

On some *Heteropoda* species from Southeast Asia with new data on their biology and distribution range and the resurrection of a new species group (Sparassidae: Heteropodinae)

Novos dados sobre algumas espécies de *Heteropoda* do sudeste asiático sobre a biologia, a área de distribuição e a ressurreição de um novo grupo de espécies (Sparassidae: Heteropodinae)

Peter Jäger^I  | Joseph K. H. Koh^{II} 

^ISenckenberg Research Institute. Arachnology. Frankfurt am Main, Germany

^{II}Lee Kong Chian Natural History Museum. National University of Singapore. Singapore

Abstract: Eight species of the huntsman spider genus *Heteropoda* Latreille, 1804 are described; *Heteropoda bufocorniculans* spec. nov. (Sabah, Sarawak; female), *H. sederhana* spec. nov. (Java; female), *H. temburong* spec. nov. (Brunei, Sabah, Sarawak; male, female), *H. trifurcata* spec. nov. (Pahang State, Malaysia; male, female), *H. tutula* spec. nov. (Singapore; female), *H. tympanum* spec. nov. (Penang, Malaysia; female), *H. ulna* spec. nov. (Sumatra, Indonesia; female), and *H. uniter* spec. nov. (Kalimantan, Indonesia; female). The latter six species, along with *H. ocyalina* (Simon, 1887) and *H. asa* Jäger, 2024, are included in the newly proposed *ocyalina* species-group. *H. fasciata* (Reimoser, 1927) is removed from synonymy of *H. ocyalina* (Simon, 1887) and considered a *nomen dubium*. The male of *Heteropoda borneensis* (Thorell, 1890) is illustrated for the first time, male and female are redescribed, new distributional data are presented, including the first records from Brunei, Indonesia (Kalimantan Utara), Malaysia (Kuala Lumpur, Sabah), and Singapore. *Heteropoda strandi* Jäger, 2002 and *H. lunula* (Doleschall, 1857) are formally documented for the first time from Singapore, the female of the former is redescribed.

Keywords: Taxonomy. New species. *Nomen dubium*. iNaturalist.

Resumo: Oito espécies do gênero de aranhas caçadoras *Heteropoda* Latreille, 1804 são reconhecidas como novas para a ciência e descritas como *Heteropoda bufocorniculans* spec. nov. (Sabah, Sarawak; fêmea), *H. sederhana* spec. nov. (Java; fêmea), *H. temburong* spec. nov. (Brunei, Sabah, Sarawak; macho, fêmea), *H. trifurcata* spec. nov. (Pahang, Malásia; macho, fêmea), *H. tutula* spec. nov. (Cingapura; fêmea), *H. tympanum* spec. nov. (Penang, Malásia; fêmea), *H. ulna* spec. nov. (Sumatra, Indonésia; fêmea) e *H. uniter* spec. nov. (Kalimantan, Indonésia; fêmea). As últimas seis espécies, juntamente com *H. ocyalina* (Simon, 1887) e *H. asa* Jäger, 2024, estão incluídas no novo grupo de espécies *ocyalina*. *H. fasciata* (Reimoser, 1927) é removido da sinonímia de *H. ocyalina* (Simon, 1887) e considerado um *nomen dubium*. O macho de *Heteropoda borneensis* (Thorell, 1890) é ilustrado pela primeira vez, com macho e fêmea sendo redescritos e apresentados novos dados de distribuição, entre eles os primeiros registros para Brunei, Indonésia (Kalimantan Utara), Malásia (Kuala Lumpur, Sabah) e Cingapura. *Heteropoda strandi* Jäger, 2002 e *H. lunula* (Doleschall, 1857) são formalmente documentados pela primeira vez em Cingapura, sendo redescrita a fêmea de *H. strandi*.

Palavras-chave: Taxonomia. Novas espécies. *Nomen dubium*. iNaturalist.

Jäger, P., & Koh, J. K. H. (2024). On some *Heteropoda* species from Southeast Asia with new data on their biology and distribution range and the resurrection of a new species group (Sparassidae: Heteropodinae). *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, 19(3), e2024-1041. <http://doi.org/10.46357/bcnaturais.v19i3.1041>

Corresponding author: Peter Jäger. Arachnology, Senckenberg Research Institute. Mertonstraße 17–21, 60325 Frankfurt am Main, Germany (peter.jaeger@senckenberg.de).

Received on 12/06/2024

Approved on 30/10/2024

Editorial responsibility: Alexandre Bragio Bonaldo



INTRODUCTION

Heteropoda Latreille, 1804 is a large genus within the subfamily Heteropodinae, with 203 nominal species and distributed mostly in Asia and Australia (World Spider Catalog, 2024), including the largely synanthropic and pantropic species *Heteropoda venatoria* (Linnaeus, 1767). Revisionary work has been done so far mainly for Southeast Asia and Australia (e.g., Jäger, 2005, 2008a, 2014, 2024; Davies, 1994). The majority of the diversity of the genus is still unrevised or undiscovered (Jäger, unpublished data).

Heteropoda borneensis (Thorell, 1890) was described from a male and a female from Borneo (Malaysia: Sarawak) in the new genus *Urgulania* Thorell, 1890. While acknowledging *Urgulania's* strong similarity in comparison with *Heteropoda* and *Panaretus* Simon, 1880, Thorell (1890, p. 143) stated in three lines in the footnote that *Urgulania* may be distinguished from the two former genera by having legs I longer than legs IV, and from *Heteropoda* by having dense pubescence at the base of the chelicerae (“as in *Panaretus*”). Simon (1880, p. 54) synonymised the genus with *Panaretus* without giving any reason. After Jäger (2002, p. 40) synonymised *Panaretus* with *Heteropoda* and formally transferred the present species to the genus *Heteropoda*, there have been no further references to the species in scientific literature. It has been difficult to identify the species based on the original eight-line description in Latin (Thorell, 1890, p. 143). After examining the type and conspecific material, the male and female are now re-described and data on the species' biology and distribution are provided.

Other material of the genus *Heteropoda* collected on various expeditions or borrowed from natural history collections was examined and eight species were recognised as new to science. They are diagnosed, described, and illustrated. A new species group is proposed to include eight species, comprising two formerly described ones and six new species described in this paper. Additionally, two previously described *Heteropoda* species are formally documented for the first time from Singapore.

MATERIAL AND METHODS

The examined spiders are preserved in 70% denatured ethanol. Observations and drawings were made using a Leica MZ 16 stereomicroscope and a Leica DLMS compound microscope, each with a camera lucida attachment. Photographs of preserved specimens were taken with a Canon EOS R and a Canon 100 mm macro lens in combination with a Canon MR 14EX ringlite (or with the same camera mounted on a Leica MZ 16 stereomicroscope). Photographs of live spiders were taken with an AF-S micro-NIKKOR 60 mm ED lens or an AF-S micro-NIKKOR 105 mm 1:2.8G ED lens, attached to a Nikon D7000 camera. Photographs of the female genitalia were taken with Nikon D800E camera either mounted on a Nikon SMZ 18 stereoscopic microscope, or with a series of extension tubes attached to a Nikon E Plan 10X compound microscope objective. Specific photo credits are given in legends. All line drawings and maps were made by P. Jäger. All measurements are given in millimetres. Prosoma length/width is the length/width of the dorsal shield of the prosoma, opisthosoma length/width is the length excluding petiolus and spinnerets. Eye distances were measured in orthogonal views. Leg formula, leg spination pattern and size classes follow Jäger (2001). Palpal and leg lengths are given as: total (femur, patella, tibia, metatarsus, tarsus). The arising points of appendages of the male bulb are given in clock-position of the left palp in ventral view. Colouration is described from specimens in ethanol and live specimens. All specimens were checked for scars as potential traces of mating bites as described in Jäger (2021, 2023) and Eudeline & Jäger (2023). Data in square brackets were retrieved subsequently. Elevation of localities are given in metres (m). The maps were produced using DIVA GIS version 7.5.0.0. Records of *H. borneensis* from iNaturalist unambiguously identifiable by photographs are included in the map, with the caveat that the precision of some of the coordinates given in iNaturalist may not necessarily be punctiliously accurate. Records for '*Heteropoda*' were searched for data associated with Singapore, Sumatra, the southern part of peninsular Malaysia, and the entire 'Borneo' region (namely



Brunei, Sabah, Sarawak, and the Indonesian provinces of Kalimantan). Valid species are listed in alphabetical order; only those close to *H. ocyalina* could be assigned to a species group.

Abbreviations used in the text: ALE = anterior lateral eyes, AME = anterior median eyes, dRTA = dorsal branch of RTA, DS = dorsal shield of prosoma, Fe = femur/femora, Mt = metatarsus/metatarsi, OL = opisthosoma length, OS = opisthosoma, OW = opisthosoma width, Pa = patella/patellae, PL = prosoma length, PLE = posterior lateral eyes, PME = posterior median eyes, PW = prosoma width, RTA = retrolateral tibial apophysis, Ta = tarsus/tarsi, Ti = tibia/tibiae, TL = total length, vRTA = ventral branch of RTA.

Museum collections (with curators): AMNH = American Museum of Natural History, New York, USA (L. Prendini); BMKB = Brunei Museum, Kota Batu, Brunei Darussalam (F. Hamdan); FRC = Forestry Research Centre, Sepilok, Sandakan, Sabah, Malaysia (A. Chung); LKCNHM = Lee Kong Chian Natural History Museum, Singapore (W. Wang); MCSN = Museo Civico di Storia Naturale, Genoa, Italy (M. Tavano); NHM = Natural History Museum, London, UK (J. Beccaloni); NHMW = Naturhistorisches Museum, Vienna, Austria (C. Hörweg); RMNH = Naturalis Biodiversity Center, Leiden, Netherlands (H. Bakker); SMF = Senckenberg Research Institute, Frankfurt am Main, Germany (J. Grüger, P. Jäger); ÜMB = Übersee Museum Bremen, Germany (V. Lohrmann); ZMUC = Zoological Museum of the University, Copenhagen, Denmark (N. Scharff).

This paper and its nomenclatural acts have been registered in ZooBank, the online registration system for the ICZN (<http://zoobank.org/urn:lsid:zoobank.org:pub:3461EAFc-DEE4-4A4A-A509-C4FA1B338C69>).

TAXONOMY

Sparassidae Bertkau, 1872
 Heteropodinae Thorell, 1873
Heteropoda Latreille, 1804
Heteropoda borneensis (Thorell, 1890)
 (Figures 1–41)

Urgulania borneensis Thorell 1890: 143 (Description of male and female; 1 female [with epigyne] lectotype; 1 male? [without palps] and 1 female [without epigyne] paralectotypes; from Borneo: [MALAYSIA:] Sarawak, Doria & Beccari, MCSN; examined).

Panaretus borneensis Simon 1897: 54 (transfer to *Panaretus*).

Heteropoda borneensis, Jäger 2002: 42 (transfer and designation of lectotype and paralectotypes).

Heteropoda sp. A—Koh & Bay 2019: 330–331, unnumbered photos of male and female. Koh et al. (2022, p. 493), unnumbered photos of male and female.

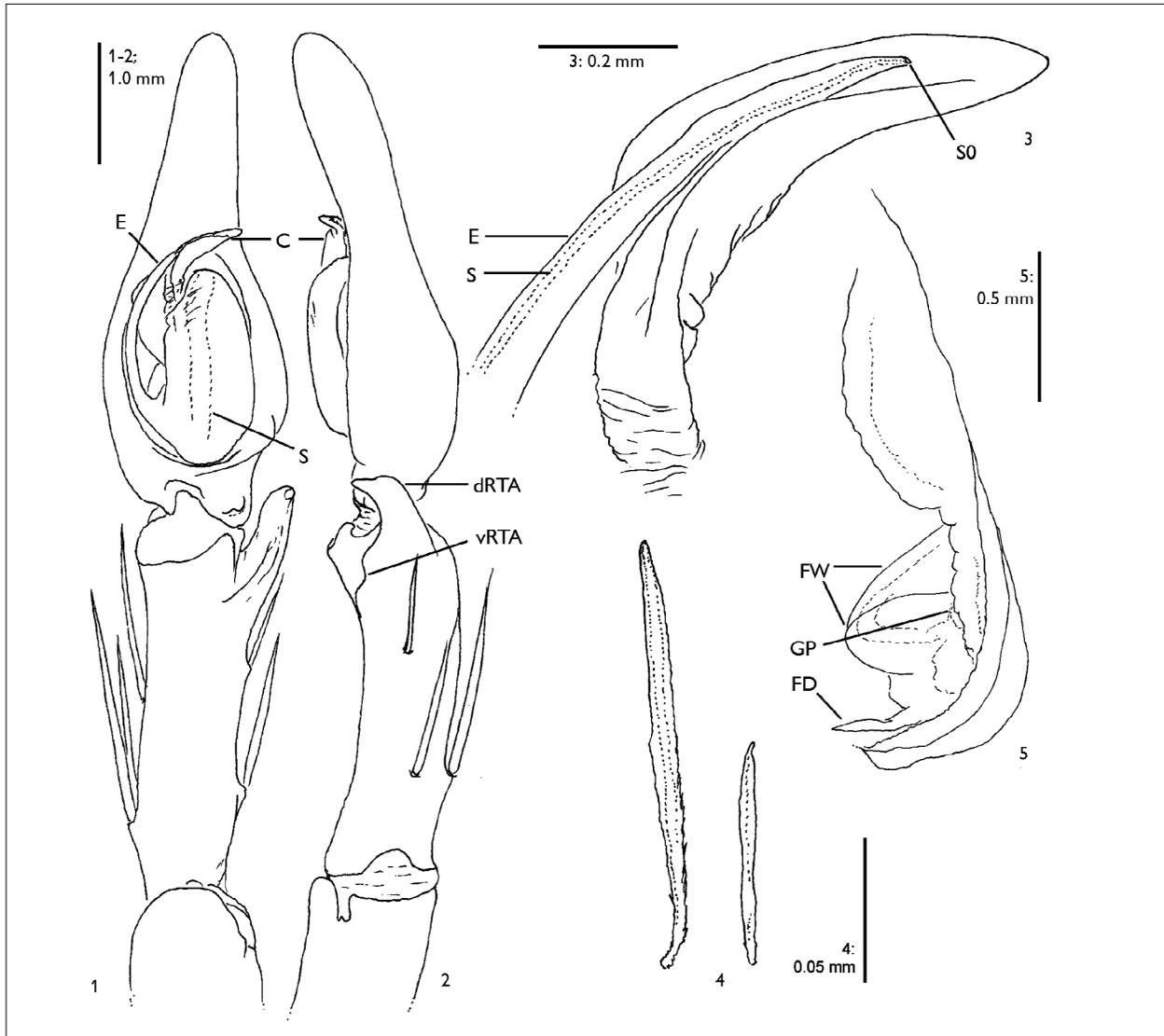
Notes. The genus *Panaretus* was synonymised by Jäger (2002, p. 40) with *Heteropoda*, thus formally transferring *Panaretus borneensis* to *Heteropoda*. In the original publication, Thorell (1890, p. 144) reported “Borneo” as its country of origin (“*patria*”). On the original labels, “Sarawak” was added and is considered a more precise indication of the type locality.

Additional material examined. BRUNEI: Belait: 1 female (JK.11.03.26.9002), Melilas, Sungai Ingei, primary forest, 4° 08' 36" N, 114° 43' 16" E [58 m elevation], J.K.H. Koh leg. 26 March 2011 (BMKB). 1 female (JK.11.03.26.9008), with same locality data as for previous specimen (LKCNHM). Tutong: 1 male (JK.11.04.16.1041), Tasek Merimbun, Botanical Trail, 4° 35' 40" N, 114° 40' 15" E [38 m elevation], Joseph K.H. Koh leg. 16 April 2011, 22.00, “orange big” (SMF). 1 female (JK.11.04.14.1012), with same data as for previous specimen (SMF). 1 female (JK.11.04.16.1006), with same locality data as for previous specimen, J.K.H. Koh leg. 16 April 2011 (LKCNHM). 4 females (JK.09.10.13.0001, JK.09.10.13.0008–9), with same locality data as for previous specimen, disturbed forest, J.K.H. Koh leg. 13 October 2009 (LKCNHM). 1 male (JK.10.01.24.3015), 2 females (JK.10.01.24.3001–2), with same locality data as for previous specimens, J.K.H. Koh leg. 24 January 2010 (LKCNHM). 1 female (JK.11.04.16.1006), with same locality data as for previous specimens, J.K.H. Koh leg. 16 April 2011 (LKCNHM). 1 female (JK.12.03.24.1002), with same locality data as for previous specimens, J.K.H.



Koh leg. 24 March 2012 (BMKB). 1 male (JK.09.10.14.2001), Tasek Merimbun Heritage Park, Banunih Trail, disturbed forest, 4° 35' 28" N, 114° 28' 44" E [43 m elevation], J.K.H. Koh leg. 14 October 2009 (BMKB). Temburong: 1 male, Ulu Temburong National Park, Kuala Belalong Field Study Centre [4° 32' 46.73" N, 115° 9' 28.15" E, 107 m elevation], O. Machač leg. 25 January–18 February 2019 (SMF). 1 female

(JK.07.04.17.0026), Kampong Lakiun, disturbed secondary forest, 4° 42' 55" N, 115° 8' 15" E [80 m elevation], J.K.H. Koh leg. 17 April 2017. (LKCNIHM). 1 male (JK.10.05.08.0008), Peradayan Forest Reserve, off Kampong Lakiun, 4° 45' 0.0" N, 115° 9' 58" E [109 m elevation], J.K.H. Koh leg. 8 May 2010 (BMKB). 4 females (JK.10.05.08.0019, JK.10.05.08.00023, JK.10.05.08.9021, JK.10.05.08.9023), with same locality



Figures 1–5. *Heteropoda borneensis* (Thorell, 1890), male (1–3) and female (4) from Brunei, holotype female (5) from Sarawak. 1–2 Left palp (1 ventral; 2 retrolateral). 3 Conductor and apical part of embolus, ventral. 4 Setae of light dorsal band on tibia IV. 5 Epigyne, lateral. Abbreviations: C = conductor, dRTA = dorsal part of RTA, E = embolus, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pore, S = spermophor, SO = spermophor opening, vRTA = ventral part of RTA.

data as for previous specimen, J.K.H. Koh leg. 8 May 2010 (LKCNDM). 1 female (JK.11.08.06.0016), with same locality data as for previous specimens, J.K.H. Koh leg. 6 July 2011 (BMKB). 2 males (JK.12.04.20.0041, JK.12.04.20.0068), 5 females (JK.12.04.20.0002–5, JK.12.04.20.0064), with same locality data as for previous specimens, J.K.H. Koh leg. 20 April 2012. (LKCNDM). MALAYSIA: Kuala Lumpur: 1 female, Pahang Road 6.5 km N Kuala Lumpur [ca. 3° 10' 56.17" N, 101° 42' 5.07" E, 39 m elevation], Robert Traub leg. March–May 1950, US Scrub Typhus Unit (AMNH). Sabah: 1 female (JK.15.06.26.0010), Tawau, Tawau Hill Park, 4° 23' 34" N, 117° 54' 52" E [291 m elevation], C.S.P. Ang & J.M.L. Yeo leg. 26 June 2015 (LKCNDM). 1 female (JK.16.11.04.0057), Maliau Basin, Sky Bridge Trail, 4° 44' 36" N, 116° 58' 13" E [260 m elevation], J.K.H. Koh leg. 4 November 2016 (FSC). Sarawak: 1 male (JK.12.01.21.1016), Gunung Mulu National Park, Night Walk Trail, near Park HQ, 4° 2' 31" N, 114° 48' 54" E [45 m elevation], J.K.H. Koh leg. 21 January 2012 (LKCNDM). SINGAPORE: 1 female (JK.15.11.16.0001), Thomson Nature Park, secondary forest floor, 1° 22' 54" N, 103° 48' 55" E [30 m elevation], J.W.B. Koh leg. 16 January 2015 (LKCNDM).

