	??????????	??????????

–, Inapplicable data; ?, unknown entries; A, polymorphic data (= [01]).