

Article

The Other Side of the Coin: Taxonomic Updates and Species Key of *Herennia* (Araneae: Nephilidae) †

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Abstract

Coin spiders of the genus *Herennia* Thorell, 1877 are species-rich nephilids distributed across South, East, and Southeast Asia and Australasia. They are notable for ladder-shaped arboricolous webs, extreme sexual size dimorphism, and complex sexual behaviors. The most recent revision recognized 11 species, only 4 of which were described from both sexes. Here, we present a taxonomic revision integrating new morphological and molecular data and recognize 14 species. We describe three new species—*H. eva* Kuntner from Sulawesi, *H. maj* Kuntner from Vietnam, and *H. tsoi* Kuntner et al. from Taiwan—and document previously unknown males of *H. oz* Kuntner, 2005 from Australia and *H. tone* Kuntner, 2005 from the Philippines. We also extend the known distribution of *H. papuana* Thorell, 1881 from New Guinea to Australia. Although several molecular species-delimitation analyses suggest *H. oz* and *H. etruscilla* Kuntner, 2005 may be conspecific, consistent and diagnostic morphological differences support their recognition as distinct species. We provide an updated identification key to all valid *Herennia* species. Additional undescribed endemics are likely to occur across the Asian mainland and the rapidly disappearing forests of Southeast Asian and Australasian islands. The genus' biogeographic pattern, shaped by an ancestrally broad distribution spanning the Wallace Line, may reflect repeated loss and regain of ballooning, a hypothesis that warrants experimental and comparative testing.

Keywords: orbweb spiders; Araneoidea; taxonomy; Wallace Line; biogeography; vicariance



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1. Introduction

Spiders of the genus *Herennia* Thorell, 1877 [1]—commonly known as coin spiders—owe their name to their flattened, often lobed abdomens that recall ancient coin artifacts (Figure 1a–c; see etymology of *Herennia etruscilla* Kuntner, 2005 [2]). Within Nephilidae Simon, 1894 [3], *Herennia* is the most readily recognizable genus, distinguishable by its overall

morphology and its characteristic web architecture [2,4]. Females are medium-sized, with a warty carapace and a lobed abdomen that is white dorsally and bright orange ventrally (Figure 1a–c). They spin vertically oriented, elongated ladder webs that contour closely to tree trunks, especially in subadult and adult females (Figure 1d; [4]). Males, by contrast, are several times smaller, lack abdominal ornamentation, and are far less conspicuous (Figure 1a,c). As a result, they are frequently missed in the field and remain underrepresented in collections. Yet it is the fine diagnostic morphology of the male pedipalps that underpins species-level taxonomy in *Herennia*.

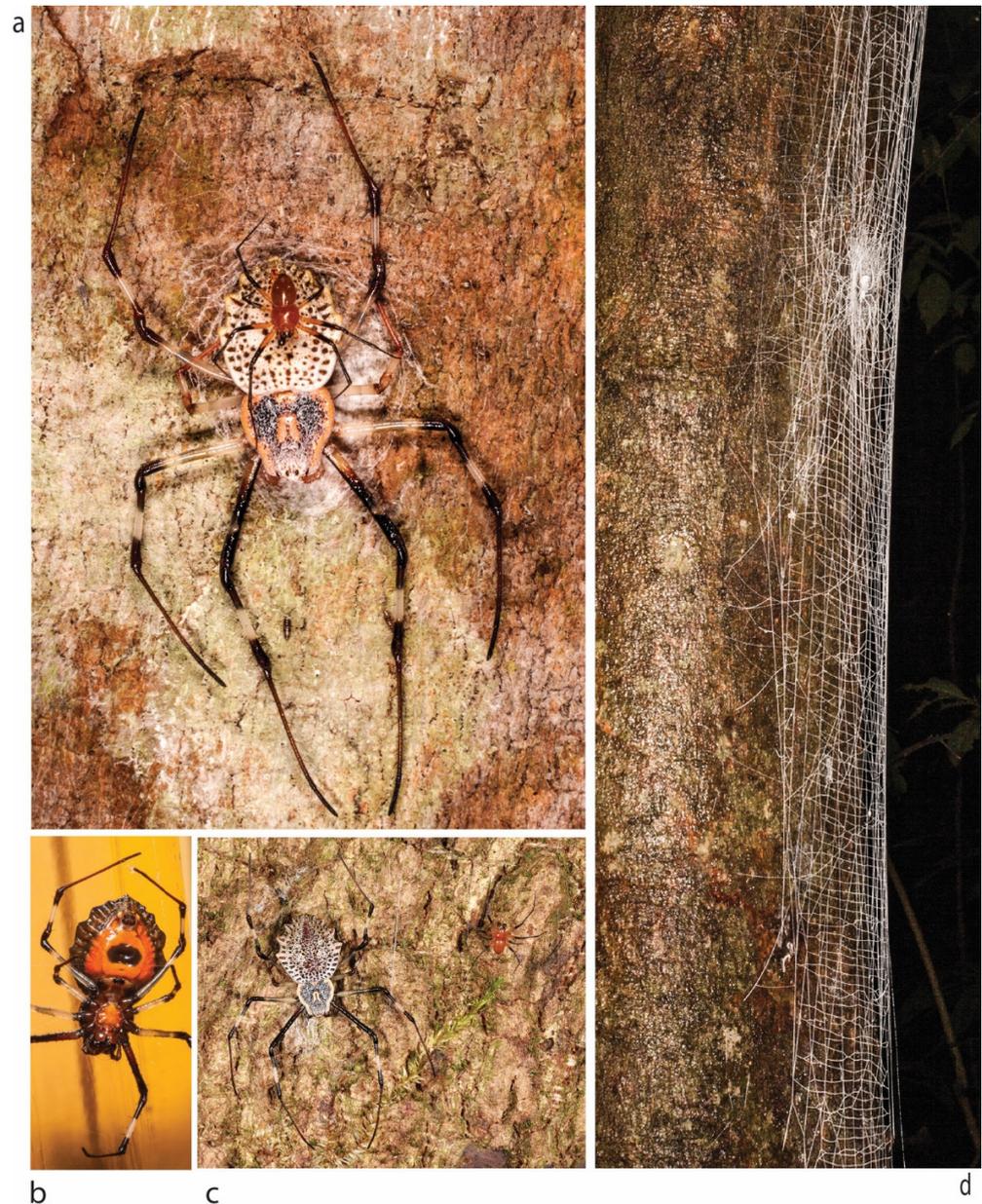


Figure 1. Coin spider species *Herennia multipuncta* (Doleschall, 1859): (a) a female from Singapore carrying her male suitor (note the absence of one of his palps—eunuch); (b) female ventral side showing the typical coloration in Singapore; (c) female (left) and male in female web, from Laos; (d) typical ladder web (dusted for contrast) on a tree trunk, female from Singapore. All photos by M. Kuntner.

The scarcity of examined males has long impeded taxonomic work on *Herennia*. In the previous revision of the genus [2], males were described for only 4 of the 11 species then known—*H. deelemanae* Kuntner, 2005, *H. etruscilla* Kuntner, 2005, *H. multipuncta* (Doleschall,

1859) [5], and *H. papuana* Thorell, 1881 [6]. The same revision diagnosed and described seven additional species based solely on female morphology: *H. agnarssoni* Kuntner, 2005, *H. gagamba* Kuntner, 2005, *H. jernej* Kuntner, 2005, *H. milleri* Kuntner, 2005, *H. oz* Kuntner, 2005, *H. sonja* Kuntner, 2005, and *H. tone* Kuntner, 2005.

Coin spiders are restricted to South and East Asia, Southeast Asia, and Australasia. The spotted coin spider, *H. multipuncta* (Figure 1), is the most widespread species, ranging from India and Sri Lanka across Nepal, Myanmar, Thailand, Laos, Cambodia, Vietnam, southern China, Malaysia, Singapore, and Indonesia to the Philippines [2]. As shown here, and contrary to the 2005 revision, it does not occur in Taiwan. The IUCN Red List currently classifies the species as “Least Concern,” with a stable population trend [7].

All remaining *Herennia* species have much narrower distributions. The Javan coin spider (*H. etruscilla*, endemic to Java and the Lesser Sunda Islands), the Papuan coin spider (*H. papuana*, endemic to Papua New Guinea and Australia), and the Australian coin spider (*H. oz*, endemic to Australia) are also listed as “Least Concern,” though their population trends remain unknown [7]. In contrast, the Philippine coin spider (*H. gagamba*) is assessed as “Vulnerable” and is confined to a small region of Luzon, where its habitat is inferred to be declining [7].

Six additional species lack sufficient distributional data and are therefore classified as “Data Deficient” [7]: the Bornean coin spider (*H. deelemanae*, Sabah, Malaysia), Sonja’s coin spider (*H. sonja*, Kalimantan and Sulawesi, Indonesia), Miller’s coin spider (*H. milleri*, Bismarck Archipelago, Papua New Guinea), Agnarsson’s coin spider (*H. agnarssoni*, Solomon Islands), Tone’s coin spider (*H. tone*, Visayas, Philippines), and Jernej’s coin spider (*H. jernej*, Sumatra, Indonesia). Among these, *H. deelemanae* shows signs of population decline. Additional specimens and updated surveys are urgently needed to refine species taxonomy and conservation assessments before further losses occur.

The biology of *Herennia*, the most species-rich nephilid genus [8], is striking but remains poorly explored. Their distinctive ladder-web architecture is unique among spiders [4]. It represents a gradual modification of the ancestral aerial orb web, passing through an intermediate hybrid stage [8] and developing ontogenetically from a small, rounded juvenile orb to the large, elongated, asymmetric ladder webs spun by adult females [4].

All *Herennia* species exhibit extreme sexual size dimorphism (eSSD), with large females and markedly small males—a pattern shaped by opposing pressures of natural and sexual selection [8,9]. eSSD, together with its characteristic mating syndrome [9], produces intense sexual conflict, including male genital damage that plugs female copulatory ducts and, in some cases, full emasculation that yields highly aggressive eunuch males [10]. These behaviors have been documented primarily in *H. multipuncta* [11], while other species remain unstudied in this context [12]. Comparative work across the genus could provide valuable insights into the evolution of sexual systems such as monogyny [13].

The primary aim of this study is to update the previous taxonomic revision of *Herennia* [2] by integrating new morphological and molecular evidence for a total of 14 species. We describe new species from Sulawesi, Vietnam, and Taiwan; document previously unknown males of *H. oz* (Australia) and *H. tone* (Philippines); and extend the known range of *H. papuana* from New Guinea into Australia. A complete identification key to all valid *Herennia* species is provided.

These taxonomic advances have already supported a revised species-level phylogeny and a reinterpreted biogeographic history of the genus [14]. The work also contributes to broader discussions on the evolution of eSSD within *Herennia* and across Nephilidae.

2. Materials and Methods

2.1. Specimens Examined

We combined new fieldwork across Asia and Australia with targeted searches in major museum collections. Materials essential for this taxonomic revision are listed in Supplementary Table S1, to be considered alongside those reported in [2]. The following museum and institute abbreviations are used: MMUE—The Manchester Museum, University of Manchester, UK; NIB—National Institute of Biology, Ljubljana, Slovenia; QM—Queensland Museum, Brisbane, Australia; SMF—Senckenberg Museum, Frankfurt, Germany; USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMMU—Zoological Museum of Moscow State University, Russia.