Diagnosis. Males may be diagnosed by the following combination of palpal characters (Figures 1–3): 1. Embolus arising in 7.30-o'clock-position from tegulum, 2. Conductor arising in 11-o'clock-position from tegulum, short, i.e. roughly as long as tegulum width, 3. Spermophor straight, longitudinally running, 4. dRTA with ventrad pointed apex, 5. vRTA with hump and building an obtuse angle with dRTA. Female copulatory organs are similar to those of *Heteropoda afghana* Roewer, 1962, *H. fischeri* Jäger 2005 and *H. robusta* Fage 1924 in having a freely visible median septum and an especially simple internal duct system with the first winding running laterad, then connecting to posterior spermathecae (Figures 6–11), but can distinguished from all three species by the short and broad anterior bands of the epigynal field (cf. Jäger, 2005, figures 7–27, 35–45). Additionally, *H. borneensis* can be distinguished from *H. fischeri* and *H. robusta* by the copulatory opening visible in dorsal view (hidden in dorsal view by first windings in *H. fischeri* and *H. robusta*).

H. borneensis can be distinguished from *H. afghana* by the round and entire outline of the spermathecae (outline with bulges in *H. afghana*; cf. Jäger, 2005, figures 8, 13, 18, 24, 26, 28). Furthermore, live spiders can be recognised by their striking colouration. Live females (Figures 23–28) are orange, with bicoloured chelicerae: the proximal part orange and distal part black. White and simple setae (i.e. not feathered, Figure 4) cover the dorsal side of tibiae and metatarsi of legs III and IV. The overall colouration of living males (Figures 29–30) is dusty brown. The tibiae and metatarsi of legs I, II, III and IV are covered dorsally by white setae. Their chelicerae are black except for a thin strip of orange hairs near the base (Figure 31). However, such contrasting colouration fades quickly in preserved specimens (Figures 12–22).

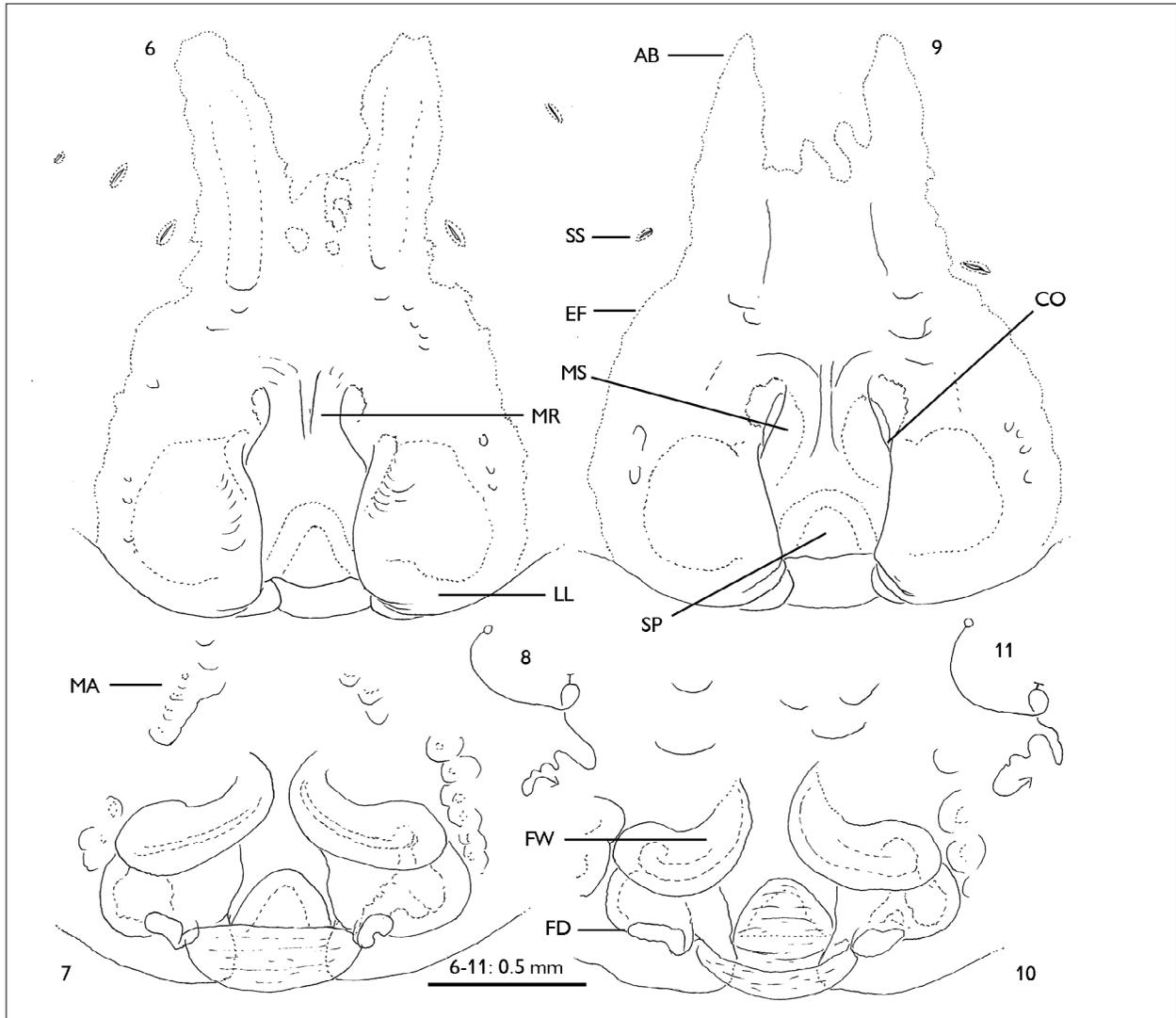
Description. Male (JK.11.04.16.1014, from Brunei): Measurements: TL 16.6, PL 9.0, PW 8.3, AW 4.1, OL 7.6, OW 4.5. Eyes: AME 0.51, ALE 0.60, PME 0.45, PLE 0.61, AME-AME 0.25, AME-ALE 0.07, PME-PME 0.42, PME-PLE 0.62, AME-PME 0.40, ALE-PLE 0.44, CH AME 0.76, CH ALE 0.75 (with especially strong setae around eyes; Figure 22). Spination: Pp 131, 101, 2121; Fe I–II 323, III 323(2), IV 321; Pa I–III 101, IV 001; Ti I–III 2126, IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 14.6 (4.9, 2.2, 3.4, –, 4.1); I 54.6 (13.8, 4.9, 15.8, 15.7, 4.4); II 58.9 (15.2, 5.1, 17.1, 17.1, 4.4); III 43.9 (12.2, 4.0, 12.5, 12.0, 3.2); IV 52.0 (14.1, 3.9, 14.1, 15.7, 4.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 75–80 denticles and 1 escort seta.

Palp (Figures 1–3). As in diagnosis. RTA arising distally to sub-distally from Ti, vRTA flat, dRTA broad, dorso-apically rounded. Cymbium distinctly longer than Ti, with indistinct small, rounded retro-proximal swelling. Spermophor running from a 12-o'clock- to 6-o'clock-position in ventral view. E with short broad base, narrowing continuously towards tip, subapically with almost undiscernible widening, spermophor opening situated apically. C with broadly pointed retrolaterad tip.



Colouration (Figures 12–14, 22). Orange-brown without distinct pattern. DS with dark fovea and margins. Chelicerae darker and with longitudinal stripes. Sternum and ventral coxae partly suffused with black especially in the anterior parts. OS dorsally with a short light-and-dark transversal pattern in posterior half, ventrally dark behind epigastric furrow with white longitudinal lines; spinnerets light brown.

Female (JK.11.04.16.1012, from Brunei with data of lectotype in square brackets, in spination pattern only when different): Measurements: TL 21.2 [22.6], PL 9.8 [11.2], PW 8.5 [10.2], AW 5.0 [5.4], OL 11.4 [11.4], OW 8.4 [6.9]. Eyes: AME 0.51 [0.52], ALE 0.63 [0.65], PME 0.46 [0.48], PLE 0.63 [0.67], AME-AME 0.26 [0.34], AME-ALE 0.11 [0.14], PME-PME 0.51 [0.53], PME-PLE 0.63 [0.75], AME-PME 0.41 [0.55], ALE-PLE 0.50 [0.56], CH AME



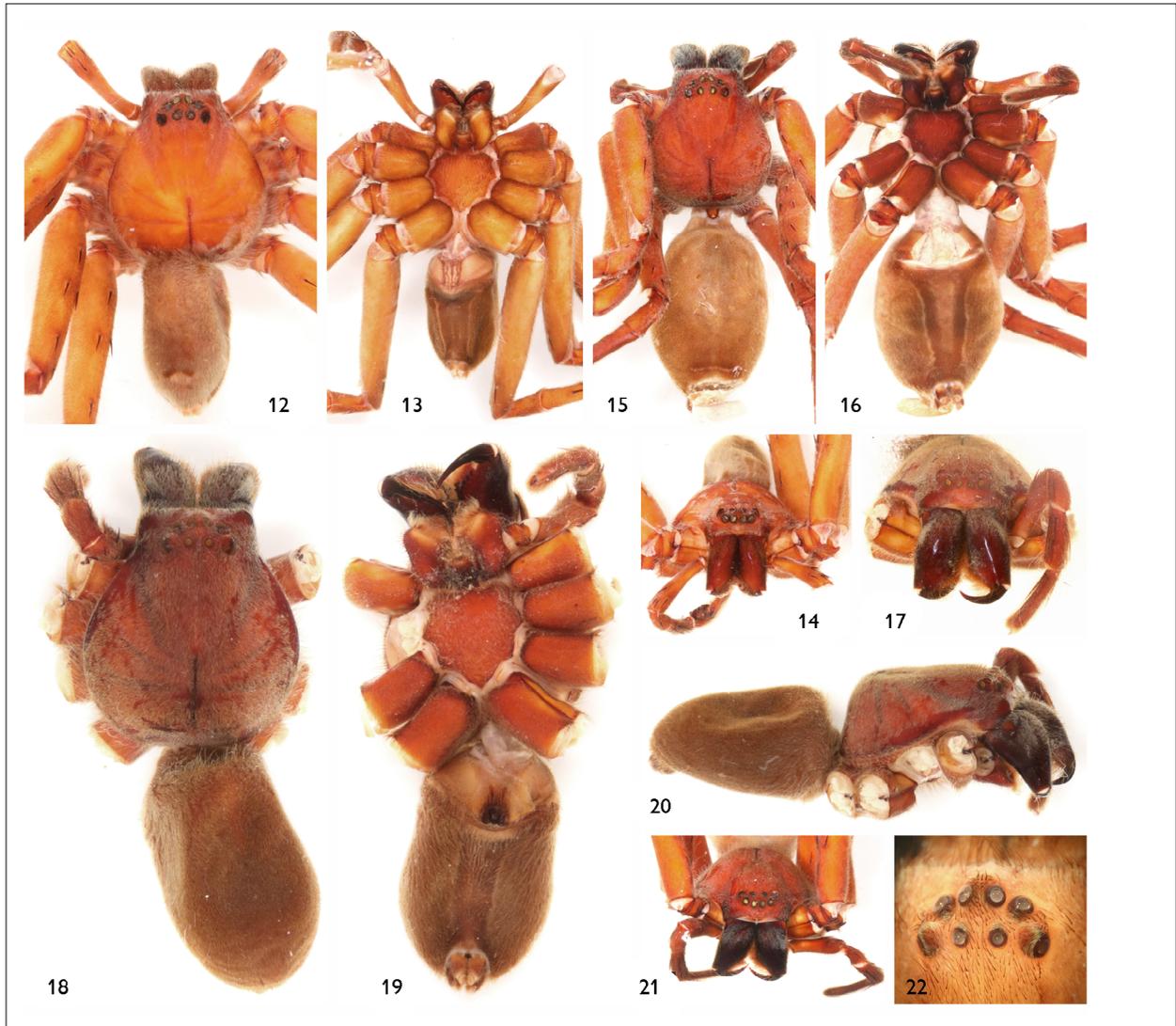
Figures 6–11. *Heteropoda borneensis* (Thorell, 1890), lectotype female from Sarawak (6–8), female from Brunei (9–11). 6, 9 Epigyne, ventral. 7, 10 Vulva, dorsal. 8, 11 Schematic course of internal duct system, dorsal. Abbreviations: AB = anterior bands, CO = copulatory opening, EF = epigynal field, FD = fertilisation duct, FW = first winding of internal duct system, LL = lateral lobes, MA = muscle attachment points, MR = median ridge, MS = median septum, SP = septal pocket, SS = slit sensillum.



0.81 [0.95], CH ALE 0.90 [1.04]. Spination: Pp 131, 101, 2121, 1014; Fe I–II 323, III 322, IV 321; Pa I–IV 001 [III 101]; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 14.3 (4.4., 2.1, 3.3, -, 4.5); I 41.7 (11.3, 4.7, 11.6, 11.0, 3.1); II 46.0 (12.7, 5.1, 13.1, 11.8, 3.3); III 35.4 (10.6, 4.3, 9.4, 8.6, 2.5); IV 43.3 (12.4, 4.0, 11.5, 12.0, 3.4) [Pp 17.0 (5.2, 2.6, 4.1,

-, 5.1); I 46.7 (12.6, 5.5, 13.3, 11.7, 3.6); II 50.2 (13.9, 6.0, 14.4, 12.3, 3.6); III 40.2 (11.7, 4.9, 11.0, 9.6, 3.0); IV 48.8 (13.9, 4.7, 12.8, 13.4, 4.0)]. Leg formula: II-IV-I-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 90 [90–100] denticles and 1 escort seta. Palpal claw with 8 [9] teeth.

Copulatory organ (Figures 6–11). As in diagnosis. Epigynal field roughly as long as wide, anterior bands fused, with 2 left and 3 right slit sensilla lateral of anterior bands and many muscle attachment points. Median septum longer



Figures 12–22. *Heteropoda borneensis* (Thorell, 1890), male (12–14) and female (15–17) from Brunei, lectotype female from Sarawak (18–21), male from Brunei (22), habitus (12, 15, 18, 22 dorsal; 13, 16, 19 ventral; 14, 17, 21 frontal; 20 lateral). Photos: P. Jäger.

than wide, septal pocket distinctly developed, with distinct median longitudinal ridge in the anterior part of the median septum. Posterior part of internal duct system separated by one width of the first winding in ventral view. Fertilisation ducts short, their tips laterad.

Colouration (Figures 15–21). As in male, but generally darker, especially, chelicerae, ventral side and palps. OS ventrally with light median band. Spinnerets proximally darker.

Variation. Male: TL 18.0–25.0, PL 9.0–12.0, OL 9.0–13.0. While the chelicerae in mature males are almost entirely black (vs bicoloured chelicerae in females), immature males have bicoloured chelicerae, like their sisters and mothers. Living males (Figures 29–32) differ from live females in overall colouration, leg colouration, and cheliceral colouration. They further differ from females in: 1. DS shows a pair of dark patches at the 4 o'clock and 8 o'clock positions (Figures 29–30, absent in the females); 2. Dark patch visible anterior to a black-and-white somewhat transversal line on the posterior half of the OS (Figures 29–30 vs. Figure 23); 3. Venter almost completely black, with only a pair of fine longitudinal lines running behind the epigastric area to the posterior end of the opisthosoma (Figure 32 vs. Figure 26). In subadult males, the chelicerae are bicoloured (Figure 33) in live specimens, like those in females, and not almost black as in adult males (Figure 31). Female: TL 20.1–27.0, PL 9.8–16.0, OL 11.2–16.3. The shape of the epigynal median septum varies rather widely. In some specimens, it is broader than those depicted in Figures 6 and 9, and the posterior margin can be straight, curved slightly backward, or angled with a blunt protrusion at the posterior end (Figures 35–40). While the median ridges of some specimens are conspicuously rugged (Figure 35), others appear merely as a slightly crested, upfolding band; in some specimens it is not recognisable at all. On both sides of the median ridge, the eyebrow-like ridges anterior to the copulatory openings are straight or concave (Figure 35 vs. Figure 38). The number of slit sensilla off the anterior bands of the epigyne varies: in some cases, only a single slit sensillum is visible on the left side; in

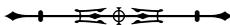
other cases, the number of sensilla ranges from one to three on one side, without necessarily a corresponding number on the other side. For instance, in one examined specimen, there are three sensilla on the left, but only one on the right. In live spiders, overall colouration is orange (Figures 23–24, 27–28), with a short transversal pattern on the posterior half (Figures 23–24). Chelicerae bicoloured with orange and black (Figures 25, 28). Palps, sternum, ventral coxae, and epigastric area black (Figure 26). A median longitudinal black band, flanked by a pair of fine white lines, running from the epigynal area to the spinnerets contrasting with the orange background, forming a T-shaped black pattern on the entire venter (Figure 26 vs. Figure 32). The orange setae on the female OS are easily dislodged, resulting in some older females showing an almost bare and brownish OS (Figure 24), differing in colouration from a DS densely carpeted by orange setae. In live males, the paired dark patches on the posterior half of the DS often differ in size and shapes. Some specimens have paired dark patches on the anterior half as well, albeit smaller and paler. In some subadult males, the size of these dark patches on the DS can be twice bigger than the norm. In subadults and mature specimens in both sexes, the light-and-dark transversal pattern on the posterior half of the OS show a wide range of differences: from a short straight or wavy line to a moustache-like bar, or a small white transversal patch (1 female from Kuala Lumpur; iNaturalist). Such a white patch on the posterior half of the opisthosoma is also present in other species of Heteropodinae, e.g., *Pseudopoda confusa* Jäger, Pathoumthong & Vedel, 2006, and may vary in size and shape (Jäger et al., 2006).

Distribution. Malaysia (Kuala Lumpur, Sabah, Sarawak), Singapore, Brunei, Indonesia (Kalimantan Utara) (Figure 41, based on specimens examined and iNaturalist records of unambiguously identified individuals of the species). Additional unmistakably identifiable records were provided on the internet platform Flickr — Malaysia: Sabah: Tawau and Maliau Basin; Selangor: close to Semenyih; Johor: Gunung Pantii. Because exact coordinates were not provided, these records are not indicated in the distribution map.





Figures 23–28. *Heteropoda borneensis* (Thorell, 1890), living females (23–24), freshly killed females (25–26), living females with egg sacs (27–28). 23 Female described in the text, from Brunei: Tütong, Tasek Merimbun Heritage Park. 24 Female from Malaysia: Sabah, Maliau Basin. 25 Frontal view showing bicoloured chelicerae, from Brunei: Temburong, Peradayan. 26 Ventral view of a specimen from Brunei: Temburong, Kuala Belalong; scale line: 5.0 mm. 27 Egg sac carried under chelicerae, from Brunei: Temburong, Peradayan Forest Reserve. 28 Egg sac fastened on foliage, from Brunei: Temburong, Peradayan Forest Reserve. Photos: J. K. H. Koh.

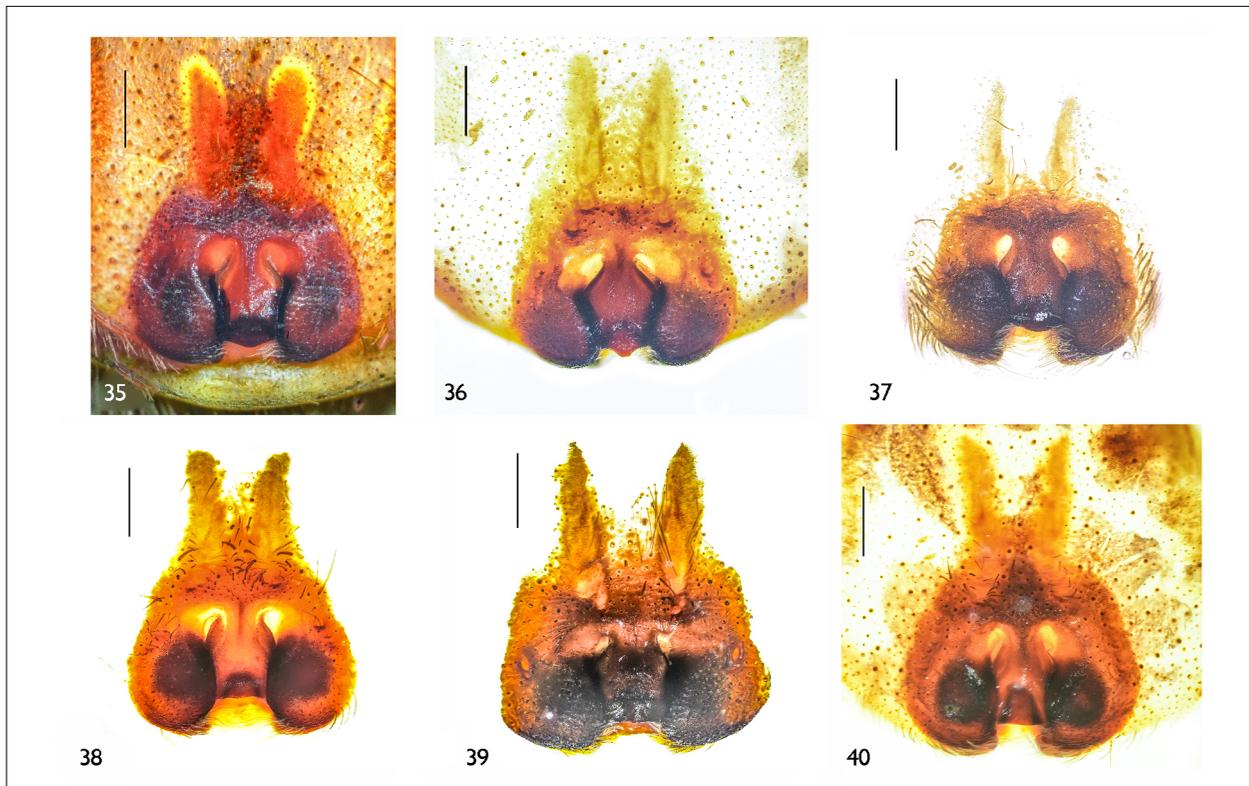




Figures 29–32. *Heteropoda borneensis* (Thorell, 1890), living males (29–30), freshly killed male (31–32). 29 the male described in text, from Brunei: Tutong, Tasek Merimbun Heritage Park. 30 Living male in resting pose, from Brunei: Temburong, Peradayan Forest Reserve. 31 Frontal view showing cheliceral colouration in adult male. 32 ventral habitus, scale bar: 5.0 mm. Photos: J. K. H. Koh.



Figures 33–34. *Heteropoda borneensis* (Thorell, 1890), freshly killed subadult male (33), living subadult male (34). 33 Frontal view showing cheliceral colouration in subadult male. 34 Habitus of subadult male. Photos: J. K. H. Koh.



Figures 35–40. *Heteropoda borneensis* (Thorell, 1890), selected epigynes from examined specimens, ventral view. Scale lines: 0.5 mm. 35 from Brunei: Beilait, Sungei Ingei Forest Reserve. 36–38 from Brunei: Temburong, Peradayan Forest Reserve. 39 from Singapore: Thomson Nature Park. 40 from Malaysia: Sabah, Tawau Hill Park. Photos: J. K. H. Koh.



Biology. This spider appears to thrive in dense, moist lowland forests (elevations between 30 and 300 metres). It forages not only on the ground, but also on the fallen logs and foliage up to a metre from the ground. Apart from insects and other spiders, slugs are among its diet (Koh & Leong, 2014, p. 242). In resting position, its legs 3 are often retracted with the femora pointing almost vertically upwards (Figures 23–24, 27, 29–30, as in the jumping spider *Portia*). A mother has been seen fastening egg sac on the upper side of leaves (Figure 28). Before that stage, the discoidal egg-sacs are carried with the fangs under the mother's prosoma, as is usually seen in this genus. In three females, scars were observed (1 female syntype from Sarawak with 1 round scar ventrodistally on coxa II; 1 female from Malaysia: with 1 irregular scar on left femur IV ventro-proximally and 1 round scar on opisthosoma dorso-anteriorly;

1 female from Kuala Lumpur with 1 round scar on left palpal tibia dorso-medially, 1 irregular and 1 round scar on left coxa II ventro-proximally, and 4 round scars on left femur II retrolatero-ventro-proximally). These scars may indicate that males bite females during the mating process as reported in some *Thunberga* spp. (Jäger, 2021; Eudeline & Jäger, 2023), *Micrommata* spp. (Jäger, 2023), and *Heteropoda* spp. (Jäger, 2024; Korai & Jäger, 2024).

Heteropoda bufocorniculans spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:64E6BBD6-1725-4D5D-9DE2-81A505DCABE4>

(Figures 42–48, 52–66, 169)

Type material. MALAYSIA: Sarawak: holotype female, Kuching, Gading National Park, 1° 41' 26.79" N, 109° 50' 45.14" E [47 m elevation], dipterocarp forest, D. Nazir

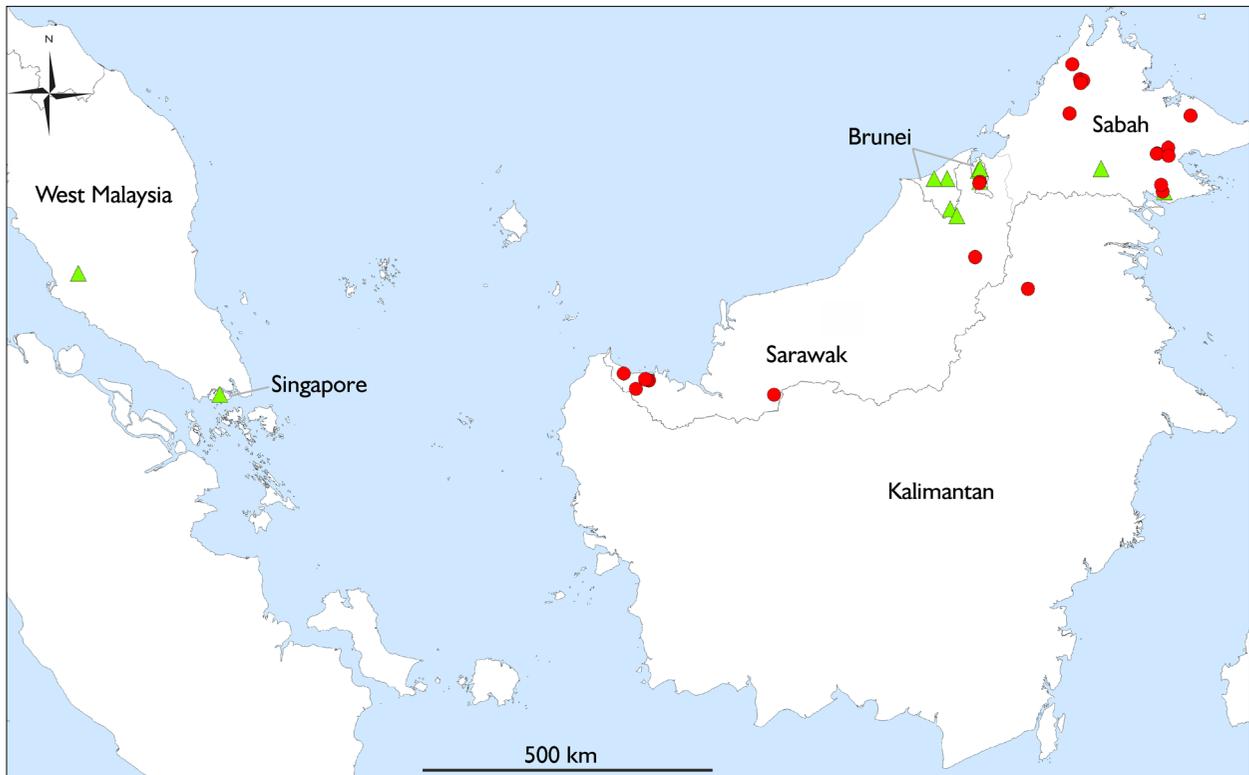


Figure 41. Distribution records of *Heteropoda borneensis* (Thorell, 1890). Green triangles—material examined for this study; red dots—photos from iNaturalist identifiable to species level. The exact type locality in Sarawak is unknown and therefore not pinpointed.

leg. 21 April 2013, DMN 00063, N. Nazir ded. (SMF). Paratype: MALAYSIA: Sabah: 1 female (JK.15.06.26.0005), Tawau, Tawau Hill Park, 4° 23' 34" N, 117° 54' 52" E [291 m elevation], C.S.P. Ang & J.M.L. Yeo leg. 26 June 2015 (FSC).

Material examined for comparison. *Heteropoda gemella* Simon, 1877: holotype female from the PHILIPPINES: Metro Manila: Manila [PL 5.7, OL 6.9; without characters 1–4 listed in the diagnosis below; DS and legs with numerous small dots] (MNHN 1774) (Figures 49–51).

Notes. Although the measured OL (6.9) of the holotype of *H. gemella* is not consistent with the length (7.5) provided by Simon in his original description, the examined specimen is considered the holotype. The ten immature specimens in the same vial as the holotype are not treated as part of the type series, as they were not mentioned in the description by Simon (1877, p. 65, “une femelle”).

Etymology. The species name is derived from the Latin ‘bufo’ meaning ‘toad’ and ‘corniculans’ meaning ‘horned’ and refers to toad-like appearance of the species with wart-shaped structures and the “horns” between lateral eyes; adjective.

Diagnosis. Females of this species are unique in having the following characters: 1. Presence of a cone-shaped bulge between lateral eyes (Figures 47–48, 55), 2. Body covered dorsally with tufts of light and dark setae (Figures 52–54, 56, 59–64), 3. Absence of most of retrolateral spines on femora, tibiae and most of lateral spines on metatarsi (see description for details), 4. Presence of erect spines on femora (Figures 57–58), 5. Reduction of metatarsal ventral scopula in legs I–III (see description for details), and 6. Posterior part of opisthosoma widened resulting in an atypical shape (Figures 52–53, 59–60, 62, 64). Female copulatory organs (Figures 42–44, 65–66) are similar to those of *Heteropoda gemella* (Figures 49–51) in having a similarly shaped median septum (narrow waist anteriorly, anterior margins laterad) and internal duct system (first winding postero-laterad, glandular pores mediad to medio-

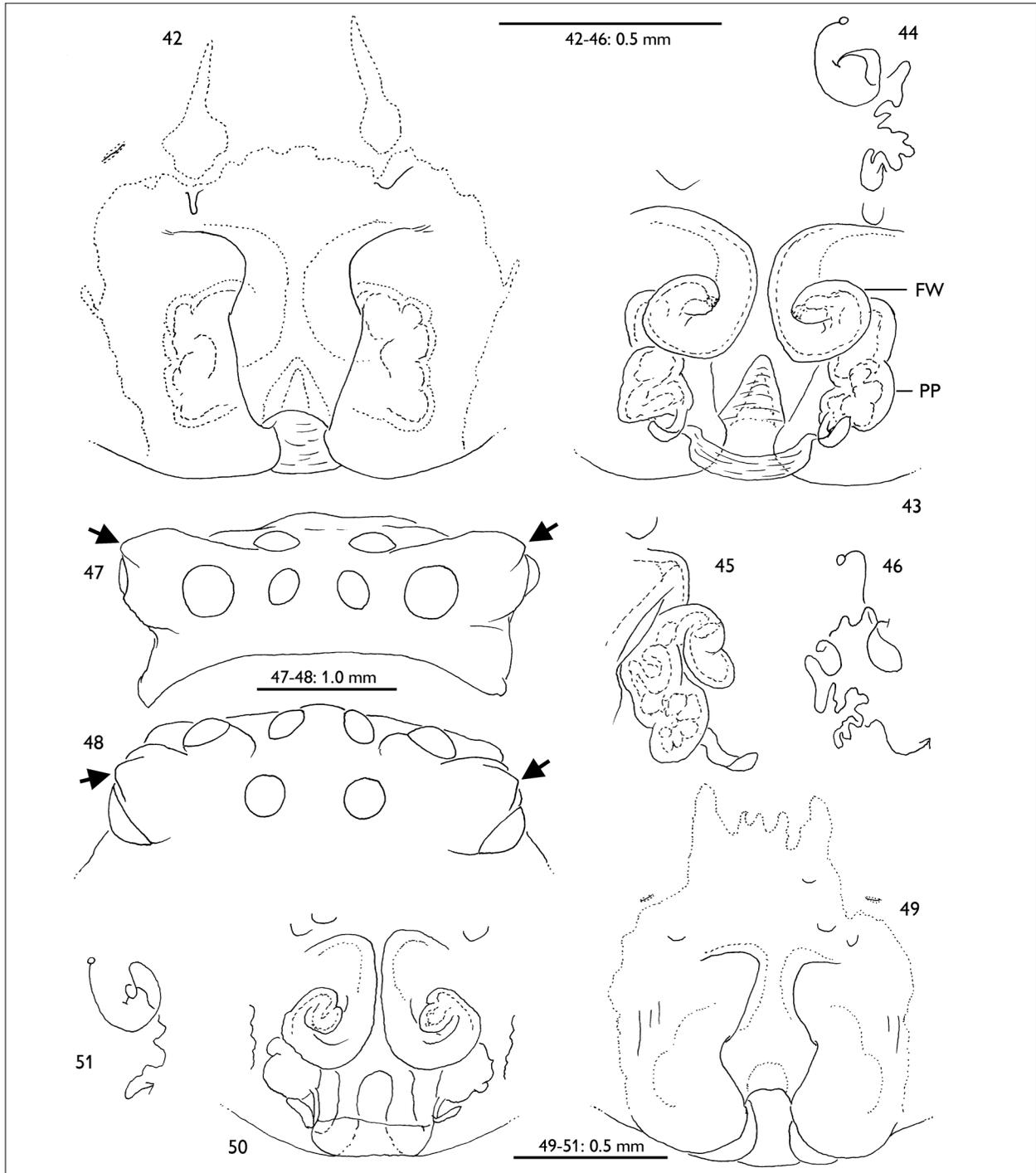
posteriad, posterior part bulging, slightly wider than anterior part), but can be distinguished by: 1. Presence of distinct anterior bands, slightly separated from the field, 2. Anterior waist of median septum wider (i.e. ratio maximum width/waist width 1.3), 3. First windings medially rounded. In contrast, in *H. gemella*, the anterior bands are indistinct, strongly fused to field, waist of median septum narrower (i.e. ratio maximum width/waist width of median septum 2.6), and the first windings are elongate (i.e. median margins partly running parallel).

Description. Male. Unknown.

Female (holotype): Measurements: TL 12.2, PL 5.6, PW 5.4, AW 2.9, OL 6.5, OW 4.5. Eyes: AME 0.30, ALE 0.44, PME 0.29, PLE 0.45, AME-AME 0.29, AME-ALE 0.22, PME-PME 0.48, PME-PLE 0.83, AME-PME 0.29, ALE-PLE 0.61, CH AME 0.37, CH ALE 0.36; lateral eyes separated by cone-shaped bulge. Spination: Pp 130, 101, 2121, 1012; Fe I 321, II 331, III–IV 330; Pa I–IV 000; Ti I 1016, II 1006, III 1004, IV 1003; Mt I 0014, II–III 0004, III 2014, IV 0006(5). Ta I–IV with moderately dense scopulae, Mt I–II with scopula in distal half and proximal field and double row of stronger setae, III with rest of sparse scopula only distally and double row of stronger setae, IV with distal field and double row of stronger setae. Measurements of palps and legs: Pp 6.6 (2.0, 1.2, 1.3, -, 2.1); I 17.3 (5.0, 2.7, 4.7, 3.7, 1.2); II 19.5 (6.0, 2.8, 5.3, 4.0, 1.4); III 16.5 (5.2, 2.3, 4.2, 3.5, 1.3); IV 16.2 (5.4, 2.0, 3.8, 3.7, 1.3). Leg formula: II-I-III-IV. CH with 3 promarginal and 4 retromarginal teeth, 35 denticles and 1 escort seta. Palpal claw with 7 teeth.

Copulatory organ (Figures 42–46). As in diagnosis. Epigynal field wider than long, with 1 slit sensillum on left side and short anteriorly acuminate anterior bands, separated from the field. Subseptal pocket developed, anteriorly tapering. Internal duct system with semicircular first winding running to the distinctly visible glandular pores; posterior part with heavily coiled ducts and bulges; fertilisation ducts long, narrow, and curved, with antero-dorsad tips.





Figures 42–51. *Heteropoda* spp., females, copulatory organs. 42–48 *Heteropoda bufocorniculans* spec. nov., holotype female from Sarawak. 49–51 *Heteropoda gemella* Simon, 1877, holotype female from Philippines. 42, 49 Epigyne, ventral. 43, 45, 50 Vulva (42, 50 dorsal; 45 left half, lateral). 44, 46, 51 Schematic course of internal duct system (44, 51 dorsal; 46 lateral). 47–48 Eye arrangement (47 frontal; 48 dorsal). Abbreviations: FW = first winding of internal duct system, PP = posterior part of the internal duct system. Arrows indicating cone-shaped bulges between lateral eyes,



Figures 52–58. *Heteropoda bufocorniculans* spec. nov., holotype female from Sarawak. 52–54 Habitus (52 dorsal; 53 ventral; 54 frontal). 55 Eye region, dorsal. 56 Opisthosoma, dorsal, showing stiff setae and tufts of light setae. 57–58 Erect femoral spines (57 shortened prolateral distal spine of leg I, dorsal; 58 dorsal spines of leg II, prolateral, with shortened prolateral spine of leg III in the background). Photos: P. Jäger.





Figures 59–66. *Heteropoda bufocorniculans* spec. nov., females from Sabah (59, with egg-sac; 60–63 carrying egg-sac; 60–61 with some freshly hatched spiderlings clinging on the mother's prosoma). 59–64 Habitus (59–62, 64 dorsal; 63 frontal). 65 Epigyne, ventral. 66 Vulva, dorsal. Photos: J. K. H. Koh (59–61, 64–66) and N. Bay (62–63).



Colouration (Figures 52–56). Pale yellow to reddish brown with vivid pattern of dots, patches, light and dark tufts of setae as well as marbled pattern. DS with lighter median band and black tufts of setae laterally. Chelicerae reddish-brown with lighter patch in proximal half. Legs with spine patches and dots in between (decreasing in intensity from leg I to IV), femora ventrally yellowish-brown with many dots. Opisthosoma dorsally with pair of dark triangular patches antero-laterally, anterior half light brown with heart region slightly darker; posterior half darker with rows of lighter tufts of setae; laterally with reticulate, strongly contrasting pattern; ventrally light brown with dots.

Variation. Female (paratype): TL 11.6, PL 5.0, OL 6.6. Chelicerae with 25 denticles in furrow. Epigyne with 1 slit sensillum on each side, anterior bands distinct, but fused to field (Figures 65–66; many setae including tufts are rubbed off).

Distribution. Malaysia (Sarawak, Sabah) (Figure 169).

Biology. These spiders were found on tree trunks in primary rain forests. The egg-sac is held like in other *Heteropoda* species mainly by fangs and palps (Figures 59–63). Hatched spiderlings were bigger in size relative to the mother's body length compared to other *Heteropoda* species (Figures 60–61; Koh & Bay, 2019, p. 335).