2.2. Morphological Methods

Specimens were examined, measured, and imaged using a Leica M205C stereomicroscope (Leica Microsystems, Wetzlar, Germany) and a Keyence VHX7000 digital microscope (Keyence International, Mechelen, Belgium). All measurements are given in millimeters. Anatomical terminology follows the previous taxonomic revision [2] and the morphological homology framework for Nephilidae and Orbipuræ [15,16]. The following abbreviations appear in the text and figures: ALE—anterior lateral eye(s); AME—anterior median eye(s); ATA—apical tegular apophysis; CB—cymbium; E—embolus; EB—embolus base; EC—embolic conductor; EC-m—membranous portion of embolic conductor; P—paracymbium; PLE—posterior lateral eye(s); PME—posterior median eye(s); ST—subtegulum; T—tegulum.

2.3. Molecular Species Delimitation

To complement the morphology-based taxonomy, we applied five molecular species delimitation approaches grounded in the phylogenetic framework of [14]: (i) multi-rate Poisson Tree Processes (mPTP) [17], (ii) Bayesian Poisson Tree Processes (bPTP) [18], (iii) Generalized Mixed Yule–Coalescent (GMYC) [19], (iv) Automatic Barcode Gap Discovery (ABGD) [20], and (v) Assemble Species by Automatic Partitioning (ASAP) [21].

The tree-based methods (mPTP, bPTP, GMYC) were applied to COI phylogenies reflecting relationships recovered in previous studies [8,14]. GMYC employing the single-threshold model was run on an ultrametric COI chronogram inferred in BEAST 2 [22], using bModelTest [23] for nucleotide substitution model selection and a strict molecular clock. Four MCMC chains were run for 10 million generations to ensure convergence. mPTP and bPTP were conducted on the corresponding non-ultrametric COI phylogenies, using online implementations with default parameters. Distance-based methods (ABGD and ASAP) were performed via their respective online servers under all available substitution models (Jukes–Cantor, Kimura, and simple distance).

Because species delimitation results for the *H. etruscilla* + *H. oz* clade conflicted with morphology, we repeated all five delimitation analyses using the 28S dataset from our previous study [14]. We did not use concatenated COI + 28S data because these tools are optimized for single-locus input. Owing to missing 28S sequences, several populations were represented by different individuals than in the COI dataset, while *H. tone*, *H. milleri*, and *H. papuana* were excluded entirely.

2.4. Taxonomy, Classification, and Nomenclature

We employed the unified species concept [24,25] to determine species validity with morphology as primary evidence (e.g., [26]). We first hypothesized morphospecies based on their diagnostic characteristics, then tested them using the above molecular species delimitation analyses. Species were considered valid if they were morphologically and

molecularly distinct. If species delimitations yielded conflicting results, we used morphological diagnosability as the final arbiter of species limits and validity.

Higher-level classification standards in arachnology are still not universally applied. Here we follow the criteria proposed specifically for nephilids and related lineages [8,16], which emphasize comparable clade ages, monophyly and exclusivity, information content of classifications, and diagnosability. Alternative nomenclatural frameworks exist [27], but apart from requiring monophyly generally lack comparable explicit criteria [28].

3. Results

3.1. Molecular Species Delimitation

Figure 2 summarizes the species delimitation outcomes plotted onto the population-level phylogeny of Turk et al. [14]. For both distance-based methods, all substitution models produced identical results, so only one set is shown. Overall, the five approaches yielded broadly similar patterns, though with several noteworthy conflicts. None of the methods reproduced fully the morphology-based species boundaries, as reflected by current species names in the tree (Figure 2).

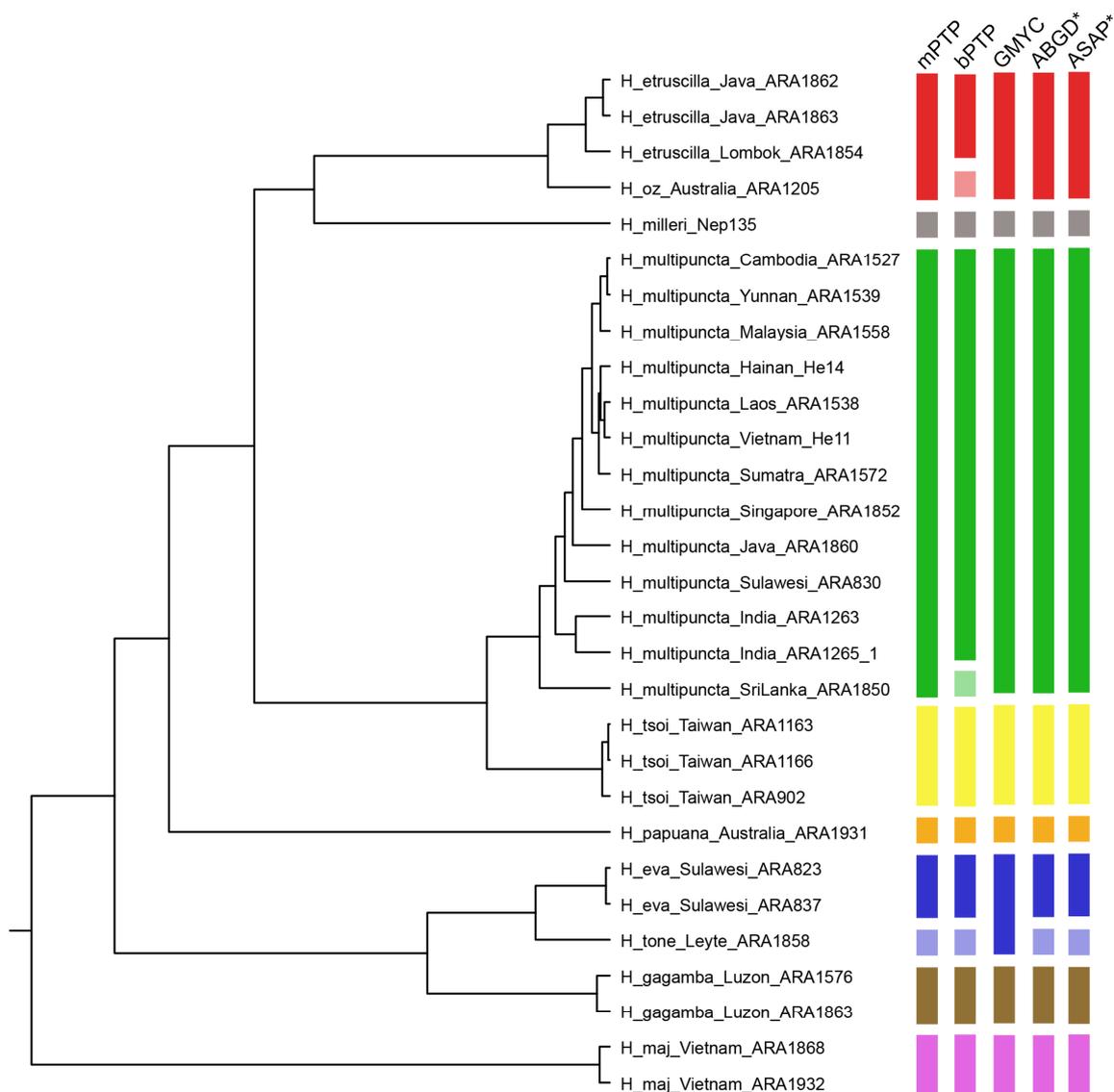


Figure 2. Species delimitation results. Results from three tree-based and two distance-based (marked with *) delimitation methods are plotted on the population-level phylogeny of *Herennia* from Turk et al. [14]. Tip names reflect morphological delimitation.

All methods consistently delimited *H. maj*, *H. gagamba*, *H. papuana*, *H. tsoi*, and *H. milleri* as distinct species. Delimitation among—and in some cases within—the remaining five species varied across methods. bPTP alone flagged the Sri Lankan *H. multipuncta* sample as a separate species. GMYC was the only method to merge *H. eva* and *H. tone* into a single unit. Every method except bPTP grouped *H. etruscilla* and *H. oz* into a single species, both using COI and 28S data. Based on morphological diagnosability and variation, our finalized taxonomy departs from some of the recovered molecular delimitations (see Discussion).

3.2. Classification

Family **Nephilidae** Simon, 1894

Remarks: For diagnosis and justification of Nephilidae, see Kuntner et al. [8,16].

Genus **Herennia** Thorell, 1877

Coin spiders

Remarks: Consult the 2005 genus revision [2] for general *Herennia* taxonomy and biology. This section adds the newly discovered species and the unknown males of *H. tone* and *H. oz.*, and updates the previously described ones.

Describing “*H. ornatissima*” (a synonym of *H. multipuncta*), Simon ([3]: 759, f. 828, 835) depicted a male palp of *H. tsoi* new species and a poorly represented female habitus of an unidentifiable species.

Composition: After this taxonomic update *Herennia* contains 14 species (Table 1).

Distribution: East Asia Southeast Asia, South Asia, and Australasia (Figure 3).

Table 1. Currently known species of coin spiders with known ranges.

Species Name	Author, Year	Comment	Known from	Range	Region
<i>Herennia agnarssoni</i>	Kuntner, 2005	Valid species	female only	Solomon Islands	Solomon Islands
<i>Herennia deelemanae</i>	Kuntner, 2005	Valid species	both sexes	Sabah	Borneo
<i>Herennia etruscilla</i>	Kuntner, 2005	Valid species	both sexes	Java, Lombok	Java, Lesser Sundas
<i>Herennia eva</i>	Kuntner, this paper	New species	both sexes	Sulawesi	Sulawesi
<i>Herennia gagamba</i>	Kuntner, 2005	Valid species	female only *	Luzon	Philippines
<i>Herennia jernej</i>	Kuntner, 2005	Valid species	female only	Sumatra	Sumatra
<i>Herennia maj</i>	Kuntner, this paper	New species	female only	Vietnam	Mainland SE Asia
<i>Herennia milleri</i>	Kuntner, 2005	Valid species	female only	Bismarck Archipelago	New Guinea
<i>Herennia multipuncta</i>	(Doleschall, 1859)	Valid species	both sexes	India to Maluku	Mainland Asia, Greater Sundas, to Maluku
<i>Herennia papuana</i>	Thorell, 1881	Valid species	both sexes	New Guinea, Australia (Queensland)	Australasia
<i>Herennia sonja</i>	Kuntner, 2005	Valid species	female only	Kalimantan, Sulawesi	Borneo, Sulawesi
<i>Herennia tone</i>	Kuntner, 2005	Valid species	both sexes	Negros, Leyte	Philippines
<i>Herennia tsoi</i>	Kuntner et al., this paper	New species	both sexes	Taiwan	Taiwan
<i>Herennia oz</i>	Kuntner, 2005	Valid species	both sexes	Northern Territory	Australia

* Male *H. gagamba* lacking palps was measured but not described (Table 2).

Table 2. Data on sexual size dimorphism (SSD) in nephilid spiders from Kuntner et al. [8], updated for *Herennia* data (in bold) from this paper. All measurements are in millimeters (mm).