Heteropoda lunula (Doleschall, 1857)
(Figures 67–71, 169)

Olios lunula Doleschall 1857: 428 (Description of female; holotype female from Java, NHMW 1858.1.30; examined).

Heteropoda lunula, Jäger 2002: 49, figures 106–117 (illustrations of male and female, removed from synonymy of *H. thoracica*, synonymy of male previously assigned to *H. lunula* with *H. venatoria*). Jäger 2006: 53, figure 9 (illustration of female).

Material examined. SINGAPORE: 4 males (JK.89.08.24.0003, JK.90.01.01.0001, 90.08.10.0001, JK.92.06.14.0001), Greenwood Avenue, inside old house (now demolished) [1° 20' 3.79" N, 103° 48' 18.87" E,

12 m], J.K.H. Koh, leg. 24 August 1989, 1 January 1990, 10 August 1990, 14 June 1992 respectively (LKCNDHM). 1 male (JK.88.10.16.0001), Malcolm Road, inside house, 1° 19' 26" N, 103° 50' 05" E [9 m elevation], J.K.H. Koh leg. 16 October 1988 (LKCNDHM), 1 male (JK.88.11.15.0002), Kent Ridge, inside old house (now demolished), 01° 17' 43" N, 103° 46' 34" E [64 m elevation], J.K.H. Koh, leg. 15 November 1988 (LKCNDHM). 1 male (JK.14.09.18.0001), Cluny Road, inside house, 01° 19' 10" N, 103° 48' 59" E [16 m elevation], J.K.H. Koh leg. 18 September 2014 (LKCNDHM). 1 female (JK.92.05.24.0001), Hillcrest Road, inside old house (now demolished), 01° 19' 48" N, 108° 48' 22" E [12 m elevation], S.C. Tiah, leg. 24 May 1992 (LKCNDHM).

Diagnosis. See Jäger (2002).

Description. See Jäger (2002). For colouration of preserved male see Figures 69–71, of live males and females see Figures 67–68 and Koh and Bay (2019, p. 326, unnumbered figures) and Koh et al. (2022, p. 505, unnumbered figures).

Distribution. India to Vietnam, Malaysia (Selangor), Indonesia (Java, Sumatra, Kalimantan, Maluku), Singapore new record (Figure 169).

Notes. Images of what can be unambiguously identified as *H. lunula* of both sexes have been taken outdoors by Nicky Bay (personal communication) near human habitation in other locations in Malaysia (Johor: Batu Pahat; Sabah: Maliau Basin).

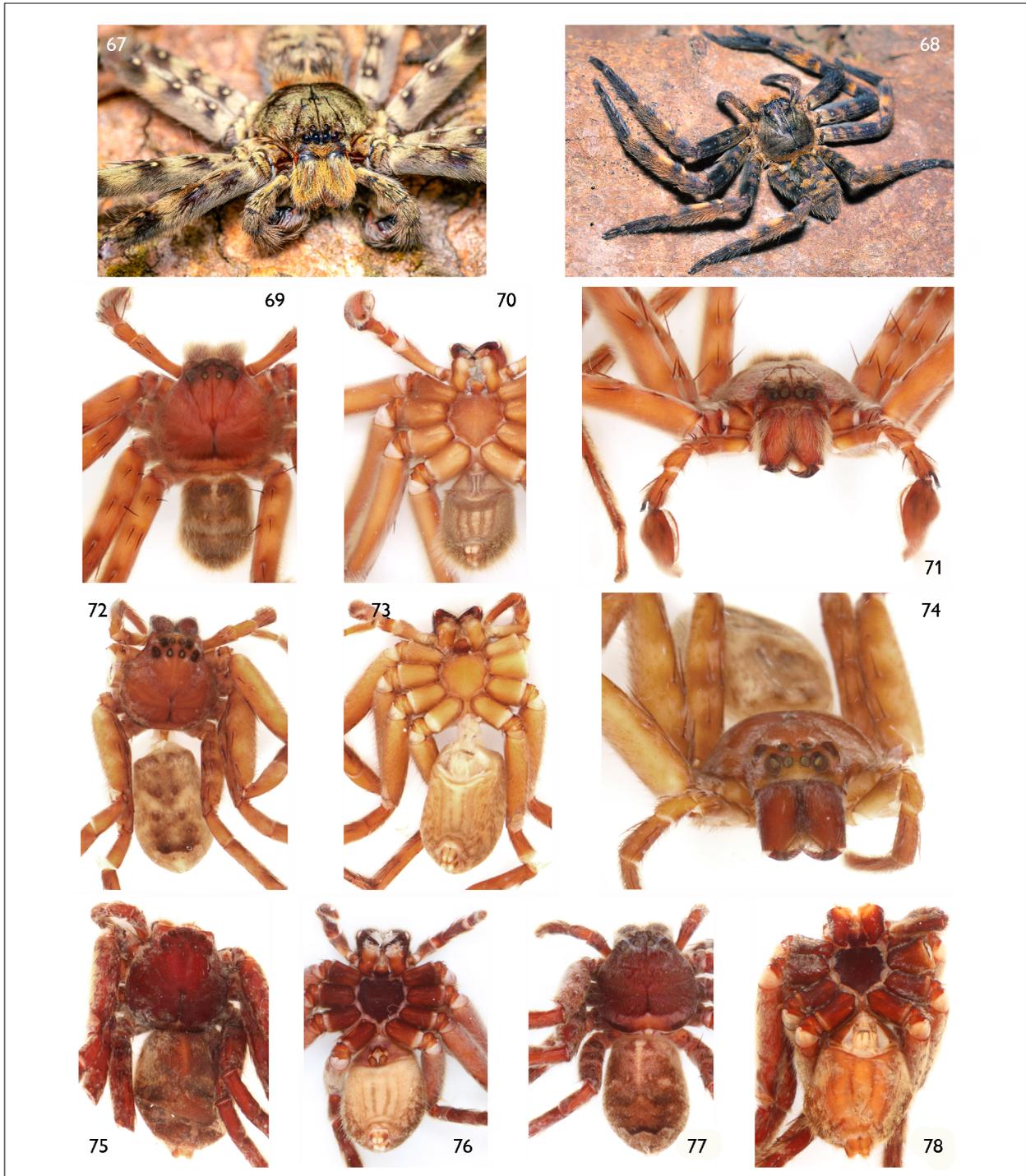
Biology. *H. lunula* may be regarded as a synanthropic species, at least in Singapore, as it is often found on walls and corners inside old houses, and on tree trunks and crevices in highly disturbed or degraded forests. The females are heavy, sluggish, and slow-moving.

Heteropoda sederhana spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:F376EB9B-3E5C-43B5-A08B-4FBF941BDF46>

(Figures 72–74, 79–81, 169)





Figures 67–78. *Heteropoda* spp., habitus. 67–71 *H. lunula* (Doleschall, 1857), male (67, 69–71) and female (68) from Singapore. 72–74 *H. sederhana* spec. nov., holotype female from Java. 75–78 *H. strandi* Jäger, 2002, females from Sumatra (75–76: holotype) and Singapore (77–78) (67, 71, 74 frontal; 68–69, 72, 75, 77 dorsal; 70, 73, 76, 78 ventral; 73, 78 with epigyne dissected). Photos: C. S. P. Ang (67); J. K. H. Koh (68); P. Jäger (69–78).



Type material. INDONESIA: Jawa Barat: Holotype female, Buitenzorg [= Bogor, ca. 6° 35' 58.46" S, 106° 47' 59.46" E, 250 m], H.J. Jensen leg. 1904, Tilg. 28.8.1916, #275 (ZMUC).

Etymology. The species name is derived from the Indonesian adjective 'sederhana', meaning 'simple,' referring to the simple internal duct system without a loop as in most other *Heteropoda* spp.; term in apposition.

Diagnosis. Females of this species and *H. strandi* are unique among *Heteropoda* spp. in having the following characters (Figures 79–81): 1. Distinct triangular pocket situated anteriorly of copulatory openings, 2. Median septum distinctly narrowing posteriorly (i.e. lateral lobes almost touching each other at posterior margin), 3. Internal duct system simple, with short first winding and one coil anteriorly. Females of *H. sederhana* spec. nov. are distinguished from those of *H. strandi* by 1. Epigynal folds with S-shaped laterad parts in anterior half. 2. Anterior pocket approximately as long as wide. 3. Plain of first winding transversal to cuticular surface (epigynal folds with simple laterad part, anterior pocket distinctly wider than long [although may be bend], plain of first winding parallel to cuticular surface in *H. strandi*, cf. Figures 82–84).

Description. Male. Unknown.

Female (holotype): Measurements: TL 13.9, PL 6.5, PW 6.2, AW 3.4, OL 7.4, OW 4.9. Eyes: AME 0.41, ALE 0.62, PME 0.42, PLE 0.67, AME-AME 0.25, AME-ALE 0.04, PME-PME 0.41, PME-PLE 0.66, AME-PME 0.46, ALE-PLE 0.50, CH AME 0.50, CH ALE 0.31. Spination: Pp 131, 101, 2121, 1014(3); Fe I–II 323, III 333, IV 331; Pa I–III 001, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Ta I–IV and Mt I–III with dense scopulae, Mt IV with distal field, double row of stronger setae and very few scopula setae. Measurements of palps and legs: Pp 8.9 (2.6, 1.5, 2.2, -, 2.6); I 23.1 (6.6, 3.1, 6.1, 5.5, 1.8); II 26.2 (7.6, 3.5, 7.0, 6.1, 2.0); III 21.2 (6.5, 2.8, 5.5, 4.8, 1.6); IV 20.7 (6.2, 2.5, 5.4, 5.0, 1.6). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 35 denticles, most of them in patch close to promarginal teeth and 1 escort seta.

Copulatory organ (Figures 79–81). As in diagnosis. Epigynal field slightly longer than wide, with 2 slit sensilla on each side and short anterior bands, the latter fused to field. Median septum narrowing to narrow posterior part. Anterior pocket regularly triangular. Internal duct system with first winding posteriorly, glandular pores not detected; posterior part with lateral bulges; fertilisation ducts narrow and curved, arising medio-posteriorly from posterior part, their tips dorsad.

Colouration (Figures 72–74). DS reddish-brown with light submarginal crescent posteriorly and sparse cover of light pubescence, the latter rubbed off in most parts; fovea, striae, and posterior margins dark. Chelicerae deep reddish-brown. Sternum ventral coxae, and gnathocoxae yellowish to reddish brown, labium deep reddish brown. Legs yellowish to dark yellowish brown with indistinct spine patches and numerous spots on ventral femora. Opisthosoma dorsally yellowish brown with four dark patches around muscle sigilla, between the two pairs a light chevron, dark median zone resulting posteriorly in dark transversal patch in posterior half; laterally mottled with elongate patches; ventrally yellowish, with four indistinct longitudinal bands of small muscle sigilla; spinnerets dorsally and laterally brown, ventrally yellowish.

Distribution. Indonesia (Java: Bogor) (Figure 169).

Heteropoda strandi Jäger, 2002
(Figures 75–78, 82–84, 169)

Torania panaretiformis Strand 1913: 119 (Description of female; holotype female from Indonesia, Sumatra, Bungar-Bondar, Schütz leg., SMF 4749; examined).

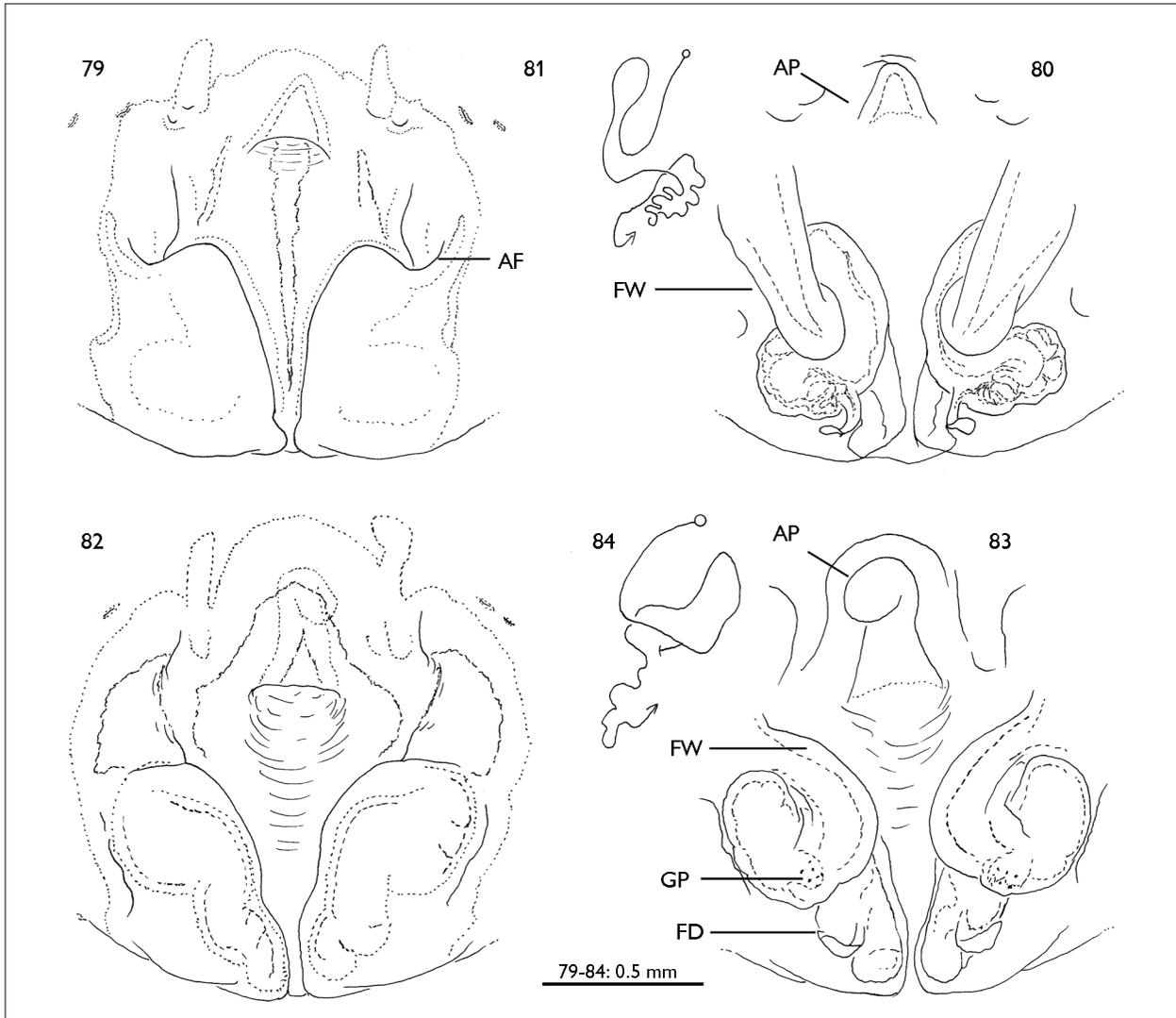
Heteropoda strandi Jäger 2002: 50, figs 129–131 (illustration of female, replacement name).

Material examined. SINGAPORE: 1 female (JK.03.07.30.0030), Upper Pierce Reservoir [1° 22' 23.65" N, 103° 48' 44.65" E, 20 m], edge of secondary forest, ground, J.K.H. Koh leg. 30 July 2003 (LKCNHM).



Diagnosis. Females of this species and *H. sederhana* spec. nov. are unique in having the following characters (Figures 82–84): 1. Distinct triangular pocket situated anteriorly of copulatory openings, 2. Freely visible median septum, narrowing posteriorly distinctly (i.e. lateral lobes almost touching each other), 3. Internal duct system simple, with short first winding and one coil anteriorly. Females of *H. strandi* are distinguished

from those of *H. sederhana* spec. nov. by: 1. Epigynal folds with simple laterad part in anterior half, 2. Anterior pocket distinctly wider than long [although may be bend], 3. Plain of first winding parallel to cuticular surface (epigynal folds with S-shaped laterad parts, anterior pocket approximately as long as wide, plain of first winding transversal to cuticular surface in *H. sederhana* spec. nov., cf. Figures 79–81).



Figures 79–84. *Heteropoda* spp., female copulatory organs. 79–81 *H. sederhana* spec. nov., holotype female from Java. 82–84 *H. strandi* Jäger, 2002, female from Singapore. 79, 82 Epigyne, ventral; 80, 83 vulva, dorsal; 81, 84 schematic course of internal duct system, dorsal. Abbreviations: AF = anterior fold of epigyne, AP = anterior pocket, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pores.

Description. Male. Unknown.

Female (Singapore): Measurements: TL 14.1, PL 6.7, PW 6.5, AW 3.7, OL 7.4, OW 5.0. Eyes: AME 0.49, ALE 0.67, PME 0.43, PLE 0.72, AME-AME 0.21, AME-ALE 0.08, PME-PME 0.47, PME-PLE 0.75, AME-PME 0.42, ALE-PLE 0.55, CH AME 0.35, CH ALE 0.24. Spination: Pp 131, 101, 2121, 1014; Fe I–II 323, III 333, IV 331; Pa I–III 001, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Ta I–IV and Mt I–III with dense scopulae, Mt IV with distal field, double row of stronger setae and very few scopula setae. Measurements of palps and legs: Pp 8.9 (2.6, 1.5, 2.0, -, 2.8); I 23.1 (6.3, 3.2, 6.3, 5.4, 1.9); II 26.1 (7.5, 3.5, 7.2, 5.9, 2.0); III 21.0 (6.4, 2.6, 5.6, 4.8, 1.6); IV 20.4 (6.1, 2.4, 5.3, 4.8, 1.8). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, 50–55 denticles in patch close to promarginal teeth and 1 escort seta. Palpal claw with 6 teeth.

Copulatory organ (Figures 82–84). As in diagnosis. Epigynal field as long as wide, with 1 slit sensillum on right and 2 slit sensilla on left side, all 3 close to the field, and short anterior bands, the latter fused to field. Median septum narrowing to thin posterior part. Anterior pocket anteriorly bent, tip ventrad. Internal duct system with first winding medio-posteriad, glandular pores indistinct; posterior part stretched converging posteriorly; fertilisation ducts narrow and curved, arising sub-terminally from posterior part, their tips antero-latero-dorsad.

Colouration (Figures 77–78). DS deep reddish-brown with distinct light submarginal crescent posteriorly and sparse cover of light pubescence, the latter denser around eyes; fovea and striae dark, with marbled pattern. Chelicerae deep reddish-brown with 2 thin dark longitudinal lines each. Sternum dark-brown, ventral coxae brown with light marbled pattern in proximal half, labium dark brown with light distal margin, gnathocoxae medially light, externally darker. Legs reddish-brown with cover of light pubescence, indistinct spine patches and numerous spots on ventral femora. Opisthosoma dorsally brown with irregular pattern, light transversal patch in posterior half, the latter anteriorly bordered by W-shaped dark zone

and posteriorly with narrow extended part. Ventral part of opisthosoma more lightly coloured in the area posterior to the epigastric groove, with four longitudinal bands of dark setae stopping short 2–3 mm anterior of the spinnerets (more obvious when the specimen was newly preserved. See also Figure 78).

Variation. Female (holotype; Figures 75–76): TL 18.0, PL 8.8, OL 9.2. Anterior pocket straight (i.e. not bent as in the Singapore specimen illustrated in Figure 83).

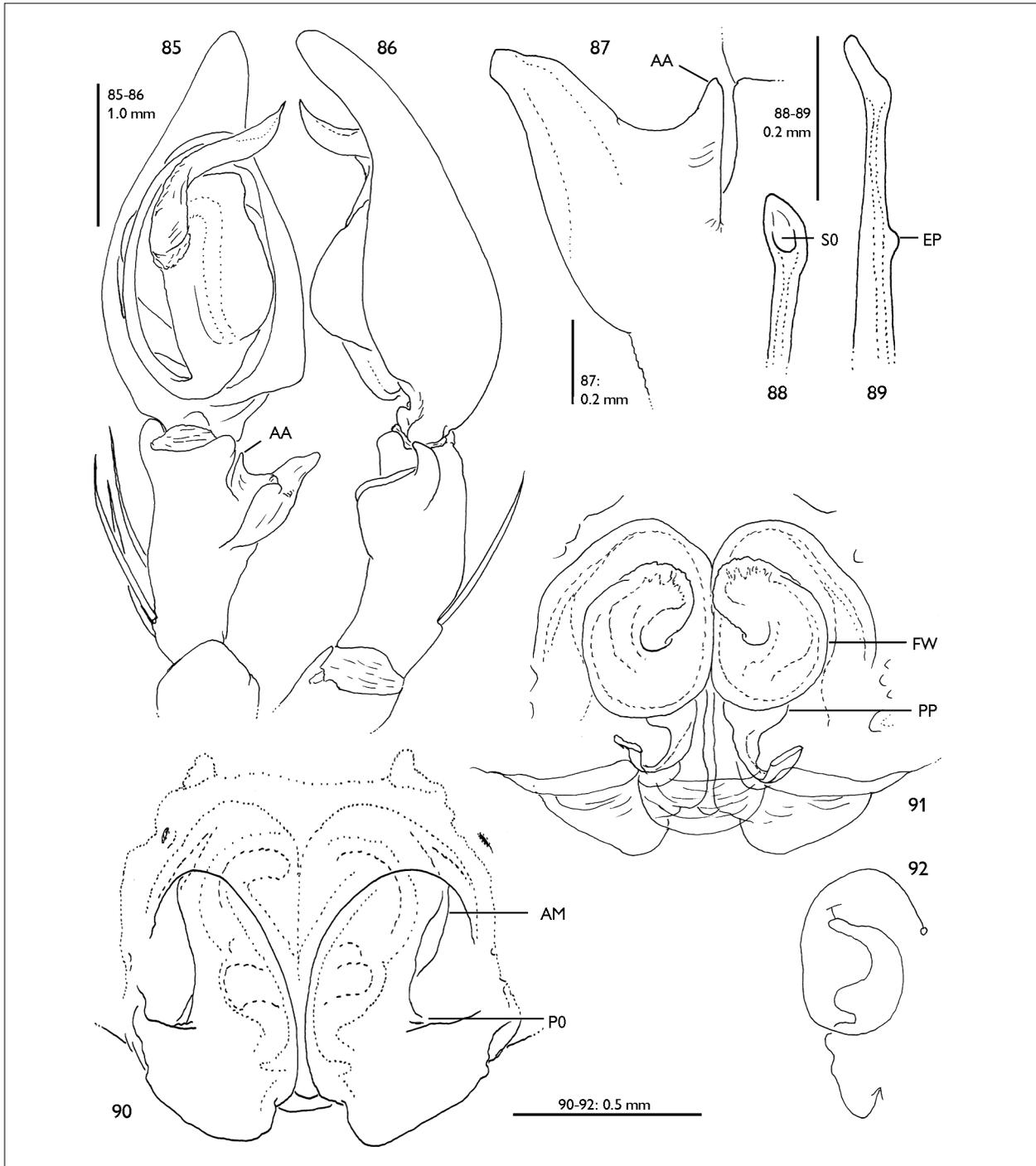
Distribution. Indonesia (Sumatra), Singapore new record (Figure 169).

Heteropoda ocyalina species-group

Among the *Heteropoda* specimens we have examined in this study are six new species that are noteworthy in having shared diagnostic characters with *H. ocyalina* (Simon, 1887) and *H. asa* Jäger, 2024. We are therefore proposing a new species-group anchored on *H. ocyalina*. Its possible phylogenetic affinities with other species-groups will be discussed at the concluding part of this paper.

Diagnosis. Males may be recognised by the following combination of characters (Figures 85–89, 102–109): 1. dRTA with at least one additional apex, this latter may be reduced and hidden, 2. Tegulum with retrolateral swelling, 3. Embolus with medial to subapical projection, and apical part carrying the spermophor opening forming in most species an obtuse angle with embolus main part. Females may be recognised by: 1. Presence of posteriorly to medially located epigynal pockets (e.g., Figures 110, 124, 144, 152, 155; Jäger & Bayer, 2009, figure 6), and 2. First windings of the internal duct system touching each other along the median line (e.g., Figures 111, 125, 140, 153, 156). Moreover, females of three species (*H. temburong* spec. nov., *H. trifurcata* spec. nov., and *H. tutula* spec. nov.) are known to make and carry an egg-sac that is more bloated, with thicker seams, rather than the flat discoidal egg-sacs more commonly seen in other *Heteropoda* species (Figures 100, 121). The opisthosoma in both sexes is elongated with





Figures 85–92. *Heteropoda temburong* spec. nov., holotype male from Brunei (85–89) and female from Sabah (90–92). 85–87 Left palp (85 ventral; 86 retrolateral; 87 RTA, dorsal). 88–89 Embolus tip (88 distal; 89 dorsal). 90 Epigyne, ventral. 91 Vulva, dorsal. 92 Schematic course of internal duct system, dorsal. Abbreviations: AA = additional apex of dRTA, AM = anterior margins of epigynal pockets, EP = embolus projection, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system, SO = spermophor opening.

an acuminate posterior end (e.g., Figures 93, 99, 114, 120, 122, 133, 158, 166). Additionally, the height of the clypeus measuring from the lower edge of the AME is about 1.5 times taller than the height measuring from the lower edge of the ALE (e.g., Figures 98, 121, 132, 160, 168). However, the last two characters (viz. elongated opisthosoma and procurved anterior eye row), by themselves, do not define the species group; they should only be used in combination with one or more of the genitalic characters defined earlier under the diagnosis of this species group. Another somatic character that may be used to discern members

of this species-group from other congeners: a bunch of stiff light bristles originating from the ocular area (e.g., Figures 99–100, 120, 161), similar to those in species of the genus *Acantheis* Thorell, 1891 (Ctenidae, Keyserling, 1877).

Species included. *H. asa* Jäger, 2024, *H. ocyalina* (Simon, 1887), *H. temburong* spec. nov., *H. trifurcata* spec. nov., *H. tutula* spec. nov., *H. tympanum* spec. nov., *H. ulna* spec. nov., *H. uniter* spec. nov.

Distribution. Malaysia (Penang, Pahang, Sabah, Sarawak), Singapore, Indonesia (Sumatra, Java, Central Kalimantan) (Figure 169).

IDENTIFICATION KEY FOR SPECIES OF THE *HETEROPODA OCYALINA* SPECIES-GROUP

- 1a. Males (those of *H. tutula* spec. nov., *H. tympanum* spec. nov., *H. ulna* spec. nov., and *H. uniter* spec. nov. unknown) 2
- 1b. Females (that of *H. asa* unknown)..... 5
- 2a. dRTA distinctly longer than vRTA in ventral view, extending retrolaterally well beyond cymbial margin, conductor with additional ventral furrow (Figures 102–103; Jäger & Bayer, 2009, figures 1–3) 3
- 2b. dRTA not extending retrolaterally well beyond cymbial margin, conductor simple, without such additional furrow 4
- 3a. dRTA distally simple, narrow (Figure 103)..... *H. trifurcata* spec. nov.
- 3b. dRTA distally widened, best seen in retrolateral view, with two apices (Jäger & Bayer, 2009, figures 3–4)....
..... *H. ocyalina*
- 4a. dRTA with one additional apex (Figures 85, 87)..... *H. temburong*
- 4b. dRTA with two additional apices (Jäger, 2024, figure 3)..... *H. asa*
- 5a. First windings overlapping medially (Figure 128)..... *H. tympanum* spec. nov.
- 5b. First windings touching each other medially, running parallel along median axis (Figures 91, 111, 126, 140, ... 153, 156)..... 6
- 6a. Median septum anteriorly distinctly broader, i.e. at least twice the posterior width, and with anteriorly diverging epigynal margins (Figures 90, 110, 113, 139, 144) 7
- 6b. Median septum anteriorly not distinctly broader, i.e. less than or just barely twice the posterior width (Figures 152, 155), or if slightly broader, anterior epigynal margins more or less parallel (Figure 124)..... 9
- 7a. Epigynal pockets situated in the mid of epigyne, i.e. not reaching epigastric furrow (Figure 90).....
..... *H. temburong* spec. nov.
- 7b. Epigynal pockets situated posteriorly, i.e. posterior of epigastric furrow (e.g., Figures 110, 113, 139, 144).... 8
- 8a. Anterior margins of first winding running towards centrally located glandular pores (Figures 140, 145), spiders with distinct, narrow median band on prosoma and opisthosoma (Figures 158, 161)..... *H. ulna* spec. nov.



- 8b. Anterior margins of first winding running directly to marginally situated glandular pores (Figure 111), spiders with broad dark patch on prosoma and dark lanceolate heart patch on opisthosoma (Figures 117, 122) *H. trifurcata* spec. nov.
- 9a. Epigynal pockets situated posteriorly, reaching epigastric furrow (Figure 152)..... *H. ocyalina*
- 9b. Epigynal pockets situated in the mid of epigyne, i.e. not reaching epigastric furrow (Figures 124, 155)..... 10
- 10a. Posterior part of internal duct system pointed, extending laterally distinctly beyond first winding, glandular pores situated centrally, dorsad (Figure 125)..... *H. tutula* spec. nov.
- 10b. Posterior part of internal duct system rounded, extending laterally not beyond first winding, glandular pores situated marginally, mediad (Figure 156) *H. uniter* spec. nov.

Heteropoda temburong spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:9496DB7E-F1D5-4778-A0A8-562C8147A941>
(Figures 85–101, 169)

Heteropoda sp. J—Koh & Bay 2019: 336, unnumbered photos of male and female.

Type material. BRUNEI: Temburong: Holotype male (JK.11.04.13.2004), Ulu Temburong National Park, Sungai Seruyu, 4° 33' 50" N, 115° 8' 55" E, 222 m elevation, primary forest, J.K.H. Koh leg. 13 April 2011, "prograde sparassid" (SMF).

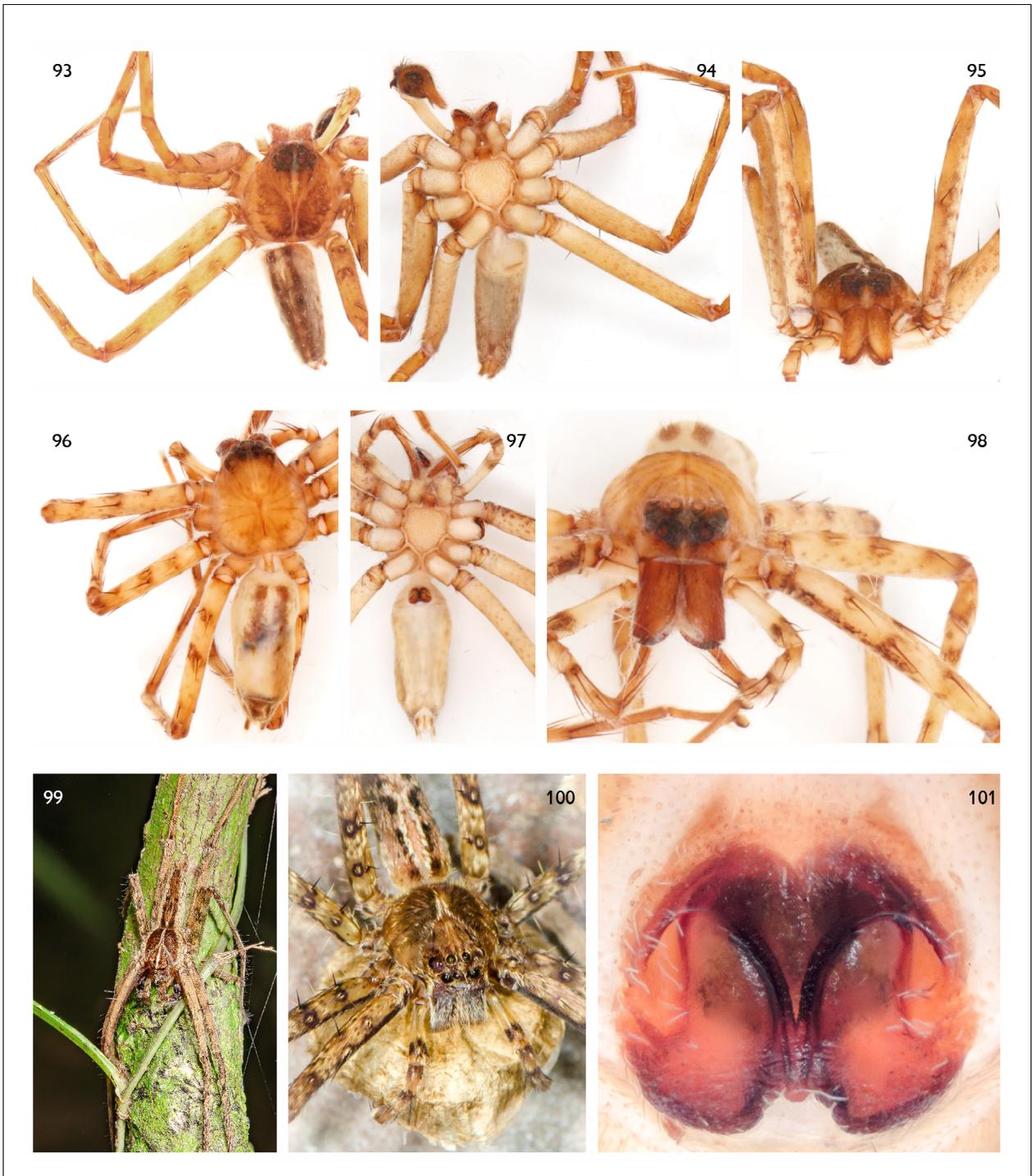
Additional material examined. BRUNEI: Temburong: 1 female (JK.12.04.20.0069), Peradayan Forest Reserve, off Kampung Lakiun, 4° 45' 0.0" N, 115° 9' 58" E [109 m elevation], J.K.H. Koh leg. 20 April 2012 (BMKB). 1 female (JK.12.04.20.0062), with same locality data as for previous specimen (LKCNHM). Belait: 1 male (JK.11.03.23.0055), Melilas, Sungai Ingei, primary forest, 4° 08' 36" N, 114° 43' 16" E [58 m elevation], J.K.H. Koh leg. 23 March 2011 (LKCNHM). MALAYSIA: Sabah: 1 female (JK.10.03.16.2017), Sepilok, Orang Utan Rehabilitation Centre, 5° 51' 37" N, 117° 57' 7" E, 49 m elevation, disturbed forest, J.K.H. Koh leg. 16 March 2010, "Prograde Unicorn" (FRC). Sarawak: 1 male (JK.12.01.23.1003), Gunung Mulu National Park, Botanical Walk near Parks' headquarters, 4° 02' 30" N, 114° 48' 52" E [44 m elevation], J.K.H. Koh leg. 23 January 2012 (LKCNHM). 1 female (JK.12.01.23.1002), same locality as for previous specimen (SMF). 1 female (JK.12.01.23.0046),

Gunung Mulu National Park, outside Fast Lane Cave 4° 02' 55" N, 114° 49' 10" E [57 m elevation] J.K.H. Koh leg. 23 January 2012 (LKCNHM).

Etymology. The species name refers to the type locality; noun in apposition.

Diagnosis. Males are similar to those of *Heteropoda asa* Jäger, 2024 by having an almost identical palpal arrangement including same arising point and shape of embolus, same arising point and shape of conductor with a pointed, retro-distad tip extending distinctly beyond cymbial margin, presence of additional apex on dRTA, tegulum with right-angled margin retro-distally and right-angled bend of spermophor (Figures 85–89), but can be distinguished by: 1. dRTA with one additional apex, 2. Embolus base narrow, 3. Retrolateral swelling of tegulum bulging distinctly ventrad, 4. Conductor tip with entire proximad margin, 5. Spermophor opening roundish (dRTA with two apices, embolus base broader, narrowing abruptly, retrolateral swelling of tegulum not bulging ventrally, conductor tip with triangular proximad outgrowth, spermophor opening elongated in *H. asa*; cf. Jäger, 2024, figures 1–5). Females similar to those of *H. trifurcata* spec. nov. in having the median septum narrowest in its posterior half, the anterior margins of posterior epigynal pockets reaching copulatory openings (Figures 90–92), but can be distinguished by: 1. Posterior pockets situated medially between copulatory openings and posterior margin of lateral lobes, 2. Lateral margins of first windings extending posteriorly distinctly beyond glandular pore area of internal duct system, 3. Posterior parts of internal duct system less





Figures 93–101. *Heteropoda temburong* spec. nov., holotype male (93–95, 99) and female (96–98, 100–101) from Brunei. 93–100 Habitus of preserved (93–98) and live (99–100) specimens (93, 96, 99–100 dorsal; 94, 97 ventral; 95, 98 frontal). 101 Epigyne, ventral. Photos: P. Jäger (93–98), J. K. H. Koh (99–101).



than one diameter apart from each other (posterior pocket extending posteriorly almost to margin of lateral lobes, lateral margins of first windings not reaching posteriorly to glandular pore area and posterior parts of internal duct system separated by more than one of their diameters in *H. trifurcata* spec. nov.; cf. Figures 110–113).

Description. Male (holotype): Measurements: TL 10.6, PL 4.9, PW 4.5, AW 2.0, OL 5.7, OW 2.2. Eyes: AME 0.28, ALE 0.49, PME 0.36, PLE 0.46, AME-AME 0.09, AME-ALE 0.08, PME-PME 0.19, PME-PLE 0.42, AME-PME 0.37, ALE-PLE 0.47, CH AME 0.41, CH ALE 0.26. Spination: Pp 131, 101, 2101; Fe I 323, III 333, IV 331; Pa I–III 101, IV 101(0); Ti I–II 2126, III 2026, IV 2126; Mt I–II 1014, III 2014, IV 3036. Mt I–III with sparse scopulae in distal half and double row of setae in proximal half, IV with distal field and double row of stronger setae. Measurements of palps and legs: Pp 8.4 (2.7, 1.0, 1.7, -, 3.0); I 33.9 (9.0, 2.5, 10.4, 9.1, 2.9); II 34.5 (9.2, 2.6, 10.4, 9.3, 3.0); III 23.3 (6.6, 1.9, 6.8, 6.0, 2.0); IV 30.7 (8.7, 2.0, 8.2, 8.9, 2.9). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 37 denticles and 1 escort seta.

Palp (Figures 85–89). As in diagnosis. RTA arising medially from Ti, vRTA flat and with right-angled margin ventrally in retrolateral view, dRTA short, slightly bent, and tapering at its tip, the additional apex distad, papering, its tip rounded. Cymbium distinctly longer than Ti, with distinct retro-proximal swelling. E arising from tegulum in 6-o'clock position running a flat semi-circle, subapically with small rounded projection, spermophor opening situated apically.