Species	Female Body Length	Male Body Length	Body Length SSD
<i>Clitaetra clathrata</i>	7.400	3.900	1.90
<i>Clitaetra episinoides</i>	7.452	4.489	1.66
<i>Clitaetra irenae</i>	6.893	2.660	2.59
<i>Clitaetra perroti</i>	4.551	2.900	1.57
<i>Herennia deelemanae</i>	7.952	3.000	2.65
<i>Herennia etruscilla</i>	10.325	3.665	2.82
<i>Herennia eva</i>	12.267	2.709	4.53
<i>Herennia gagamba</i>	12.950	3.500	3.70
<i>Herennia multipuncta</i>	12.668	2.856	4.43
<i>Herennia papuana</i>	13.600	3.652	3.72
<i>Herennia tone</i>	9.500	2.542	3.74
<i>Herennia tsoi</i>	15.957	3.167	5.04
<i>Herennia oz</i>	12.600	3.390	3.72

Table 2. Cont.

Species	Female Body Length	Male Body Length	Body Length SSD
<i>Indoetra thisbe</i>	3.500	2.570	1.36
<i>Nephila constricta</i>	34.282	2.997	11.44
<i>Nephila pilipes</i>	30.357	4.396	6.91
<i>Nephilengys malabarensis</i>	14.833	2.876	5.16
<i>Nephilengys papuana</i>	14.487	4.193	3.46
<i>Nephilingis borbonica</i>	16.450	3.800	4.33
<i>Nephilingis cruentata</i>	22.328	3.635	6.14
<i>Nephilingis dodo</i>	20.771	6.600	3.15
<i>Nephilingis livida</i>	23.270	3.903	5.96
<i>Trichonephila antipodiana</i>	32.935	3.873	8.50
<i>Trichonephila clavata</i>	21.385	5.184	4.12
<i>Trichonephila clavipes</i>	24.984	3.975	6.28
<i>Trichonephila edulis</i>	18.037	7.108	2.54
<i>Trichonephila fenestrata</i>	21.095	4.129	5.11
<i>Trichonephila inaurata</i>	30.630	5.856	5.23
<i>Trichonephila komaci</i>	32.089	4.415	7.27
<i>Trichonephila plumipes</i>	20.516	4.743	4.33
<i>Trichonephila senegalensis</i>	25.929	7.022	3.69
<i>Trichonephila sexpunctata</i>	27.124	3.478	7.80
<i>Trichonephila sumptuosa</i>	34.863	4.400	7.92
<i>Trichonephila turneri</i>	36.129	4.334	8.34

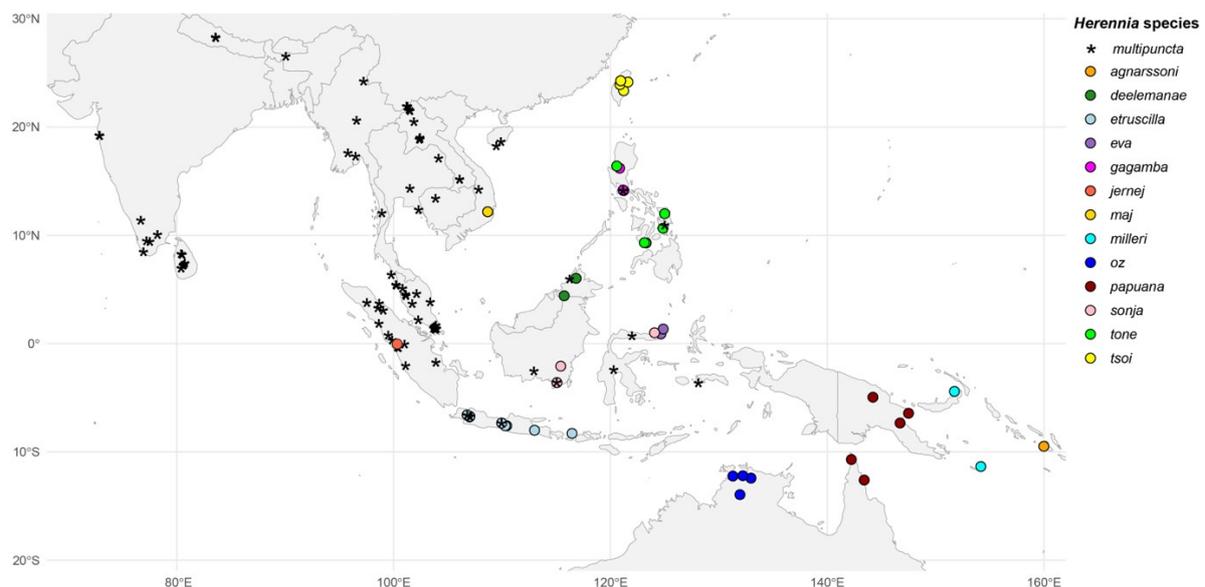


Figure 3. Distributions of currently valid *Herennia* species based on originally examined material (Table S1).

3.3. A Key to *Herennia* Species

This key to the currently known *Herennia* species supersedes the key in Kuntner [2].

Female I.

Male II.

I. (females)

1.

(A) Female carapace has a conspicuous V-shaped mark in its center (Figures 1a and 4a)

2

(B) Female carapace V-shaped mark absent or inconspicuous (Figure 4b)

7

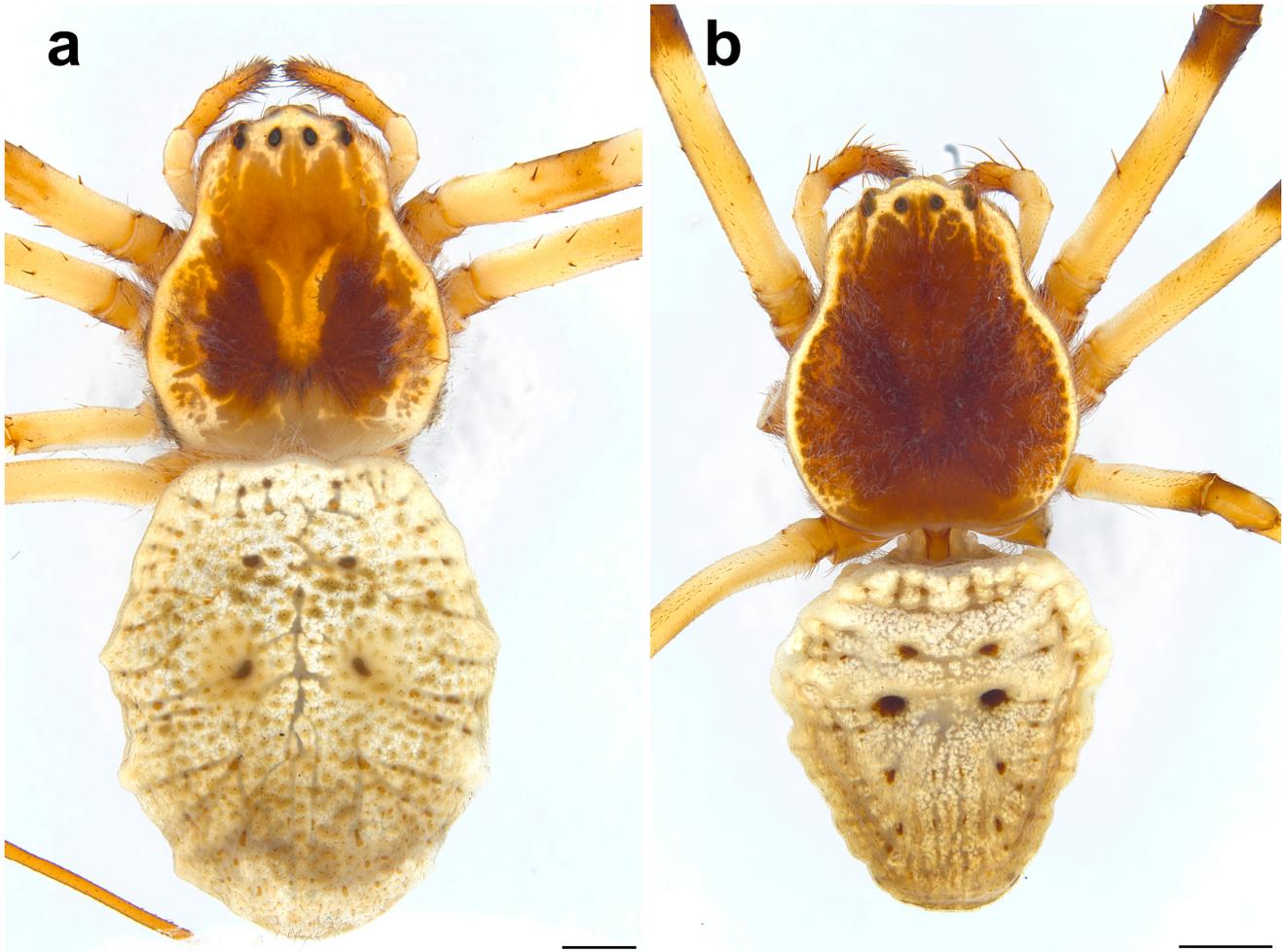


Figure 4. Female somatic characteristics of *Herennia* species: (a) *H. maj* sp. nov. (holotype, ARA1866); (b) *H. deelemanae* Kuntner, 2005 (paratype, HE114). Scale bars: 1 mm.

2.

(A) Epigynal area round, with a thin posterior sclerotized edge (Figure 5a,b)

3

(B) Epigynal area wide, with a broad posterior sclerotized edge (Figure 5c–f)

4

3.

(A) Epigynum with a thin septum and round chambers (Figure 5a); Kalimantan, Sulawesi *H. sonja*

(B) Epigynum with a broad septum and ear-shaped chambers (Figure 5b); Philippines *H. gagamba*

4.

(A) Epigynal lateral sclerotized edge well-sclerotized and sharp where curved around chambers (Figure 5c,d) 5

(B) Epigynal lateral sclerotized edge not sharply defined where curved around chambers (Figure 5e,f) 6

5.

(A) Epigynal chambers round, poorly defined by septum and frontal sclerotized edge (Figure 5c); South and Southeast Asia *H. multipuncta*

(B) Epigynal chambers oval, well defined by septum and frontal sclerotized edge (Figure 5d); Sumatra *H. jernej*

6.

(A) Epigynum with massive chambers and a broad posterior sclerotized edge (Figure 5e); Vietnam *H. maj*

(B) Epigynum with medium sized chambers and a massive posterior sclerotized edge (Figure 5f); Taiwan *H. tsoi*

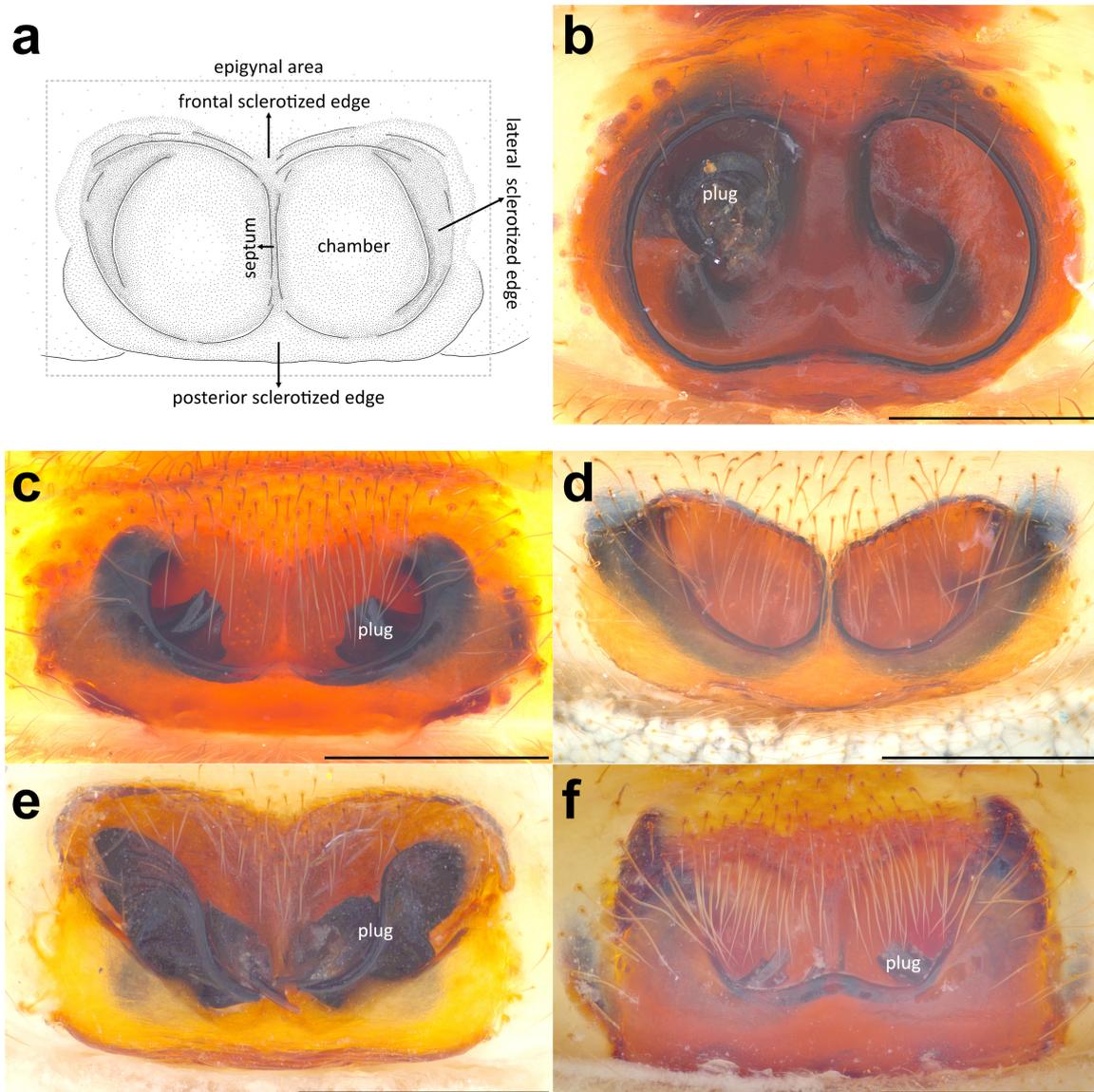


Figure 5. Epigyna of *Herennia* species in ventral view: (a) *H. sonja* Kuntner, 2005 (holotype, redrawn from Kuntner [2]); (b) *H. gagamba* Kuntner, 2005 (paratype, HE54/f1); (c) *H. multipuncta* (Doleschall, 1859) from Java, Indonesia (ARA1860, NIB); (d) *H. jernej* Kuntner, 2005 (holotype, HE19); (e) *H. maj* sp. nov. (holotype, ARA1866); (f) *H. tsoi* sp. nov. (paratype, ARA1222). Scale bars: (a) not available; (b–f) 0.5 mm.

7.

(A) Epigynum with a thin posterior sclerotized edge and inconspicuously defined chambers (Figure 6a,c) 8

(B) Epigynum with a broad posterior sclerotized edge and conspicuous chambers (Figure 6d–h) 10

8.

(A) Epigynal frontal sclerotized edge rounded (Figure 6a); North Borneo

H. deelemanae

(B) Epigynal frontal sclerotized edge straight (Figure 6b,c) 9

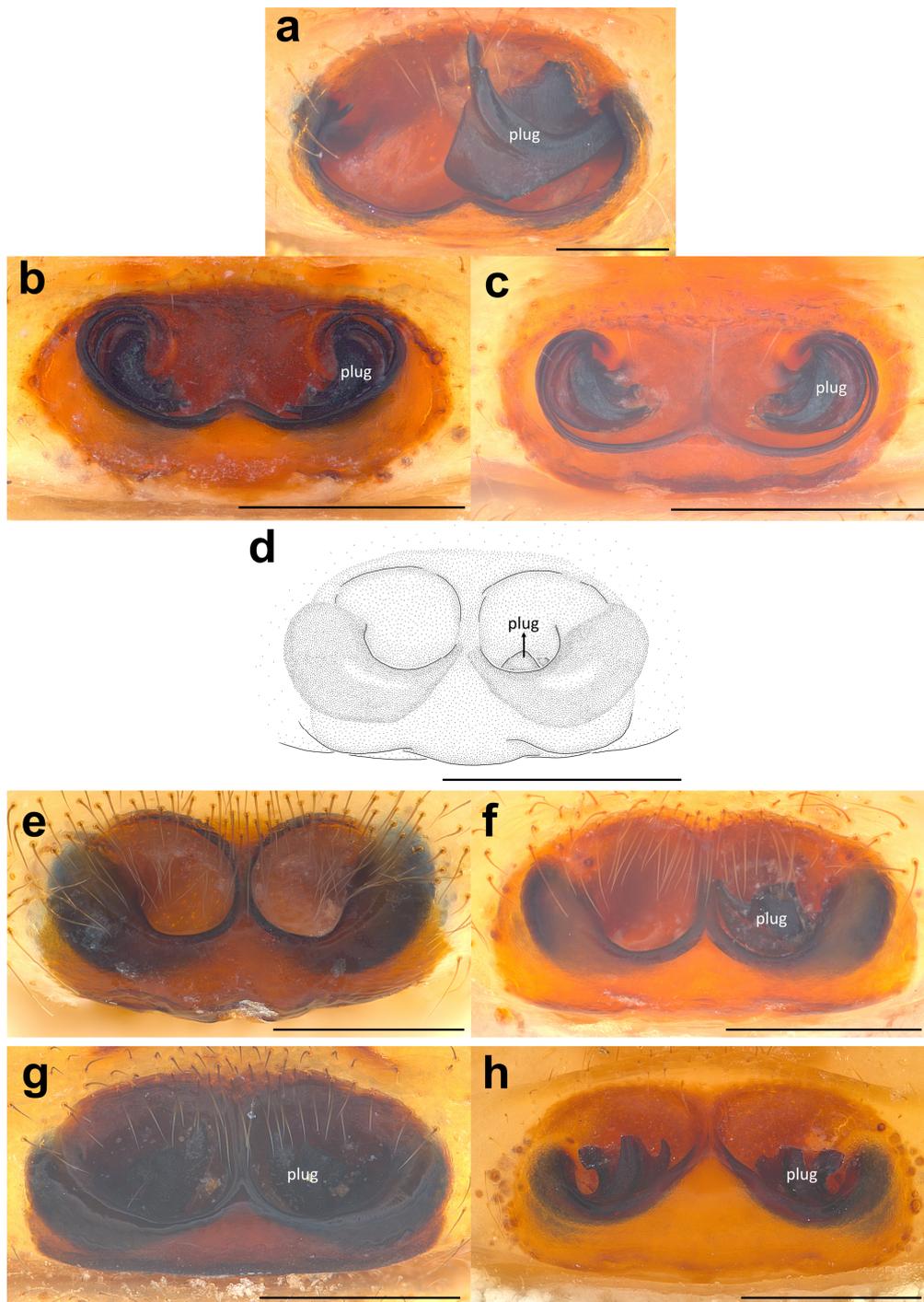


Figure 6. Epigyna of *Herennia* species in ventral view: (a) *H. deelemanae* Kuntner, 2005 (paratype, HE114); (b) *H. eva* sp. nov. (paratype, ARA840); (c) *H. tone* Kuntner, 2005 (ARA1858, NIB); (d) *H. agnarssoni* Kuntner, 2005 (holotype, redrawn from Kuntner [2]); (e) *H. papuana* Thorell, 1881 from Queensland, Australia (QM-S91352); (f) *H. milleri* Kuntner, 2005 (holotype, HE113); (g) *H. etruscilla* Kuntner, 2005 (ARA1854, NIB); (h) *H. oz* Kuntner, 2005 (holotype, HE22). Scale bars: (a) 0.2 mm; (b–h) 0.5 mm.

9.

(A) Epigynal lateral sclerotized edge ear-shaped (Figure 6b); Sulawesi *H. eva*

(B) Epigynal lateral sclerotized edge rounded (Figure 6c); Philippines *H. tone*

10.

(A) Epigynal lateral sclerotized edge massive, reaching into the frontal third of the epigynal area (Figure 6d–f) 11

(B) Epigynal lateral sclerotized edge moderately broad and confined to the posterior half of the epigynal area (Figure 6g,h) 13

11.

(A) Epigynal septum inconspicuous (Figure 6d); Solomon Islands *H. agnarssoni*

(B) Epigynal septum well defined (Figure 6e,f) 12

12.

(A) Epigynal chambers ovoid (Figure 6e); Papua New Guinea, Australia (QLD)

H. papuana

(B) Epigynal chambers round (Figure 6f); Bismarck Archipelago, Papua New Guinea
H. milleri

13.

(A) Posterior epigynal sclerotized edge defines a conspicuous but not exaggerated septum and spherical chambers (Figure 6g); Java, Lombok *H. etruscilla*

(B) Massive posterior epigynal sclerotized edge defines an exaggerated septum and ovoid chambers (Figure 6h); Australia (NT) *H. oz*

II. (males)

NB: Males of *H. agnarssoni*, *H. jernej*, *H. maj*, *H. milleri*, *H. sonja* remain unknown. The single male of *H. gagamba* was measured (Table 2) but lacked the palps, hence its diagnostic morphology remains unknown.

1.

(A) Distal part of the EC with a distinct hook (Figure 7a-red arrow) 2

(B) Distal part of the EC without a distinct hook (Figure 8) 5

2.

(A) In lateral view, EC tip is bent outwards (Figure 7a,b) 3

(B) In lateral view, EC tip is bent inwards (Figure 7c,d) 4

3.

(A) Distally, EC is broad, with an undulating flap (Figure 7a); South and Southeast Asia

H. multipuncta

(B) Distally, EC is thin and square-shaped (Figure 7b); Taiwan *H. tsoi*

4.

(A) EC tip curve is long, over half EC length (Figure 7c); Java, Lombok

H. etruscilla

(B) EC tip curve is short, about a third EC length (Figure 7d); Australia (NT)

H. oz

5.

(A) In lateral view, EC tip points down (Figure 8a,b) 6

(B) In lateral view, EC tip points up (Figure 8c,d) 7

6.

(A) Subdistal part of the EC with a bump (Figure 8a); Sulawesi *H. eva*

(B) Subdistal part of the EC smooth (Figure 8b); Philippines *H. tone*

7.