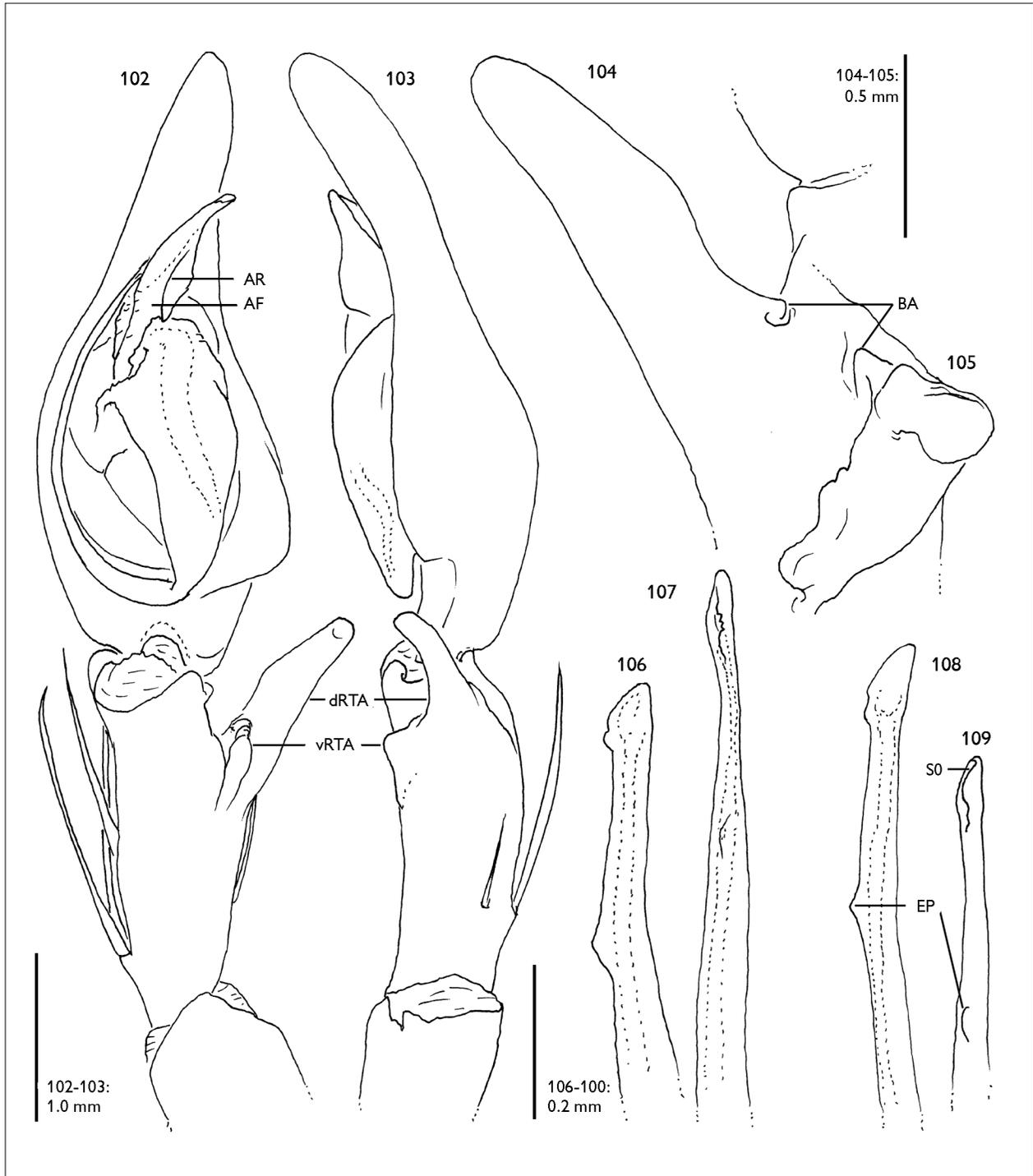
Colouration (Figures 93–95). Yellowish-brown with dark pattern consisting of dark setae. DS with light narrow lateral bands and median dark band with an anteriorly trifurcated light line, clypeus with light median patch in front of AME. Chelicerae brown, disto-medially lighter. Sternum, gnathocoxae, ventral coxae light yellow, labium brown. Legs yellowish-brown with dark patches and femora, additionally, with dots ventrally. Opisthosoma dorsally with two dark narrow posteriorly converging bands, these consisting of dark patches, between and

lateral to these bands light-brown; laterally light with dots; ventrally pale yellowish-brown with elongate triangle in front of spinnerets, the latter dorsally pale yellowish brown, ventrally and laterally brown. Live spiders or freshly preserved specimens with more distinctly contrasting colouration, with the trifurcate pattern on DS more conspicuous than that in preserved specimens (Figure 99). As median part of the trifurcate pattern, a narrow band of long and forward-directed white seta runs from the fovea, through the gap between the PME, to the anterior edge of the DS between the AME. 2 long and stiff bristles between the AME projects beyond the anterior edge of the DS.

Female (from Sepilok, Sabah): Measurements: TL 10.8, PL 4.6, PW 3.9, AW 2.2, OL 6.2, OW 2.7. Eyes: AME 0.29, ALE 0.49, PME 0.36, PLE 0.43, AME-AME 0.18, AME-ALE 0.02, PME-PME 0.24, PME-PLE 0.46, AME-PME 0.37, ALE-PLE 0.45, CH AME 0.72, CH ALE 0.45. Spination: Pp 131, 101, 2121, 1014; Fe I 323, II–III 333, IV 331; Pa I–II 001, III 101, IV 100; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with moderately dense scopulae along entire length and few stiff setae very proximally (I–II) or with double row of stiff setae over entire length (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.1 (2.2, 1.0, 2.0, -, 2.9); I 24.3 (6.5, 2.2, 7.3, 6.2, 2.1); II 24.5 (6.8, 2.3, 7.3, 6.0, 2.1); III 17.9 (5.2, 1.7, 5.0, 4.3, 1.7); IV 23.4 (6.8, 1.8, 6.1, 6.5, 2.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4(5) retromarginal teeth, ca. 30 denticles and 1 escort seta.

Copulatory organ (Figures 90–92). As in diagnosis. Epigynal field with one slit sensillum on each side, one very close to field, one included in the field. Median septum longer than wide, becoming gradually narrower towards posterior end. Posterior pockets postero-medial, wide, their internal margin running close to copulatory organ. Copulatory openings situated laterally. Glandular pores of internal duct system antero-medial, fertilisation ducts arising postero-medially from spermathecae, long and bent, their tips dorsad.





Figures 102–109. *Heteropoda trifurcata* spec. nov., holotype male (102–107) and paratype male (108–109) from Malay peninsula, copulatory organs (102 left palp, ventral; 103 same, retrolateral; 104 RTA, dorsal; 105 same, disto-retrolateral; 106, 108 embolus, ventral; 107, 109 same, distal). Abbreviations: AF = additional furrow of conductor; AR = additional ridge of conductor; BA = basal apex of dRTA, dRTA = dorsal part of RTA, EP = embolus projection, SO = spermophor opening, vRTA = ventral part of RTA.



Colouration (Figures 96–98). As in male, but patch on DS not as distinct. Fe I with dark pattern ventrally, this pattern turning gradually to a dotted pattern towards Fe IV. OS dorsally with less distinct pattern, ventrally paler and many light erect spines on OS. Living spiders with much more distinctly developed pattern (Figure 100). 2 broken bristles and another base of a broken off setae are present between the AME.

Variation. Males: TL 10.2 to 10.8. Female: TL 9.2 to 11.2. Epigyne with both slit sensilla separated from epigynal field (Figure 101). In both sexes, the stiff bristles projecting between the AME in both sexes may vary from one to three. In some specimens, one of the bristles may point upward (dorsally) instead of forward (anteriorly). The dorsal patterns of opisthosoma vary: some do not have a white longitudinal band.

Distribution. Brunei (Temburong, Belait) and Malaysia (Sabah, Sarawak) (Figure 169).

Biology. Although it is occasionally found among forest leaf litter, the species lives and hunts at night mainly above ground: on foliage, twigs and stems, and tree trunks. In their resting position, the males and females of this species (and the two new species described below) tend to direct their legs I and II forward, instead of spreading them sideway, as in other congeners. The egg-sac is more bloated or inflated in shape compared to the flattish discoid egg-sacs more commonly seen in other *Heteropoda* species (Figure 100). Measurements of an egg-sac carried by specimen JK. 12.40.30.0069 from Brunei: 10.3 mm (maximum width) by 8.7 mm (minimum width), and 7.4 mm (thickness).

Heteropoda trifurcata spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:302C8C8A-F0A9-4A40-A6BC-454989F9E755>

(Figures 102–123, 169)

Type material. MALAYSIA: Pahang State: Holotype male, Bukit Fraser, Jeriau Waterfall, 3° 43' 26.07" N, 101° 42' 36.22" 'E, 1040 m elevation, disturbed primary forest,

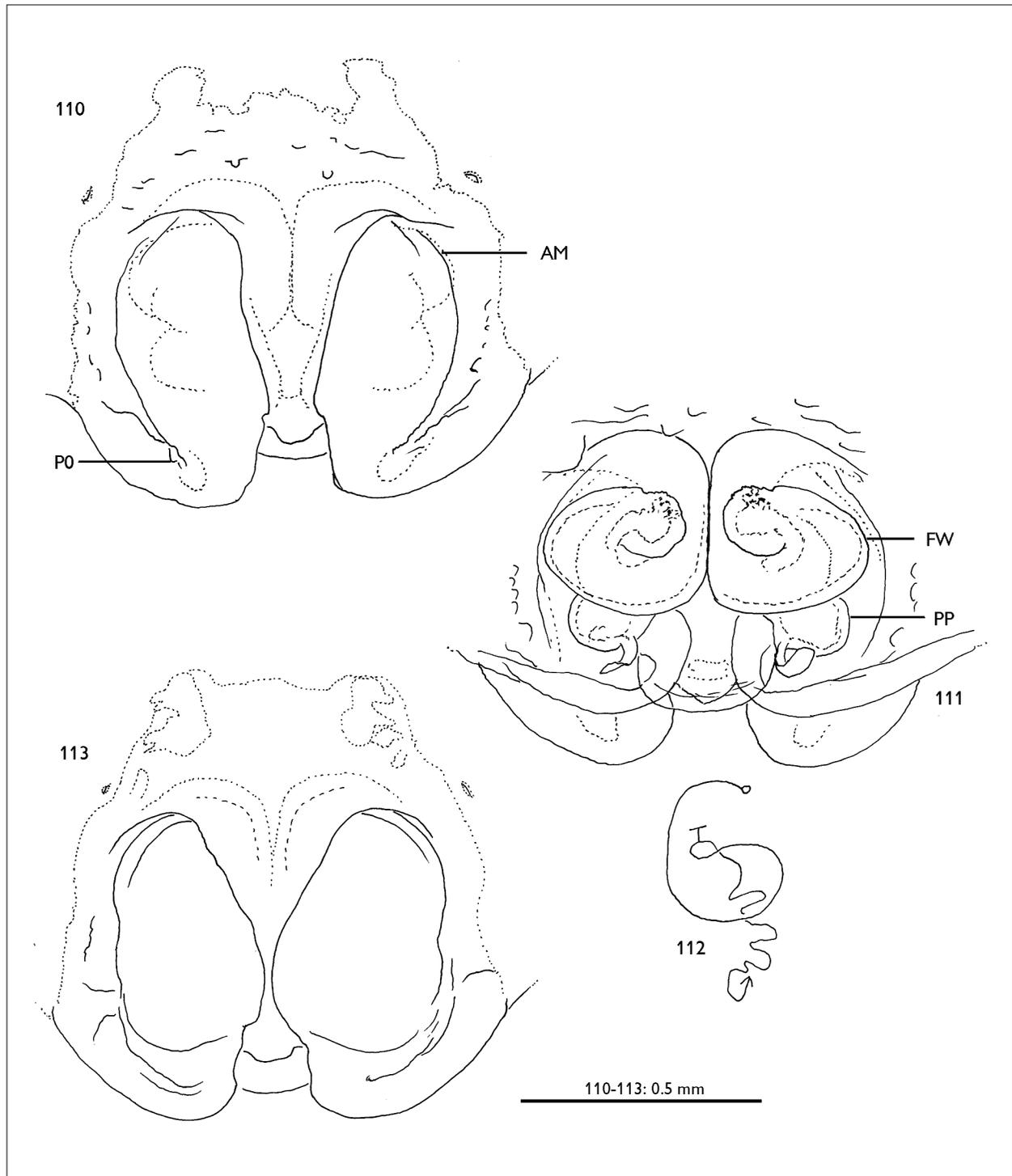
along trail, at night, by hand, P. Jäger & T. Laufs leg. 13 February 2014 (SMF). Paratypes: 1 female, with same data as for holotype (SMF). 1 male, 1 female, with same data as for holotype, except for: 11 February 2014 (LKCNHM).

Additional material examined. 1 immature, with same data as for holotype (SMF). 2 immatures, with same data as for holotype, except for: 11 February 2014 (LKCNHM).

Etymology. The species name is derived from the Latin 'trifurcatus, -a, -um' meaning 'trifurcated' and refers to the trifurcate pattern on the dorsal shield of prosoma especially of males, characteristic for the *ocyalina* species-group; adjective.

Diagnosis. Males of *H. trifurcata* spec. nov. similar to those of *H. ocyalina* in having a similar arrangement of the palp including almost the same arising point and shape of embolus and conductor, the retro-proximal margin of the conductor with additional furrow and ridge, spermophor very slightly S-shaped, running from 12.30-o'clock-position to the retrolateral part of the embolus base (Figures 102–109), but can be distinguished by: 1. dRTA long and with simple apex, 2. Embolus projection situated freely visible outside of the conductor sheath (dRTA with two small plier-shaped apices, embolus projection situated sub-apically within the conductor sheath in *H. ocyalina*; cf. Jäger & Bayer, 2009, figures 1–5). Female copulatory organs similar to those of *H. ocyalina* in having an epigynal field roughly as long as wide and with only very short or entirely included anterior bands, a very similar internal duct system with first winding running one coil up to glandular pores, these latter anterior to mediad (Figures 110–112), but can be distinguished by: 1. Median septum narrowest in posterior half, 2. Posterior epigynal pockets extending into anterior half, 3. First winding of internal duct system wider than posterior part, i.e. posterior part extending only posteriorly beyond first winding (median septum roughly with the same width over entire length, slightly narrower in anterior half, posterior pockets situated exclusively in posterior half, first winding not as wide as posterior part of internal duct system, i.e. the latter part extending beyond first winding laterally in *H. ocyalina*; cf. Figures 152–154).





Figures 110–113. *Heteropoda trifurcata* spec. nov., paratype females, copulatory organs (110, 113 Epigyne, ventral; 111 vulva, dorsal; 112 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system.

Description. Male (holotype): Measurements: TL 15.0, PL 6.2, PW 5.8, AW 2.8, OL 8.8, OW 4.5. Eyes: AME 0.38, ALE 0.56, PME 0.41, PLE 0.52, AME-AME 0.19, AME-ALE 0.05, PME-PME 0.19, PME-PLE 0.49, AME-PME 0.42, ALE-PLE 0.59, CH AME 0.95, CH ALE 0.60. Spination: Pp 131, 101, 2101; Fe I 323, II–III 333, IV 331; Pa I–II 101, III 1(0)01, IV 100; Ti I–II 2326, III–IV 2126; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and stiff setae in proximal half, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 11.2 (3.9, 1.6, 2.3, -, 3.4); I 45.7 (12.4, 3.5, 14.0, 12.3, 3.5); II 47.3 (13.1, 3.6, 14.3, 12.7, 3.6); III 32.3 (9.4, 2.9, 9.3, 8.3, 2.4); IV 39.5 (11.5, 2.8, 10.6, 11.4, 3.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 65 denticles and 1 escort seta.

Palp (Figures 102–107). As in diagnosis. RTA medially to sub-distally from Ti, vRTA developed as small hump, internally connected to basal dRTA apex, the latter small and seen only in dorsal or retrolatero-distal view, dRTA only very slightly bent, distally rounded. Cymbium distinctly longer than Ti, with distinct, rounded retro-proximal swelling. E arising in 5.30-o'clock-position from tegulum, running a flat semicircle to its tip, subapically with small triangular projection, spermophor opening situated apically. C with pointed disto-retrolaterad tip, extending slightly beyond cymbial margin.

Colouration (Figures 114–116). Yellowish-brown with moderately dark pattern. DS with broad black median band with a narrow trifurcate light pattern, reaching from fovea between AME and along border between thoracic and cephalic area; 5 sockets of setae present between AME in a triangular arrangement, with 1 median long stiff seta and shorter lateral setae. Chelicerae light yellowish-brown. Legs yellowish-brown with spine patches on femora and further patches on patellae and tibiae, and many dots on femora ventrally. Opisthosoma dorsally light reddish-brown with dark median lanceolate patch above heart; ventrally yellowish-brown with

reddish-brown median band ending in triangle anterior of spinnerets, the latter dorsally reddish-brown, ventrally pale yellowish-brown. Living spiders with much more vividly developed pattern (Figure 120).

Female (paratype, SMF): Measurements: TL 20.1, PL 8.3, PW 7.1, AW 4.1, OL 11.8, OW 6.1. Eyes: AME 0.46, ALE 0.67, PME 0.53, PLE 0.62, AME-AME 0.25, AME-ALE 0.06, PME-PME 0.30, PME-PLE 0.64, AME-PME 0.54, ALE-PLE 0.64, CH AME 1.24, CH ALE 0.84. Spination: Pp 131, 101, 212(1)1, 1014; Fe I 323, II–III 333, IV 331; Pa I 001, II–III 101, IV 100; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and stiff setae in proximal half, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 15.9 (4.5, 2.1, 3.8, -, 5.5); I 45.9 (12.6, 4.6, 13.9, 11.6, 3.2); II 47.0 (13.2, 4.8, 14.1, 11.6, 3.3); III 34.7 (10.4, 3.5, 10.2, 8.4, 2.2); IV 41.6 (12.3, 3.3, 11.3, 11.6, 3.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 75 denticles and 1 escort seta.

Copulatory organ (Figures 110–112). As in diagnosis. Epigynal field with one slit sensillum on each side, very close to field. Median septum longer than wide, with posteriorly bulging transversal margin. Posterior pockets postero-mediad, slit-like, their internal margin running close to copulatory opening. Copulatory openings situated antero-laterally. Glandular pores of internal duct system antero-mediad, fertilisation ducts arising postero-mediad from spermathecae, bent, their tips dorsad to antero-dorsad.

Colouration (Figures 117–119). As in male, but generally darker, dark reddish-brown. DS with pair of distinct light patches submarginally in posterior half; 5 sockets of broken off setae between AME. Coxae ventrally vividly dotted. OS dorsally with few long light setae standing upright; laterally dotted; ventrally with dark triangle anterior of spinnerets. In living spiders especially pattern on DS more distinctly developed (Figures 121–123).





Figures 114–123. *Heteropoda trifurcata* spec. nov., holotype male (114–116, 120) and paratype female (117–119, 121–123) from Malay peninsula, habitus of preserved (114–119) and live (120–123) specimens (114, 117, 120, 122 dorsal; 115, 118, 123 ventral; 116, 119, 121 frontal). Photos: P. Jäger.



Variation. Male: TL 16.4, PL 7.3, OL 9.1. Distinctly darker than holotype, DS and OS dorsally with more complete colour pattern; 2 long stiff setae present between AME. Coxae ventrally with few pale dots. Embolus tip with spermophor opening and subapical projection only slightly different from that of holotype (Figures 108–109). Female: TL 18.1, PL 7.2, OL 10.9. Chelicerae laterally with narrow band of light setae. OS dorsally with light patches anterior and posterior of dark lanceolate heart patch. Lateral lobes in paratype (11.2.2014) almost touching each other, anterior bands integrated in epigynal field (Figure 113).

Distribution. Known only from type locality in Pahang State, Malaysia (Figure 169).

Biology. Little is known about the biology of this species. One male was caught on the rooftop of a forest hut, suggesting that the species inhabits also higher strata. One female with an egg-sac was found on the ground in a disturbed primary forest. The egg-sac is similar to those of *H. temburong* spec. nov. and *H. tutula* spec. nov., in contrast to the typically discoidal egg-sacs of most other *Heteropoda* spp. Additionally, it has unique dark streaks of silk on its surface such as those on the egg-sacs of *Argiope bruennichi* (Scopoli, 1772) (Bellmann, 2001, p. 121, unnumbered photo).