(A) Distal part of EC broad and square-shaped (Figure 8c); North Borneo

H. deelemanae

(B) Distal part of EC thin, finger-shaped (Figure 8d); Papua New Guinea, Australia (QLD) *H. papuana*

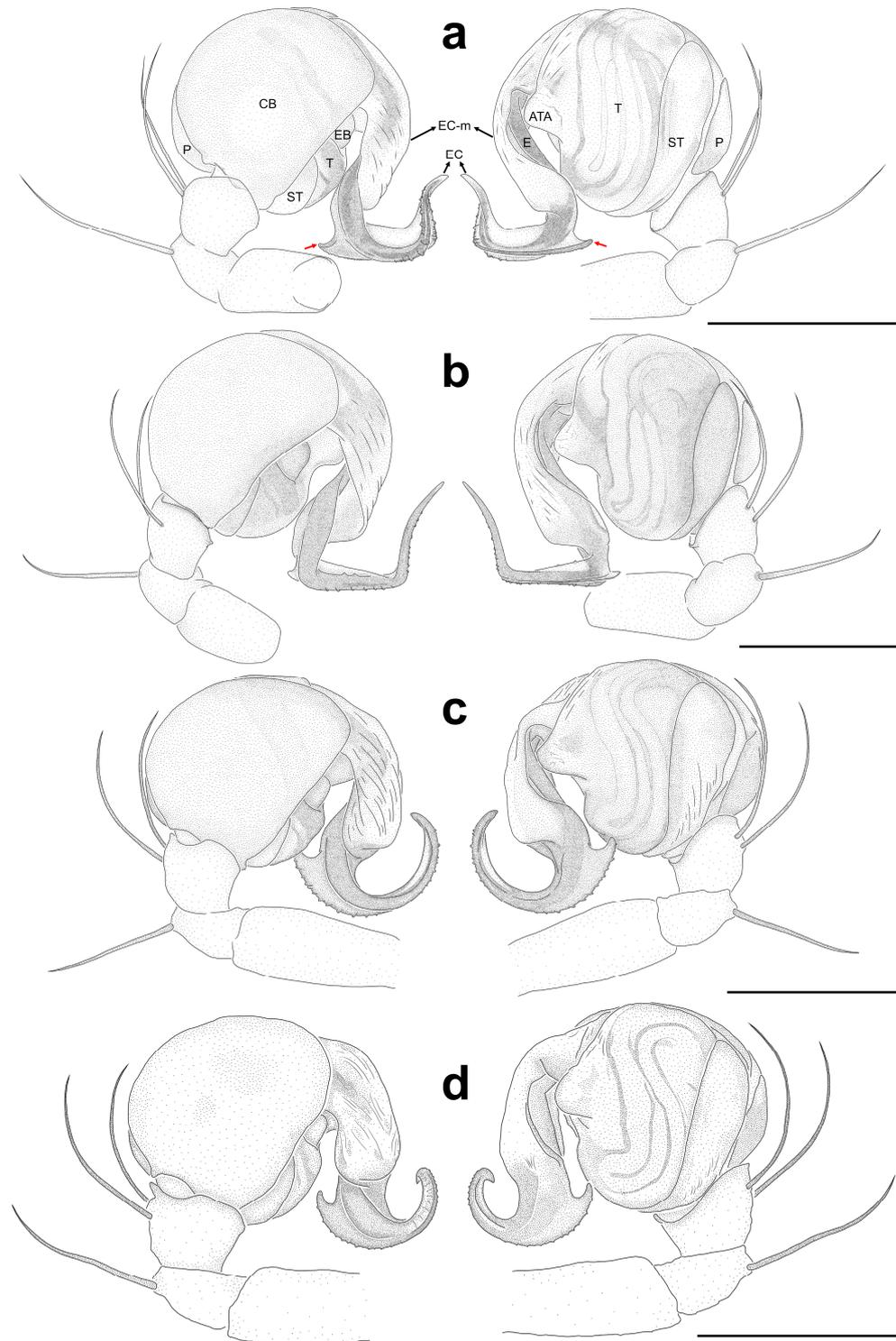


Figure 7. Palps of *Herennia* species in mesal (left) and ectal (right) views: (a) *H. multipuncta* (Doleschall, 1859) from India (ARA1264, NIB). Red arrows highlight the hook on the embolic conductor (EC); (b) *H. tsoi* sp. nov. (holotype, ARA1222); (c) *H. etruscilla* Kuntner, 2005 (ARA1857, NIB); (d) *H. oz* Kuntner, 2005 (QM-S124106). Scale bars: 0.5 mm.

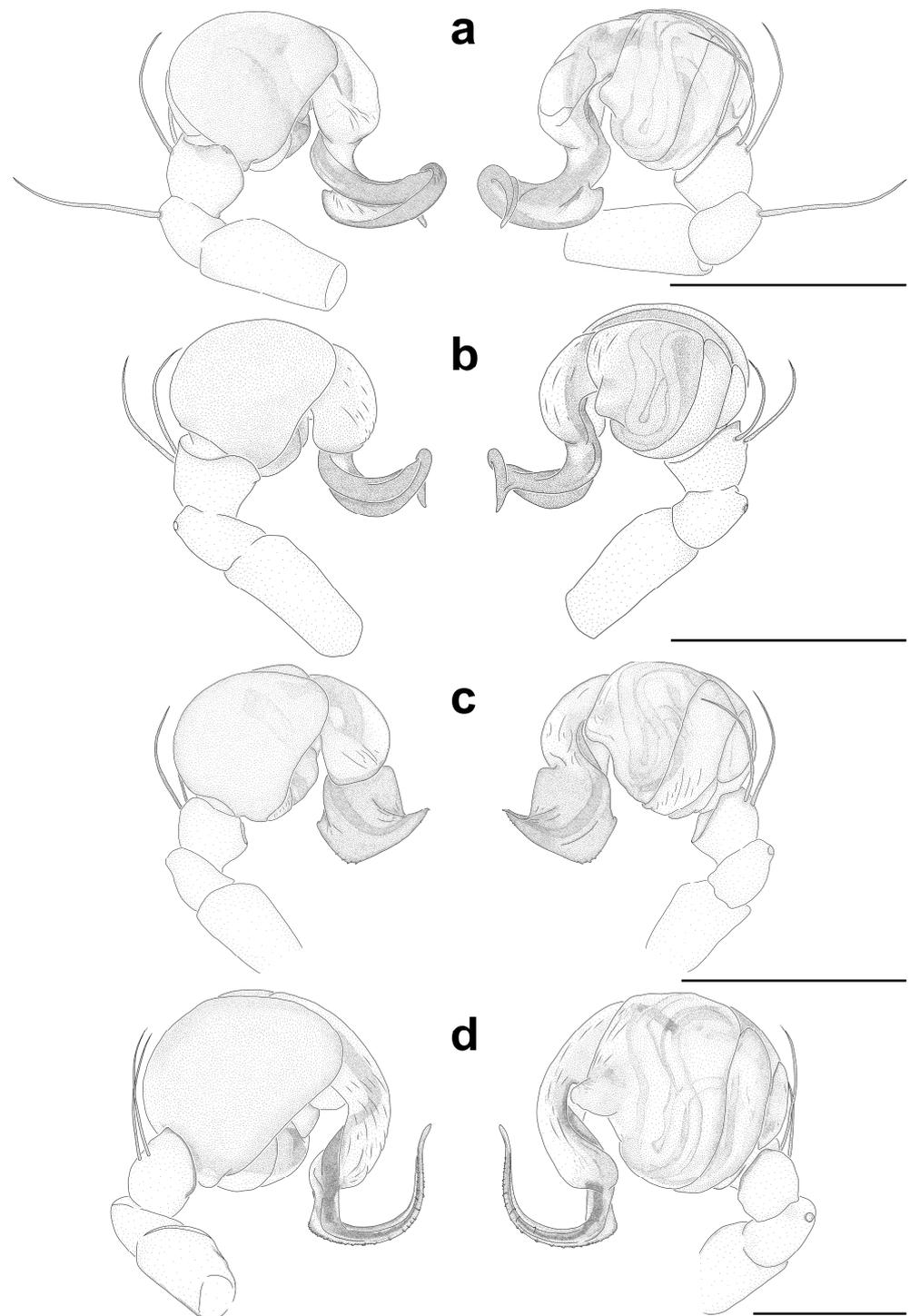


Figure 8. Palps of *Herennia* species in mesal (**left**) and ectal (**right**) views: **(a)** *H. eva* sp. nov. (holotype, ARA826); **(b)** *H. tone* Kuntner, 2005 (holotype, ARA1859); **(c)** *H. deelemanae* Kuntner, 2005 (holotype, HE115); **(d)** *H. papuana* Kuntner, 2005 from Queensland, Australia (ARA1931). Scale bars: 0.5 mm.

3.4. Taxonomic Updates

Herennia eva Kuntner, new species

Eva's coin spider

Figures 6b, 8a and 9a–f

ZooBank ID: urn:lsid:zoobank.org:act:D09054BB-DFE2-4C8D-BBD5-960F1522BBE4

Types: Holotype male (ARA825) and paratype female (ARA840), both deposited in USNM from: “Sulawesi: Mahawu Mt. Area near Tomahon, 8.vii.2013, N1.3468, E124.8709, M. Kuntner coll.”

Additional material examined: See Table S1.

Etymology: The first author is naming this species to honor his daughter Eva. The species epithet is to be treated as a noun in apposition.

Diagnosis: In contrast to *H. multipunctata*, *H. tsoi*, *H. maj* (Figure 4a), *H. jernej*, *H. sonja*, and *H. gagamba*, the female carapace in *H. eva* lacks a distinct V-shaped mark (Figure 9a,c). The female resembles that of *H. tone*, but their epigyna are diagnosable: in *H. eva*, the epigynal lateral sclerotized edge is ear-shaped (Figures 6b and 9d) rather than rounded. The *H. eva* male palp has a massive embolic conductor with a distinct proximal bump (Figures 8a and 9e,f).