Heteropoda tutula spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:9D7F591E-9070-4EB3-89C8-14D1FDC767A5>

(Figures 124–126, 130–133, 169)

Type material. SINGAPORE: Holotype female (JK.91.01.30.0008), Upper Peirce Reservoir, Pipeline Trail, 1° 23' 11" N, 103° 48' 40" E [42 m elevation], forest floor; J.K.H. Koh leg. 30 September 1991 (LKC�HM).

Etymology. The species name refers to the stiff setae between the AME characteristic for the *ocyalina* species-group and derived from the Latin 'tutulus, -a, -um' meaning 'hair dressed in a high cone over the forehead'; adjective.

Diagnosis. Females of *H. tutula* spec. nov. are similar to those of *H. ocyalina* in having indistinct epigynal

pockets and the posterior part of internal duct system wider than first winding (Figures 124–126), but can be distinguished by: 1. Posterior pockets with their anterior margins reaching copulatory openings, 2. Lateral margins of first winding extending posteriorly beyond glandular pores, 3. Posterior part of internal duct system distinctly bent laterally (posterior pockets situated in posterior half, lateral margins of first winding situated anterior of glandular pores, posterior part of internal duct system longitudinally straight in *H. ocyalina*; cf. Figures 152–154).

Description. Male: Unknown.

Female (holotype): Measurements: TL 12.1, PL 4.6, PW 4.3, AW 2.3, OL 7.5, OW 3.8. Eyes: AME 0.30, ALE 0.49, PME 0.37, PLE 0.47, AME-AME 0.19, AME-ALE 0.05, PME-PME 0.20, PME-PLE 0.46, AME-PME 0.37, ALE-PLE 0.41, CH AME 0.77, CH ALE 0.45. Spination: Pp 131, 101, 2(1)121, 1014; Fe I 323, II–III 333, IV 331; Pa I 001, II 101, III 100, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and few stiff setae very proximally (I–II) or double row of setae in proximal half (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.5 (2.4, 1.2, 2.0, -, 2.9); I 24.3 (6.6, 2.3, 7.3, 6.0, 2.1); II 24.6 (6.8, 2.3, 7.3, 6.1, 2.1); III 17.7 (5.2, 1.8, 4.9, 4.2, 1.6); IV 23.2 (6.8, 1.9, 6.0, 6.4, 2.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 55–60 denticles and 1 escort seta.

Copulatory organ (Figures 124–126). As in diagnosis. Epigynal field slightly trapezoid, narrowing anteriorly, with one slit sensillum on each side. Median septum longer than wide covered by lateral lobes a bit in posterior half, with posteriorly concave transversal margin. Posterior pockets posteriad, slit-like. Copulatory openings situated antero-laterally. Glandular pores of internal duct system anteriad, turning point wide, fertilisation ducts arising postero-medially from spermathecae, bent, their tips latero-dorsad.

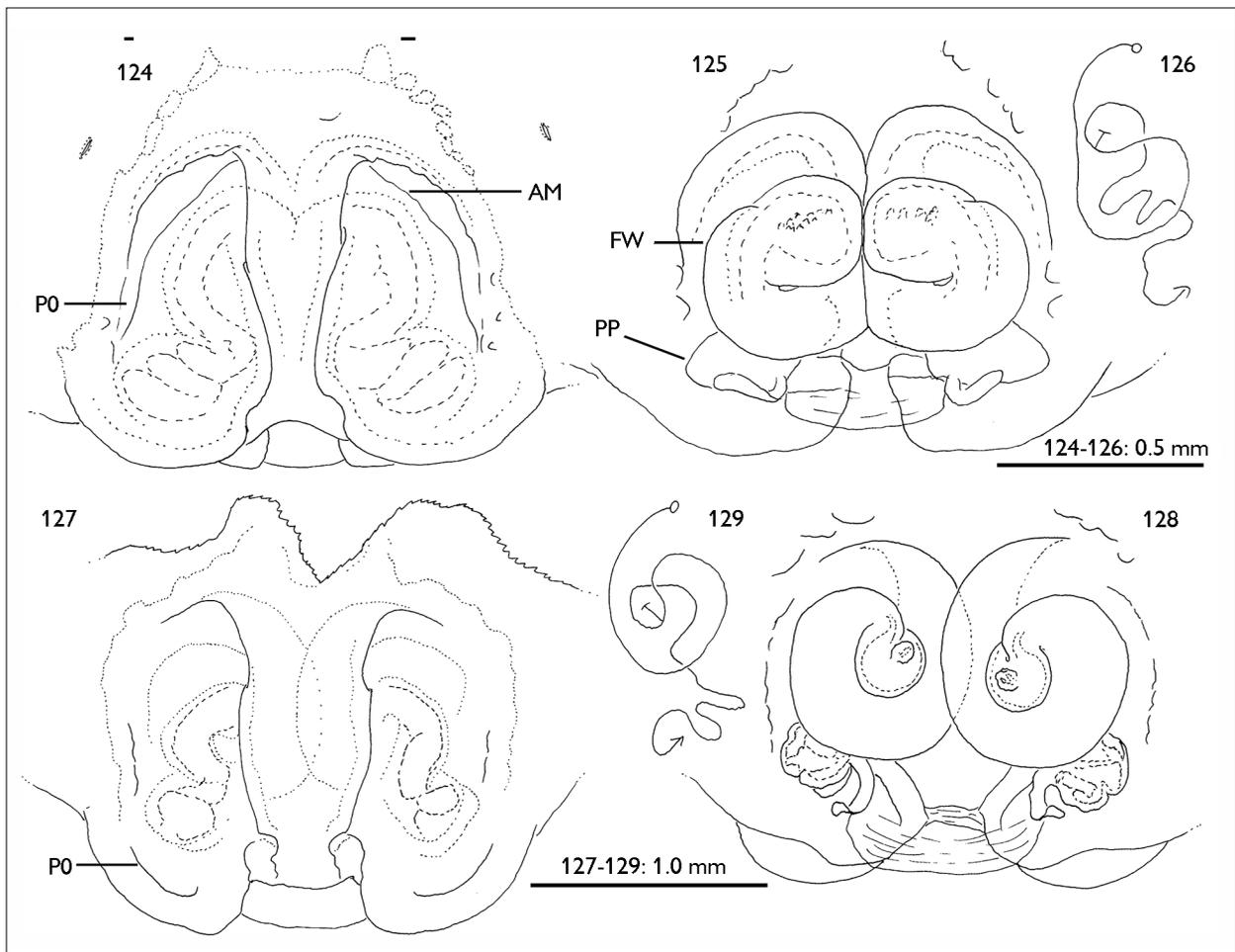


Colouration (Figures 130–132). Deep yellowish-to light reddish-brown with reddish-brown pattern. DS reddish brown with broad margins and median stripe light yellowish, the latter over entire length of DS; with 5 sockets of broken off setae between AME. PS ventrally pale yellow, without pattern. Chelicerae darker reddish-brown than DS, with 3 longitudinal bands each. Legs yellowish-brown with patches at spines on femora and on patellae and proximal tibia, femora ventrally dotted. Opisthosoma dorsally reddish-brown, becoming darker posteriorly, with light median band along entire

length; ventrally pale yellowish, with indistinct patch anterior of spinnerets, the latter dorsally and laterally reddish-brown, ventrally pale yellow. Living spiders with distinctly more contrasting pattern and more details (Figure 133).

Distribution. Known only from type locality in Singapore (Figure 169).

Biology. Like the egg-sacs of the two preceding species in the oyalina species-group, the egg-sac is more inflated and thicker than those seen in most other *Heteropoda* species.



Figures 124–129. *Heteropoda* spp., females, copulatory organs. 124–126 *Heteropoda tutula* spec. nov., holotype from Singapore. 127–129 *Heteropoda tympanum* spec. nov., holotype from Penang, Malaysia (124, 127 epigyne, ventral; 125, 128 vulva, dorsal; 126, 129 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system.

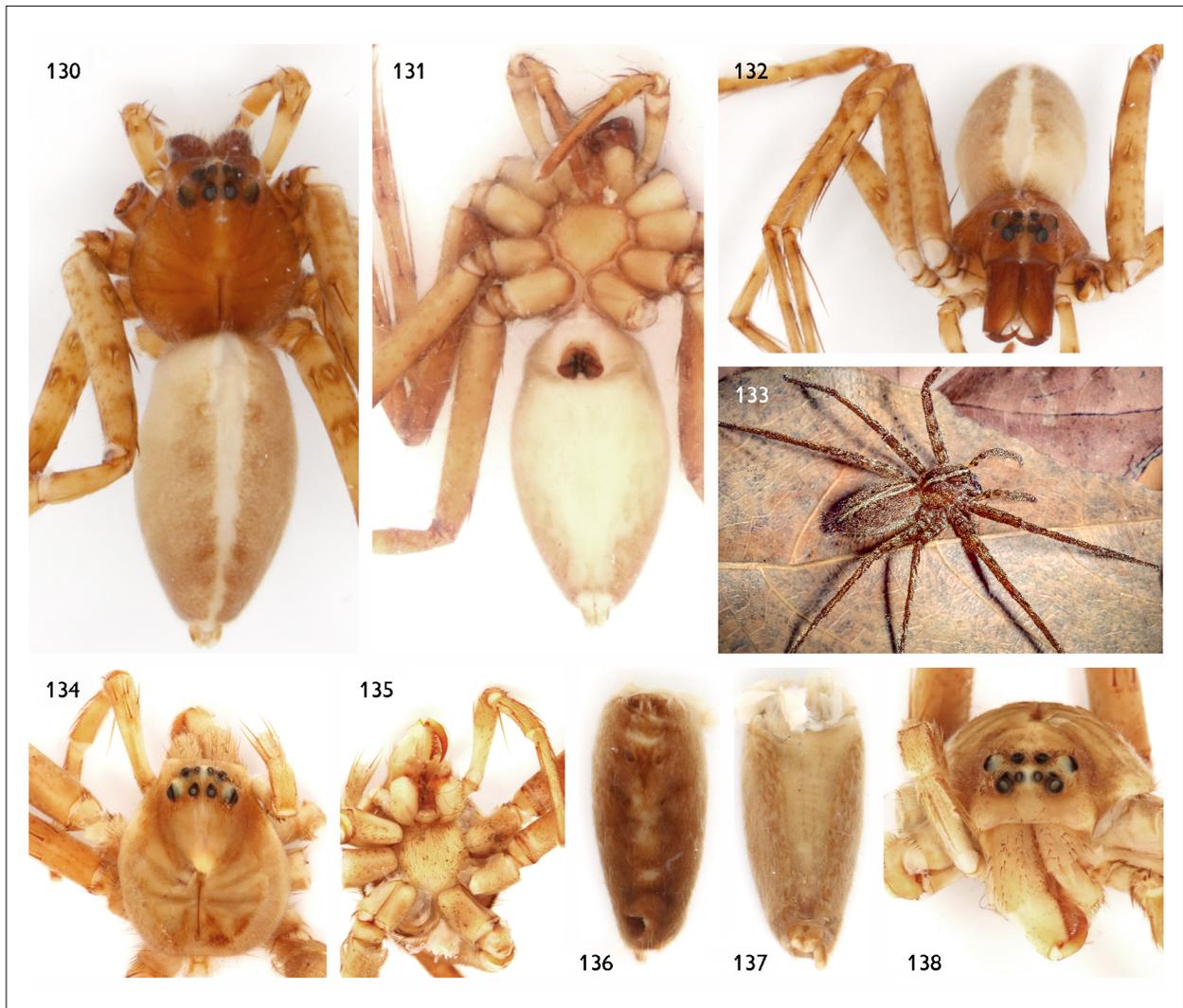
Heteropoda tympanum spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:845687EE-2CE1-4071-A136-BD8C760EA78B>
(Figures 127–129, 134–138, 169)

Type material. MALAYSIA: Penang: Holotype female, Penang [ca. 5° 22' 46.64" N, 100° 15' 12.08" E, 352 m elevation], March 1898, 42., F.H. Gravely det. 1930 as *Heteropoda* sp. (NHM).

Etymology. The species name is derived from the Latin word 'tympanum', meaning 'tambourine-shaped drum' and refers to the round medially overlapping first winding of the internal duct system; noun in apposition.

Diagnosis. Females of *H. tympanum* spec. nov. are similar to those of the *H. ocyalina* species-group in having a similar course of internal duct system, posterior pockets (although indistinct), and an elongate opisthosoma, but can be distinguished from all females by the medially overlapping



Figures 130–138. *Heteropoda* spp., habitus of preserved (130–132, 134–138) and live (133) specimens. 130–133 *Heteropoda tutula* spec. nov., holotype female from Singapore. 134–138 *Heteropoda tympanum* spec. nov., holotype female from Penang, Malaysia (130, 133–134, 136 dorsal; 131, 135, 137 ventral; 132, 138 frontal). Photos: P. Jäger (130–132, 134–138), C. S. P. Ang (133).

first winding (first winding not overlapping medially, but running parallel along median axis in all other species of that group).

Description. Male: Unknown.

Female (holotype): Measurements: TL 18.0, PL 7.8, PW 7.0, AW 3.6, OL 10.2, OW 4.7. Eyes: AME 0.40, ALE 0.61, PME 0.46, PLE 0.57, AME-AME 0.27, AME-ALE 0.07, PME-PME 0.28, PME-PL 0.55, AME-PME 0.43, ALE-PL 0.56, CH AME 1.16, CH ALE 0.81. Spination: Pp 131, 101, 2121, 1014; Fe I -, II 333, III 332, IV 331; Pa I-II 101, III -, IV 100; Ti I-IV 2026; Mt I-II 1014, III 2014, IV 3036. Mt I-III with dense scopulae along entire length and few stiff single setae very proximally (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 15.1 (4.3, 2.1, 3.2, -, 5.5); I -; II - (13.3, -, -, -, -); III 17.1 (10.1, 3.4, 10.7, 8.8, 2.7); IV - (10.2, -, -, 12.1, 3.2). Leg formula: -. CH with 3 promarginal and 4 retromarginal teeth, ca. 100 denticles and 1 escort seta.

Copulatory organ (Figures 127–129). As in diagnosis. Epigynal field roughly rectangular, anterior part not recognisable due to damage. Median septum longer than wide, with posteriorly slightly convex transversal margin. Posterior pockets and their anterior margins indistinct. Copulatory openings situated anteriorly. Glandular pores of internal duct system medio-anteriad, situated on small hump, turning point narrower than first winding, dorsal part of internal duct system wider posteriorly, fertilisation ducts arising postero-medially to medially from spermathecae, bent, their tips dorsad.

Colouration (Figures 134–138). Yellowish-brown with opisthosoma darker. No pattern recognisable due to degraded condition of specimen.

Distribution. Known only from type locality in Penang, Malaysia (Figure 169).

Heteropoda ulna spec. nov.

[http://zoobank.org/urn:lsid:zoobank.org:act:6B5F7D26-](http://zoobank.org/urn:lsid:zoobank.org:act:6B5F7D26-3BAA-4BB5-A644-BA40826799F4)

[3BAA-4BB5-A644-BA40826799F4](http://zoobank.org/urn:lsid:zoobank.org:act:6B5F7D26-3BAA-4BB5-A644-BA40826799F4)

(Figures 139-151, 158-165, 169)

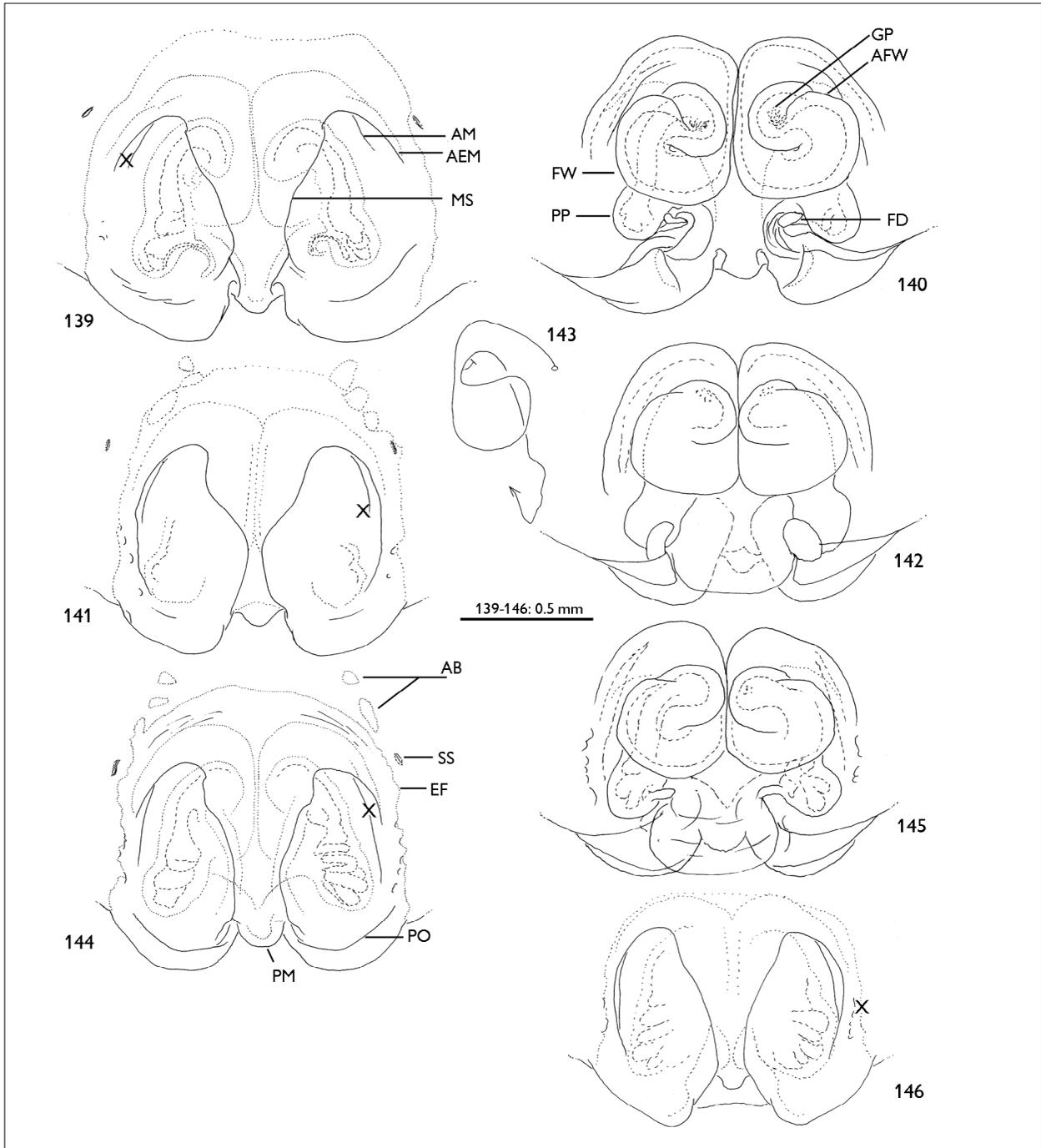
Type material. INDONESIA: Sumatera Barat: Holotype female, Fort de Kock [Bukittinggi, ca. 0° 19' 29.51" S, 100° 22' 12.22" E, 910 m elevation], Eusparassidae, Coll. Roewer, No. 12974, PJ 85 (SMF 9912974). Paratypes: 2 females, with same data as for holotype, PJ 86–87 (SMF).