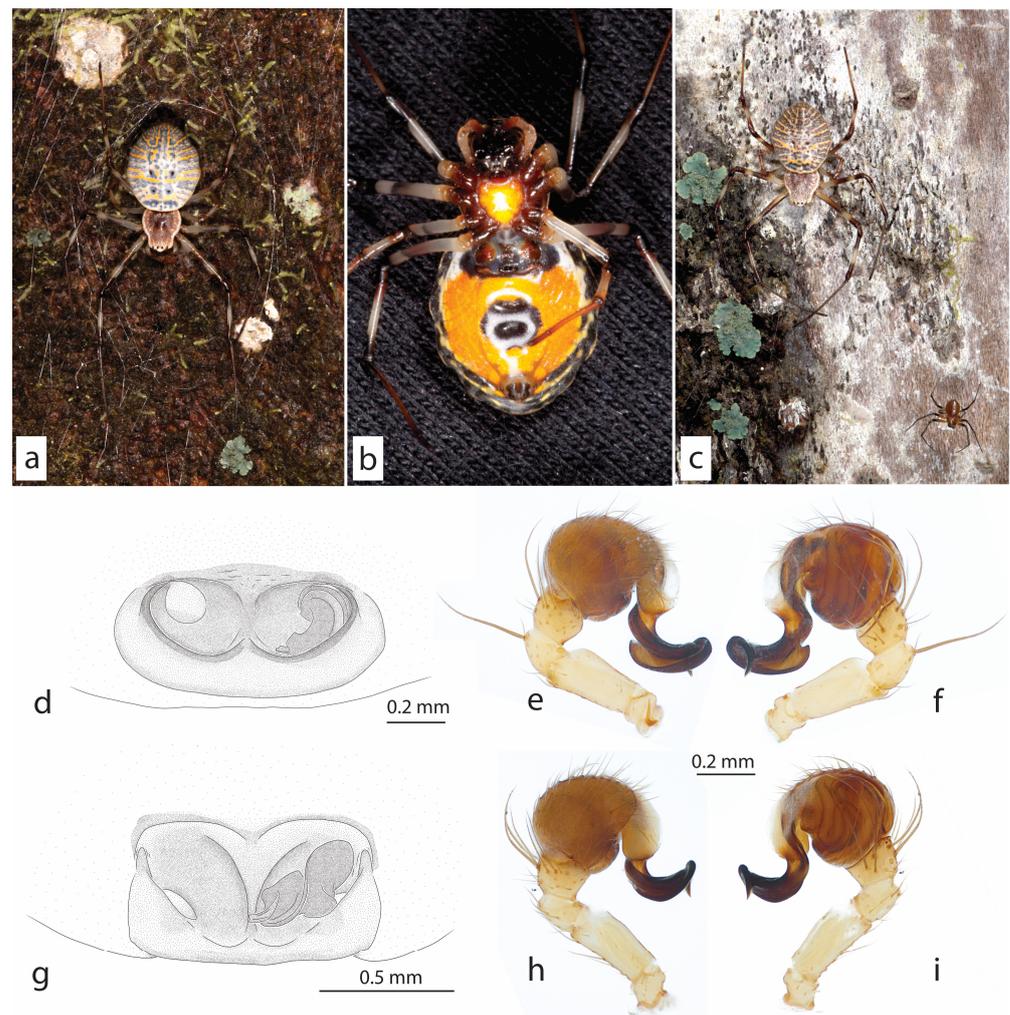


Figure 9. New *Herennia* morphology described in this article: (a) a live female of *H. eva* sp. nov., dorsal view; (b) *idem*, ventral view; (c) a live female (top left) and a live male (bottom right) of *H. eva*; (d) epigynum of paratype female *H. eva* (ARA826), ventral view; (e) left palp of holotype male *H. eva* (ARA840), mesal view; (f) *idem*, ectal view; (g) epigynum of holotype female *H. maj* sp. nov. (ARA1866); (h) left palp of *H. tone* Kuntner, 2005 (ARA1859), dorsal view; (i) *idem*, ectal view.

Molecular evidence: The species is supported by delimitation analyses, except for GMYC (Figure 2).

Description: Female (paratype; Figures 6a and 9d). Total length 12.97. *Prosoma* 4.41 long, 4.04 wide. Sternum 2.11 long, 2.10 wide. AME diameter 0.24, ALE 0.14, PME 0.14, PLE 0.13. AME separation 0.22, PME separation 0.31, PME-PLE separation 0.35, AME-ALE

separation 0.24, AME-PME separation 0.30, ALE-PLE separation 0.10. Clypeus height 0.34. *Appendages* Leg I length 21.53 (Fe 6.33, Pa 1.50, Ti 4.75, Me 6.92, Ta 2.02). *Opisthosoma* 6.68 long, 8.61 wide, 4.34 high. Male (holotype; Figures 8a and 9e,f). Total length 2.54. *Prosoma* 1.35 long, 1.15 wide. Sternum 0.62 long, 0.56 wide. AME diameter 0.14, ALE 0.07, PME 0.10, PLE 0.08. AME separation 0.06, PME separation 0.08, PME-PLE separation 0.05, AME-ALE separation 0.04, AME-PME separation 0.06, ALE-PLE separation 0.04. Clypeus height 0.04. *Appendages* Leg I length 7.48 (Fe 1.67, Pa 0.48, Ti 1.46, Me 2.5, Ta 1.37). *Opisthosoma* 1.77 long, 1.35 wide, 0.76 high.

Variation: Female total body length from 11.70 to 12.97 (N = 4), male total body length from 2.54 to 2.84 (N = 3).

Natural History: The type locality, Mahawu Mt. Area near Tomahon, had appropriately sized trees for *H. eva* to construct their ladder webs (female web was 28 cm wide, 65 cm high, and 22 cm from top frame to the hub). At the other locality near Ratatok, *H. eva* inhabited trees in both rain forest as well as plantation. A female web with egg sac in the dense canopy forest was 35 cm wide, 70 cm high, and 45 cm from top frame to the hub.

Distribution: The species is endemic to northern Sulawesi, Indonesia.

Herennia tone Kuntner, 2005

Tone's coin spider

Figures 6c, 8b and 9h,i

Remarks: No males have been available during prior revision [2], but one has since become available that was matched with the described *H. tone* female.

For types and etymology, see [2].

Material examined since prior revision [2]: Female and male (ARA1858-9) deposited at SMF from "PHILIPPINES: Leyte, Visca, N Baybay, primary forest, 200–500 m, W. Schawaller et al. leg. 10.3.1991". Very roughly, this locality lies at N10.66 and E124.85.

Diagnosis: In contrast to *H. multipuncta*, *H. tsoi*, *H. maj* (Figure 4a), *H. jernej*, *H. sonja*, and *H. gagamba*, the female carapace in *H. tone* lacks a distinct V-shaped mark. The female resembles that of *H. eva*, but their epigyna are diagnosable: the epigynal lateral sclerotized edge in *H. tone* is rounded (Figure 6c) and not ear-shaped. Male palp has a massive, twisting embolic conductor that resembles that of *H. eva*. However, unlike in that of *H. eva*, this embolic conductor is not as broad and lacks a distinct proximal bump (Figure 8b).

Molecular evidence: The species is supported by delimitation analyses, except for GMYC (Figure 2).

Description: Male (ARA1859; Figures 8b and 9h,i). Total length 2.78. *Prosoma* 1.46 long, 1.18 wide. Sternum 0.71 long, 0.62 wide. AME diameter 0.16, ALE 0.10, PME 0.11, PLE 0.09. AME separation 0.08, PME separation 0.10, PME-PLE separation 0.05, AME-ALE separation 0.03, AME-PME separation 0.09, ALE-PLE separation. Clypeus height 0.63. *Appendages* Leg I length (Fe 1.87, Pa 0.40, Ti 1.44, Me 1.87, Ta 0.91). *Opisthosoma* 1.64 long, 1.38 wide, 0.77 high.

Variation: Unknown male variation.

Natural History: Unknown but presumed to be confined to primary forest as collection label suggests.

Distribution: The species is endemic to Visayas group of islands in the Philippines with a questionable additional record from Luzon [2].

Herennia maj Kuntner, new species

Maj's coin spider

Figures 4a, 5e and 9g

ZooBank ID: urn:lsid:zoobank.org:act:2C5105E0-8313-490F-B19B-A453C8BFD504

Types: Holotype female, designated herein with a manuscript label code ARA1866 and originally labeled as “Vietnam, Lam Dong Province, Lac Duong Distr., 5 km NE of Long Lahn Vil. Bi Dup–Nui Ba Nature Reserve. 12d10'44" N, 108d40'44" E, 1400 m a.s.l. May 2009, A.V. Abramov (exp. of Russia-Vietnam Tropical Centre)”, deposited at ZMMU. Paratype female with a manuscript label code ARA1868 and originally labeled as holotype above, deposited at MMUE.

Additional material examined: None.

Etymology: The first author is naming this species to honor his son Maj. The species epithet is to be treated as a noun in apposition.

Diagnosis: Unlike in *H. eva*, *H. tone*, *H. agnarssoni*, *H. papuana*, *H. milleri*, *H. etruscilla*, *H. oz*, and *H. deelemanae* (Figure 4b), the female carapace in *H. maj* bears a distinct V-shaped mark (Figure 4a). Somatically, female *H. maj* resemble small specimens of *H. multipuncta* and *H. tsoi*. However, in *H. maj* the epigynal posterior sclerotized edge is broad and not massive, the lateral sclerotized edge is not sharply defined where curved around the chambers, and the chambers are massive and square shaped rather than circular (Figure 5e).

Description: Female (holotype; Figures 4a, 5e and 9g). Total length 10.10. *Prosoma* 4.94 long, 3.76 wide. Sternum 1.76 long, 1.95 wide. AME diameter 0.23, ALE 0.13, PME 0.15, PLE 0.12. AME separation 0.25, PME separation 0.32, PME-PLE separation 0.30, AME-ALE separation 0.31, AME-PME separation 0.30, ALE-PLE separation 0.10. Clypeus height 0.32. *Appendages* Leg I length 20.83 (Fe 6.35, Pa 1.48, Ti 4.44, Me 6.19, Ta 1.92). *Opisthosoma* 5.88 long, 5.30 wide, 3.98 high. Male unknown.

Variation: Female total body length from 8.89 to 10.10 (N = 2).

Natural History: Unknown.

Distribution: Only known from the type locality in southern Vietnam.

Herennia tsoi Kuntner & al., new species

Tso's coin spider

Figures 5f, 7b and 10

ZooBank ID: urn:lsid:zoobank.org:act:D56D3637-1F4B-4742-8FDF-FCA16AB14CB2

H. multipuncta, in part: [2]

Remarks: No males from Taiwan have been available, and a single museum female was tentatively identified as *H. multipuncta* in the prior revision [2]. With the newly collected material treated here, the Taiwanese population of *Herennia* belongs to a distinct species, *H. tsoi* described herein.

Types: Holotype male ARA1223 from Nantou County, Taiwan and paratype female ARA1222 from Nantou County, Taiwan, both deposited in USNM (Smithsonian Institution).

Additional material examined: See Table S1.

Etymology: Named to honor our colleague I-Min Tso of Taiwan who helped us to discover the uniqueness of this species;. The species epithet is a Latinized masculine adjective.

Diagnosis: Unlike in *H. eva*, *H. tone*, *H. agnarssoni*, *H. papuana*, *H. milleri*, *H. etruscilla*, *H. oz*, and *H. deelemanae* (Figure 4b), the female carapace in *H. tsoi* bears a distinct V-shaped mark (Figure 10a). Somatically, the females resemble *H. multipuncta* and *H. maj*. The male palp, however, has a distinctly shaped embolic conductor with a much narrower flap and a longer and more proximally bent tip (Figures 7b and 10e,f) compared with *H. multipuncta* (male *H. maj* is unknown). The epigynum has distinct chambers that unlike in *H. multipuncta* are not fully circular but rather distorted in shape. Unlike in *H. multipuncta*, the epigynal edges are strongly sclerotized (Figures 5f and 10d). Unlike in *H. maj*, the *H. tsoi* epigynum has medium-sized chambers and a massive posterior sclerotized edge (Figures 5f and 10d).

Description: Female (paratype; Figures 5f and 10a,b,d). Total length 16.18. *Prosoma* 5.89 long, 5.75 wide. Sternum 2.45 long, 2.51 wide. AME diameter 0.23, ALE 0.21, PME 0.15,

PLE 0.14. AME separation 0.32, PME separation 0.45, PME-PLE separation 0.54, AME-ALE separation 0.38, AME-PME separation 0.27, ALE-PLE separation 0.15. Clypeus height 0.25. *Appendages* Leg I length 24.51 (Fe 6.52, Pa 1.78, Ti 5.58, Me 8.32, Ta 2.31). *Opisthosoma* 11.42 long, 10.23 wide, 4.96 high. Male (holotype; Figures 7b and 10e,f). Total length 3.17. *Prosoma* 2.00 long, 1.55 wide. Sternum 1.03 long, 0.81 wide. AME diameter 0.16, ALE 0.09, PME 0.73, PLE 0.08. AME separation 1.04, PME separation 0.17, PME-PLE separation 0.11, AME-ALE separation 0.05, AME-PME separation 0.12, ALE-PLE separation 0.07. Clypeus height 0.08. *Appendages* Leg I length 9.03 (Fe 2.35, Pa 0.63, Ti 1.99, Me 2.78, Ta 1.28). *Opisthosoma* 1.8 long, 1.37 wide, 0.94 high.

Variation: Female total body length from 14.96 to 16.53 (N = 13). Male total body length from 3.17 to 3.71 (N = 2).

Natural History: The natural history of *H. tsoi* is classical *Herennia* in the way juveniles and females inhabit ever larger trees to construct their arboricolous webs adhering to tree trunks. Webs can be very large: in Yushan NP we observed a web with the female and her egg sacs in it that was 30 cm wide, 160 cm high, and 27 cm from top frame to the hub. This massive web hosted seven coinhabiting kleptoparasitic theridiid spiders of the genus *Famakytta* Pett & Agnarsson, 2025 [29] (Figure 10c).

Distribution: Endemic to Taiwan.

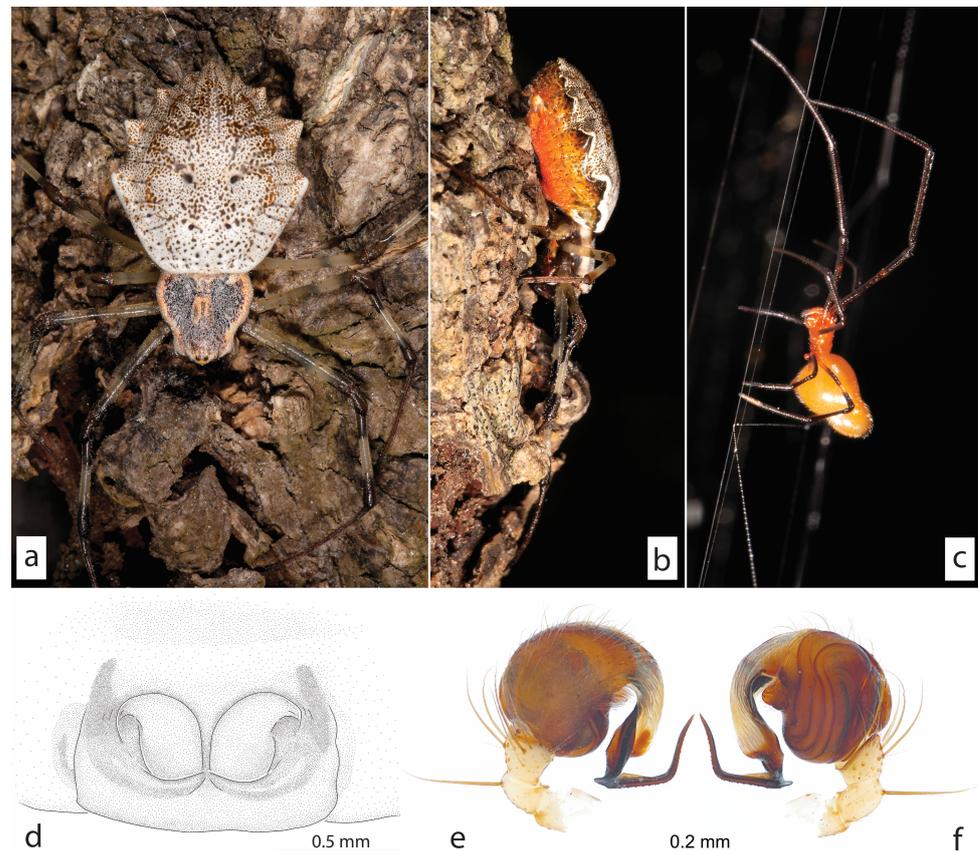


Figure 10. Morphology and ecology of *Herennia tsoi* sp. nov.: (a) a live female, dorsal view; (b) *idem*, lateral view; (c) a kleptoparasitic theridiid (*Famakytta* sp.) found on the web of *H. tsoi*; (d) epigynum of paratype female (ARA1222), ventral view; (e) left palp of holotype male (ARA1223), mesal view; (f) *idem*, ectal view.

Herennia oz Kuntner, 2005

Australian coin spider

Figures 6h, 7d, 11a–f and 12a

Remarks: No males have been available during prior revision [2].

For types and etymology, see [2].

Material examined since prior revision [2]: Male, QM-S124106, Northern Territory, Darwin, East Point. 12d24'34.5" S, 130d49'05.4" E, 17 m a.s.l. 1 September 2023, G.J. Anderson, deposited at QM.

Diagnosis: In contrast to *H. multipuncta*, *H. tsoi*, *H. maj* (Figure 4a), *H. jernej*, *H. sonja*, and *H. gagamba*, the female carapace in *H. oz* lacks a distinct V-shaped mark (Figure 12a). The female resembles that of *H. etruscilla* (Figures 6g and 11g), but their epigyna are diagnosable: in *H. oz*, a massive posterior epigynal sclerotized edge defines an exaggerated septum and ovoid chambers (Figures 6h and 11d). Unlike in *H. eua*, *H. tone*, *H. deelemanae*, and *H. papuana*, the male palp in *H. oz* bears an EC whose distal part has a distinct hook (Figure 7d). As in *H. etruscilla*, the EC tip in lateral view is bent inwards (Figure 7c,d), but in *H. oz* the EC tip curve is short, only about a third of EC length (Figures 7d and 11e,f) rather than over half EC length as in *H. etruscilla* (Figures 7c and 11h,i).

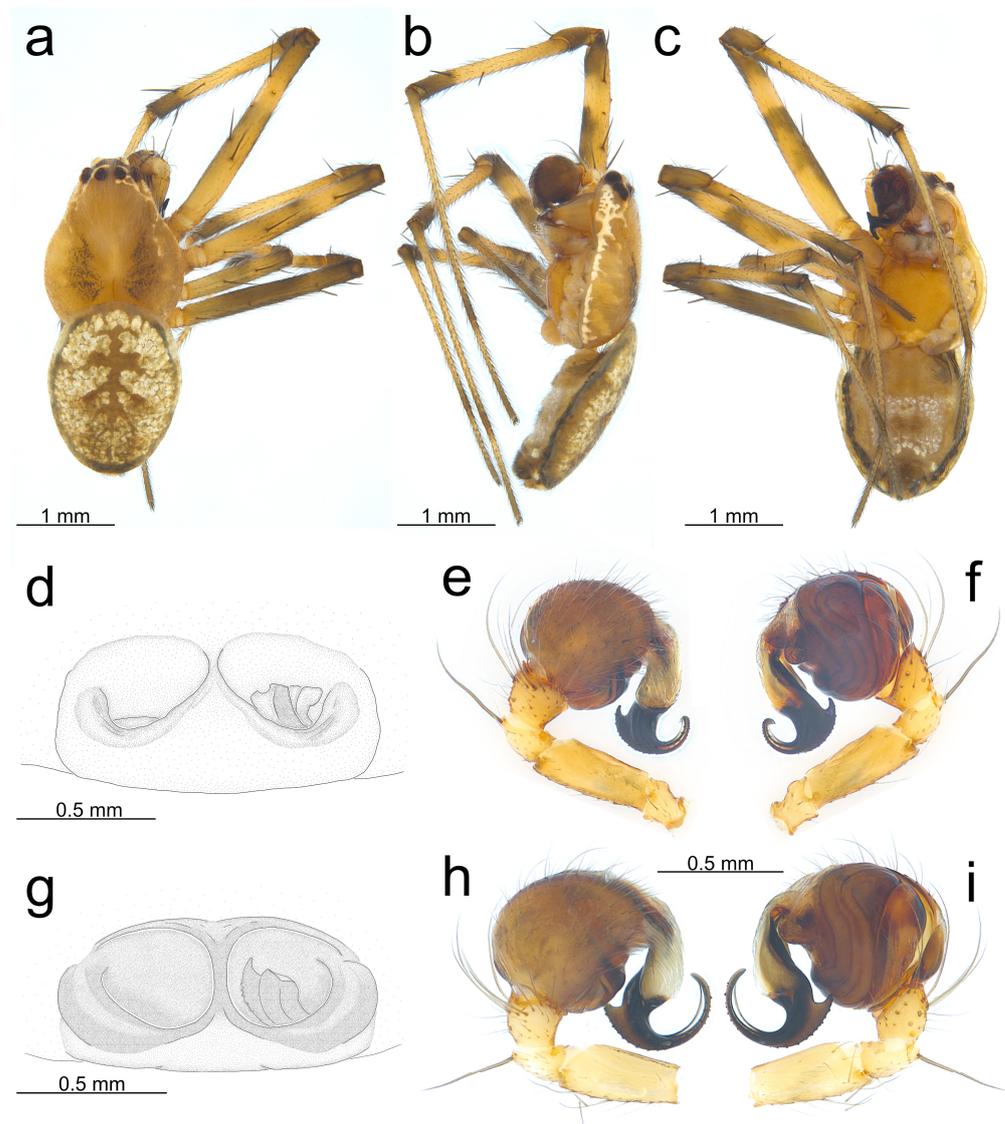


Figure 11. Morphological comparison between *Herennia oz* Kuntner, 2005 (a–f) and *H. etruscilla* Kuntner, 2005 (g–i): (a) male *H. oz* (QM-S124106), dorsal view; (b) *idem*, lateral view; (c) *idem*, ventral view; (d) epigynum of holotype female *H. oz* (HE22), ventral view; (e) left palp of male *H. oz* (QM-S124106), mesal view; (f) *idem*, ectal view; (g) epigynum of *H. etruscilla* (ARA1854), ventral view; (h) left palp of male *H. etruscilla* (ARA1857), mesal view; (i) *idem*, ectal view.

Molecular evidence: Among all species delimitation analyses, *H. oz* is supported as distinct from *H. etruscilla* only by bPTP (Figure 2).

Description: Male (QM-S124106; Figures 7d and 11a,f). Total length 3.39. *Prosoma* 1.86 long, 1.45 wide. Sternum 0.81 long, 0.81 wide. AME diameter 0.18, ALE 0.10, PME 0.11, PLE 0.10. AME separation 0.11, PME separation 0.15, PME-PLE separation 0.13, AME-ALE separation 0.05, AME-PME separation 0.11, ALE-PLE separation 0.02. Clypeus height 0.01. *Appendages* Leg I length (Fe 2.49, Pa 0.54, Ti 2.12, Me 2.62, Ta 1.13). *Opisthosoma* 1.98 long, 1.4 wide, 0.73 high.

Variation: Unknown male variation.

Natural History: Unknown.

Distribution: The species is endemic to Australia's Northern Territory.

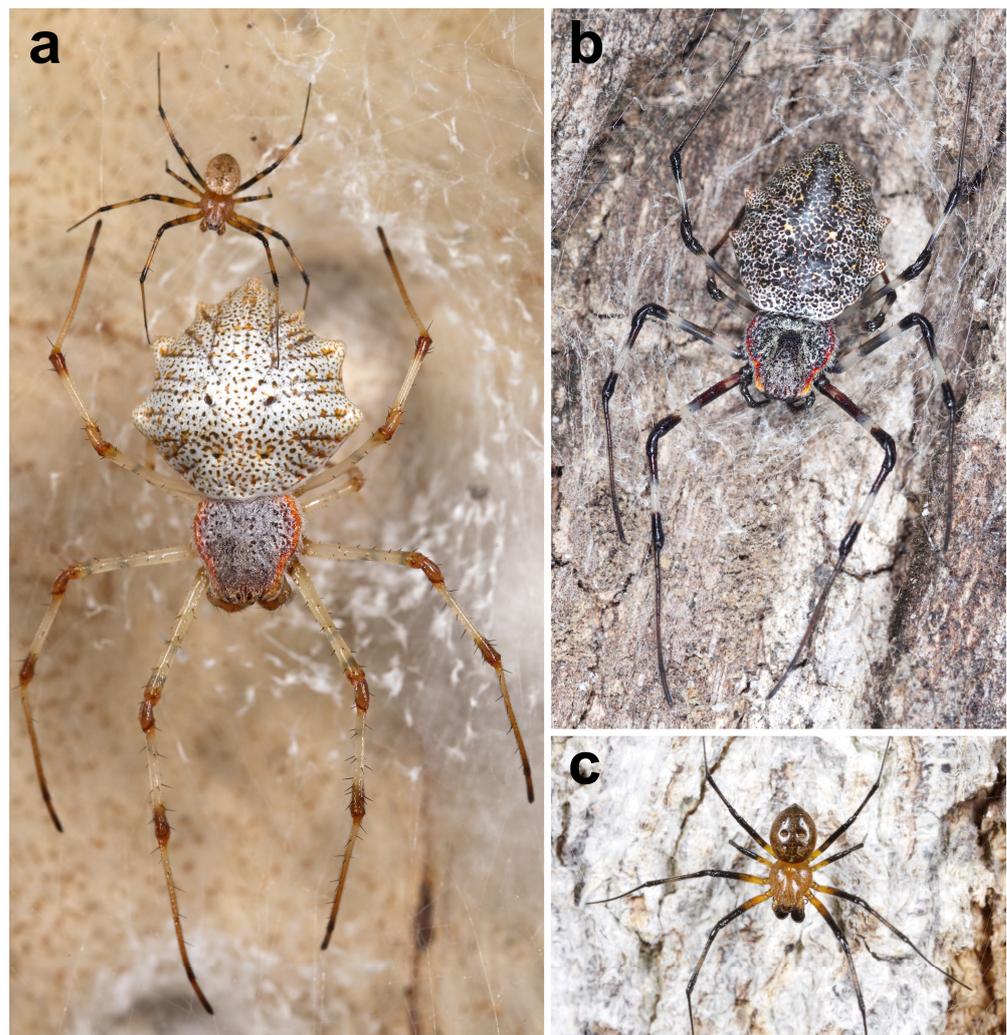


Figure 12. Coin spiders of Australia: (a) female (lower) *Herennia oz* Kuntner, 2005 from Darwin, Northern Territory with a male suitor (above); (b) female *Herennia papuana* Thorell, 1881 from northern Queensland, dorsal view; (c) male *Herennia papuana* from northern Queensland, dorsal view. All photos by G. J. Anderson.

4. Discussion

The taxonomy presented here adds three new species to the genus *Herennia* on the basis of morphological and molecular evidence and thus raises the number of recognized coin spider species to 14 (Table 1). It also describes first male records of *H. tone* and *H. oz*, further refining diagnostic traits and improving taxonomic resolution. The newly recorded

males were measured for body size, and these data add to the overall understanding of sexual size dimorphism in *Herennia* (Table 2). Despite this progress, the scarcity of museum material—especially males—continues to limit taxonomic resolution. This constraint is now partly alleviated by molecular species delimitation analyses, providing an independent line of evidence.

However, it is well documented that molecular species delimitation methods can be prone to oversplitting or overlumping hypothetical species, highlighting the value of an integrative taxonomic framework [30–33]. Although molecular delimitation broadly agrees with morphology in our case study, some conflicts arose. For example, we treat *H. oz* as a separate species on the grounds of clear genital diagnosability, despite contradicting molecular delimitation results with all methods except bPTP. Similarly, GMYC lumps *H. eva* and *H. tone*, but given their compelling morphological characteristics, we treat them as valid species. In contrast, bPTP is the only method to distinguish Sri Lankan *H. multipuncta* as a separate species; however, such a distinction is not supported by morphology.

In this paper we summarize the taxonomic advances since the 2005 revision of *Herennia* [2], add original field images of several species that facilitate their overall recognition and initial identification (Figure 1, Figure 9a–c, Figure 10a,b and Figure 12), and provide a fully illustrated identification key to all 14 currently recognized coin spider species that supersedes the 2005 key [2]. The new species formalized here were already included—under provisional names—in a phylogenetic and biogeographic analysis of *Herennia* [14]. That study reconstructed the historical biogeography of ten species, inferring their likely geographic origin and major dispersal pathways. Because the dominant dispersal mode in coin spiders remains uncertain, two parallel models were evaluated: one assuming active ballooning [34] and the other emphasizing short-distance walking. Following earlier work on nephilid dispersal probabilities [35], geographic distances among areas were used as proxies for dispersal likelihood, informing ancestral area reconstruction [36,37]. Both models supported a broad ancestral range encompassing Australia, mainland Southeast Asia, and the Philippines [14]. The ballooning-based model yielded the more parsimonious scenario, invoking fewer long-distance dispersal events.

Notably, the inferred ancestral range of the genus spans both sides of Wallace’s Line and its later refinements, which broadly separate Asian from Australian biotas [38,39]. In the ballooning-based model, only three dispersal events crossed this barrier: two from Australia into mainland Southeast Asia and the Lesser Sunda Islands, and one from mainland Southeast Asia into Sulawesi [14]. These patterns may suggest that vicariance is the dominant driver of diversification in *Herennia*, consistent with the presumed low dispersal propensity of most species and, consequently, their narrow endemism, with some exceptions.

Spiders, in particular orbweavers, are known to disperse aerially via ballooning [34,40–44]. We therefore reaffirm our earlier conclusion that the common ancestor of *Herennia* likely had a broad Asian–Australasian distribution but subsequently lost the capacity—or propensity—for ballooning [14]. As recognized in biogeographic literature, natural selection often favors reduced dispersal following successful colonization [45]. However, some lineages, notably *H. multipuncta*, might have secondarily regained effective dispersal ability, facilitating their extensive geographic range. Continued comparative work on dispersal biology will be essential to further clarify species boundaries and the evolutionary history of coin spiders.

Herennia is currently the most species-rich genus within Nephilidae [8], yet available evidence indicates that its diversity remains incompletely documented. A common way of estimating uncovered species diversity is an extrapolation of the accumulation curve derived from Chao2 [46] species richness estimator (e.g., [47,48]). Our estimation based

on 127 unique localities (Figure 13) suggests that considerably expanded sampling—likely exceeding 250 unique localities—will be required before species richness approaches an asymptote. Given the genus' pronounced geographic structuring and high levels of local endemism (Figure 3), we hypothesize that much of the remaining undocumented diversity is confined to poorly sampled regions of the Asian mainland and the island systems of Southeast Asia and Australasia. Targeted sampling in these regions will be essential for testing this hypothesis and for achieving a more complete understanding of *Herennia* diversity and evolution.

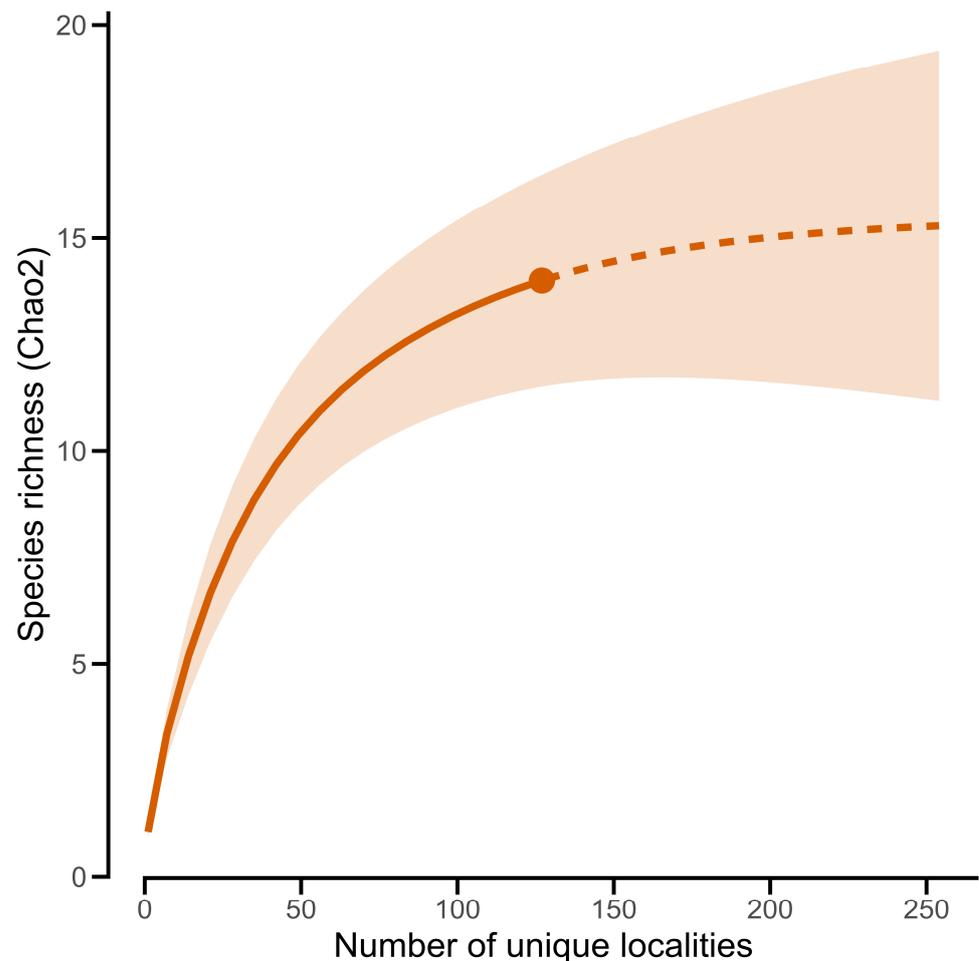


Figure 13. Accumulation curve (orange line) of Chao2 [46] species richness estimator and the 95% confidence intervals (orange shade) derived from 1000 permutations of 127 unique localities (see Table S1 and Kuntner [2]) with the presence of 14 known *Herennia* species (orange point). The extrapolation of the curve (orange dotted line) to 250 localities shows potentially uncovered *Herennia* species with the additional sampling effort required to detect them. These analyses were performed in R v4.3.3 [49] using the package “iNEXT” [50].

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18010054/s1>, Table S1: Coin spider specimens examined.

Author Contributions: Conceptualization, M.K. and R.-C.C.; methodology, M.K. and R.-C.C.; software, K.-P.Y., E.T., K.Č. and R.-C.C.; validation, all authors; formal analysis, M.K., K.-P.Y., E.T., K.Č., M.G. and R.-C.C.; resources, all authors; data curation, M.K., K.-P.Y., E.T., K.Č., M.G., G.J.A., J.A.C. and R.-C.C.; writing—original draft preparation, M.K. and R.-C.C.; writing—review and editing, all authors; visualization, M.K., K.-P.Y., K.Č., E.T. and R.-C.C.; supervision, M.K.; project administra-

tion, M.K.; funding acquisition, M.K. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All specimen information is in Table S1.

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Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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