Additional material examined. Sumatera Utara: 2 females, Soekaranda [south of Medan, ca. 3° 26' 21.99" N, 98° 40' 44.56" E, 108 m elevation], Dohrn [leg.], Jenner [=January] [18]82, PJ 3144–3145 (ÜMB). Aceh: 1 female, Ketambe, Gunung Leuser [ca. 3° 32' 56.47" N, 97° 41' 51.55" E, 470 m elevation], fr[om] leaves, tr. 4.2., Suh. Djojodharmo leg. 3 May [19]86, *Urgularius* [Deeleman det.], Coll. Deeleman, PJ 3146 (RMNH). Riau: 1 female, Buru [ca. 0° 56' 26.76" N, 103° 27' 18.01" E, 13 m elevation], 034. (NHMW).

Etymology. The species name is derived from the Latin noun 'ulna', meaning 'elbow' and refers to the anterior epigynal margins bent like an elbow; noun in apposition.

Diagnosis. Females of *H. ulna* spec. nov. are similar to those of *H. trifurcata* spec. nov. in having a posteriorly distinctly converging median septum in combination with the dorsal part of internal duct system posteriorly widening (Figures 139–151), but can be distinguished by: 1. Posterior pockets and their anterior margins discontinuous, 2. First winding running into central part of glandular region, 3. Prosoma length 4.1–5.2 (posterior pockets connected with their anterior margins, first winding running marginally to glandular region, prosoma length 7.2–8.3 in *H. trifurcata* spec. nov.; cf. Figures 110–113). Females are also similar to those of *H. tutula* spec. nov. in having a similar internal duct system with a similar arrangement of the glandular pores in the centre of the turning point region and anterior margin of first winding running into this area (Figures 139–151), but can be distinguished by: 1. Anterolateral epigynal margin and anterior margin of posterior pocket leaving a narrow slit-like space, 2. Median septum distinctly diverging anteriorly, 3. Epigynal field only little narrower anteriorly than posteriorly, i.e. roughly square, 4. Posterior part of internal duct system





Figures 139–146. *Heteropoda ulna* spec. nov., females from Sumatra, Indonesia (139–140 holotype from Bukittinggi; 141–143 paratype from Bukittinggi; 144–146 specimens from Soekaranda), copulatory organs (139, 141, 144, 146 epigyne, ventral; 140, 142, 145 vulva, dorsal; 143 schematic course of internal duct system, dorsal). Abbreviations: AB = anterior band, AEM = anterior epigynal margin, AFW = anterior margin of first winding, AM = anterior margin of epigynal pocket, EF = epigynal field, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pores, MS = median septum, PM = convex posterior margin of median septum, PO = epigynal pocket, PP = posterior part of internal duct system, SS = slit sensillum, x indicating narrow slit.



laterally rounded (anterolateral epigynal margin and anterior margin of posterior pockets leaving a wide space, median septum in its anterior half with parallel margins, and posterior part of internal duct system with pointed laterad bulges in *H. tutula* spec. nov.; cf. Figures 124–126). In addition, *H. ulna* spec. nov. has a wide light median band on the opisthosoma dorsally distinctly bordered by a dark pattern (Figures 158, 161, 163), whereas in *H. tutula* spec. nov. this band is distinctly narrower and without distinct dark border (Figures 130, 133).

Description. Male: Unknown.

Female (holotype): Measurements: TL 10.8, PL 4.6, PW 4.1, AW 2.2, OL 6.2, OW 2.5. Eyes: AME 0.22, ALE 0.41, PME 0.30, PLE 0.41, AME-AME 0.20, AME-ALE 0.05, PME-PME 0.16, PME-PLE 0.39, AME-PME 0.33, ALE-PLE 0.42, CH AME 0.75, CHALE 0.47. Spination: Pp 131, 101, 2121, 1014; Fe I 323, II–III 333, IV 331; Pa I–II 000(1), III–IV 100; Ti I 2(1)024, II 2025, III 2024, IV 2025(6); Mt I–II 1014, III 2014, IV 3036(5). Mt I–III with dense scopulae along entire length and few stiff setae very proximally (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.5 (2.5, 1.2, 1.8, -, 3.0); I 26.2 (7.3, 2.4, 7.8, 6.5, 2.2); II 26.4 (7.5, 2.4, 7.7, 6.6, 2.2); III 18.9 (5.5, 1.8, 5.3, 4.5, 1.8); IV 24.5 (7.4, 1.8, 6.3, 6.9, 2.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 45 denticles and 1 escort seta; palpal claw with 6 teeth.

Copulatory organ (Figures 139–140). As in diagnosis. Epigynal field anteriorly rounded, anterior bands indistinct, with one slit sensillum on each side. Median septum longer than wide covered by lateral lobes in posterior half, with convex posterior transversal margin. Posterior pockets indistinct, shallow. Copulatory openings situated antero-laterally. Glandular pores of internal duct system anteriorly, situated in the centre of the second winding, fertilisation ducts arising medially from spermathecae, bent, their tips latero-dorsad.

Colouration (Figures 158–160). Pale yellowish- to light reddish-brown with reddish-brown pattern. DS yellowish

brown with broad slightly darker margins and pale median stripe, the latter over entire length of DS; with 5 sockets (4 of which with broken off setae, 1 with stiff white setae) between AME. PS ventrally pale yellow, without pattern. Chelicerae yellowish-brown, with indistinct pattern. Legs yellowish-brown with indistinct small spine patches on femora, femora ventrally dotted. Opisthosoma dorsally pale reddish-brown, becoming darker posteriorly, with light median band along entire length, this latter bordered by reddish-brown pattern; ventrally pale yellowish, with indistinct pattern in posterior half; spinnerets dorsally and laterally reddish-brown, ventrally pale yellow.

Variation. Female TL 10.0–14.2, PL 4.1–5.2, OL 5.9–9.0. Spination: Pa I–II 001, III 100(1), IV 101; Ti I 2024(5/6), II 2024(6), III 2024(5/6), IV 2026. Chelicerae with ca. 50 intermarginal denticles. Colouration (Figures 161–165): Some specimens darker. Femoral dots may fused proximally or along entire femora. White stiff setae between AME present in female from Gunung Leuser. Epigynal field with anterior bands, these partly fragmented (Figures 141–151).

Distribution. Known from various localities in Indonesia: Sumatra (Figure 169).

Heteropoda uniter spec. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:79B5AB44-58BA-43AE-8427-2921DC4F4F60>
(Figures 155–157, 166–169)

Type material. INDONESIA: Kalimantan Tengah: Holotype female, Kaharian, 2° 2' N, 113° 40' E [c. 50 m elevation], swampy primary forest, leaf litter, Suh. Djojosedharmo leg. 2–16 September 1985, 0208–0217; PJ 3147 (RMNH).

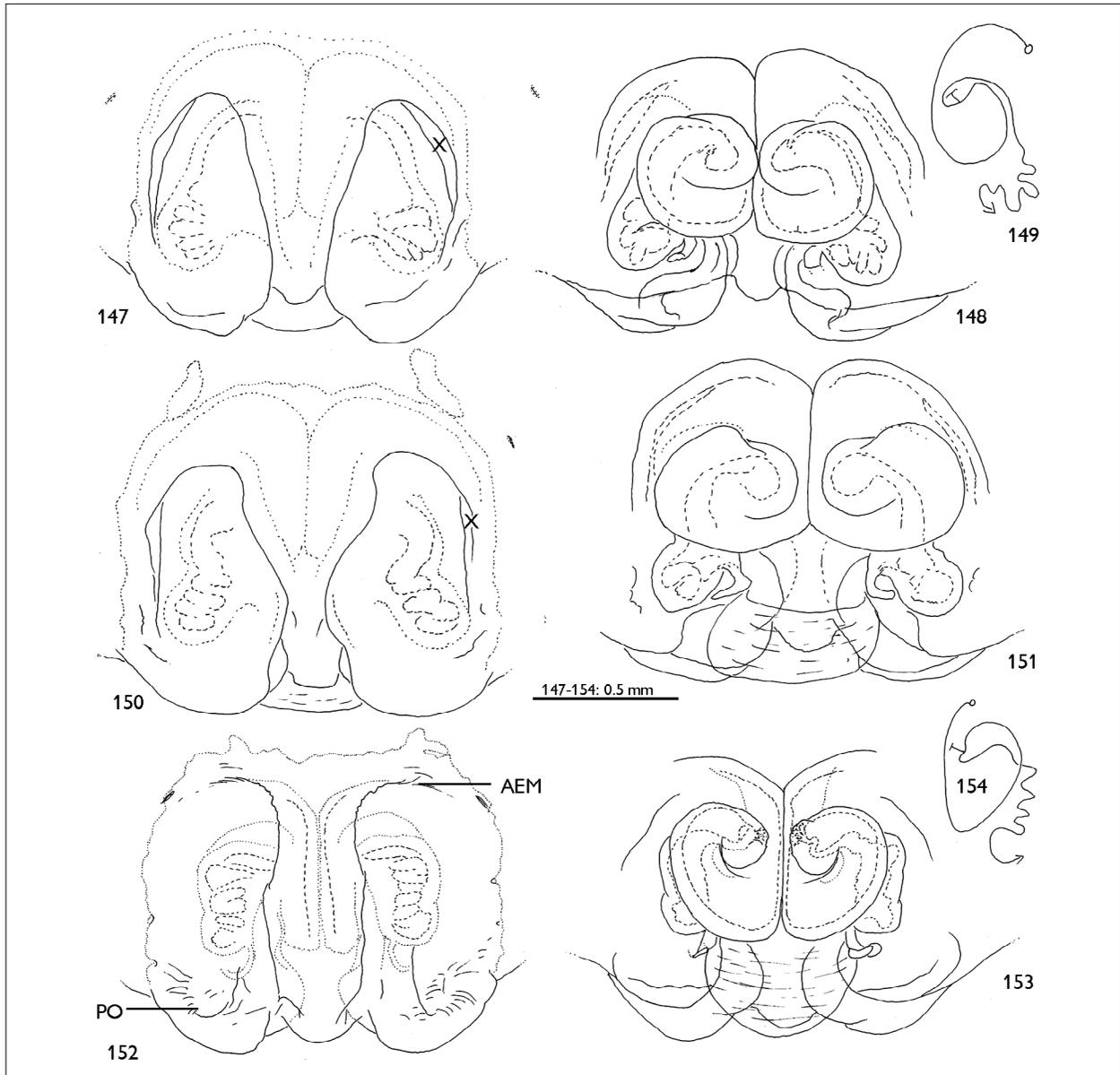
Etymology. The species name is derived from the Latin 'uniter,' meaning 'united in one' and refers to the first windings of the internal duct system joining along the median axis; adverb in apposition.

Diagnosis. Females of *H. uniter* spec. nov. are similar to those of *H. temburong* spec. nov. in having epigynal pockets with their anterior margins extending to the middle



part of epigyne and the anterior bands short and attached to epigynal field (Figures 155–157), but can be distinguished by:
 1. Glandular pores mediad, glandular regions touching each other medially, 2. Lateral lobes distinctly separated over their entire length, 3. Posterior part of internal duct system as wide

as first winding (glandular pores anteriad, glandular regions separated, lateral lobes almost touching each other medially in posterior half, posterior part of internal duct system distinctly narrower than first winding in *H. temburong* spec. nov.; cf. Figures 90–92).



Figures 147–154. *Heteropoda* spp., females from Indonesia (147–151 *H. ulna* spec. nov. from Pulau Buru [147–149] and Gunung Leuser [150–151], 152–154 *H. ocyalina* from the South coast of Java), copulatory organs (147, 150, 152 epigyne, ventral; 148, 151, 153 vulva, dorsal; 149, 154 schematic course of internal duct system, dorsal). Abbreviations: AEM = anterior epigynal margin, PO = epigynal pocket, x indicating narrow slit (152–154 from Jäger & Bayer, 2009).



Description. Male: Unknown.

Female (holotype): Measurements: TL 9.3, PL 4.4, PW 3.4, AW 2.0, OL 4.9, OW 2.0. Eyes: AME 0.25, ALE 0.45, PME 0.32, PLE 0.42, AME-AME 0.16, AME-ALE 0.03, PME-PME 0.17, PME-PLE 0.40, AME-PME 0.29, ALE-PLE 0.57, CH AME 0.67, CH ALE 0.40. Spination: Pp 131, 101, 2121, 1014; Fe I-II 323, III 333, IV 331; Pa I-II 001, III-IV 000; Ti I 2024, II-III 2025, IV 2024(5); Mt I-II 1014, III 2014, IV 3036. Mt I-III with dense scopulae along entire length and four stiff setae in proximal half (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 7.6 (2.2, 1.0, 1.8, -, 2.6); I 22.4 (6.3, 2.0, 6.7, 5.6, 1.8); II 29.0 (8.4, 2.7, 8.6, 7.0, 2.3); III 22.0 (6.0, 2.1, 6.7, 5.4, 1.8); IV 22.0 (6.6, 1.8, 5.7, 6.0, 1.9). Leg formula: II-I-(IV-III). CH with 3 promarginal and 4 retromarginal teeth, ca. 45 denticles and 1 escort seta.

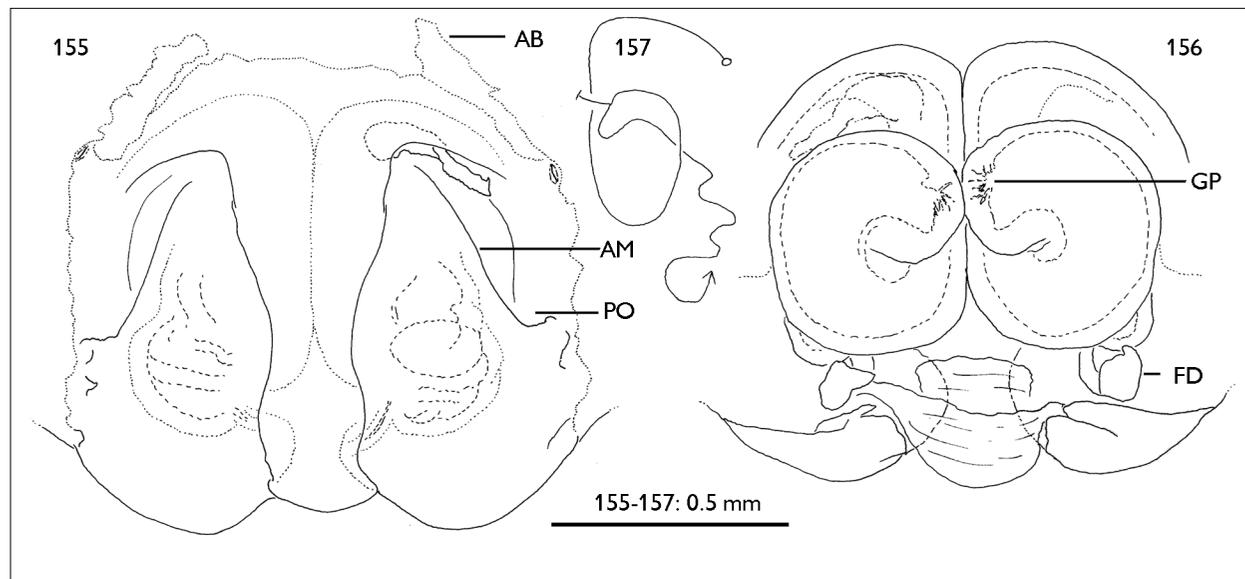
Copulatory organ (Figures 155–157). As in diagnosis. Epigynal field roughly rectangular, with one slit sensillum on each side, included in the field. Median septum longer than wide, slightly wider anteriorly, with posteriorly

convex transversal margin. Posterior pockets slit-like, running diagonally. Copulatory openings situated antero-laterally. Fertilisation ducts arising postero-medially from spermathecae, bent, their tips antero-dorsad.

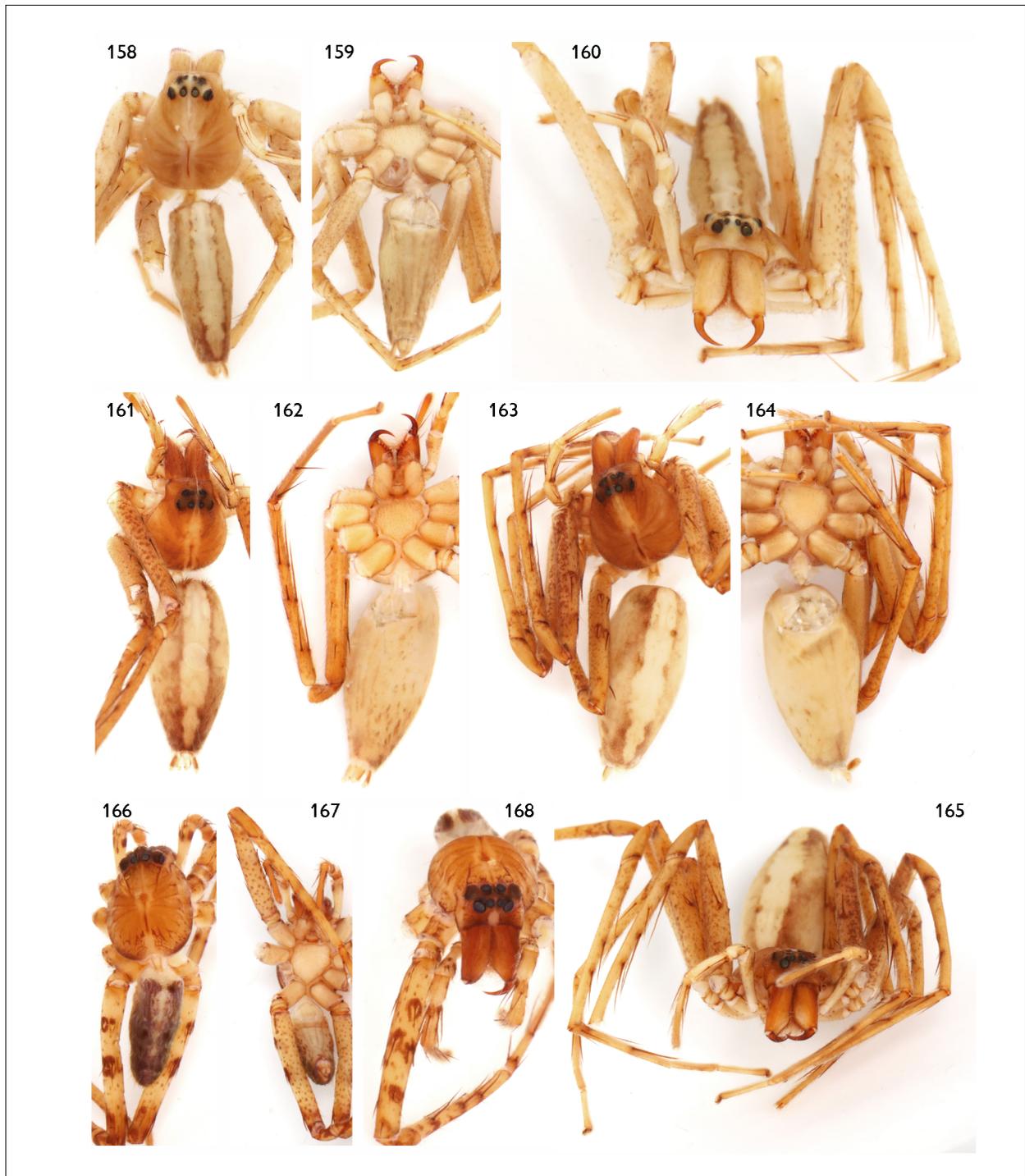
Colouration (Figures 166–168). Deep yellowish- to light reddish-brown with distinct reddish-brown pattern. DS reddish brown with indistinct light median stripe, fovea dark with round dark patch in front; with 4 sockets in a linear arrangement of broken off setae between AME. PS ventrally pale yellow, without pattern. Chelicerae slightly darker reddish-brown. Legs yellowish-brown with distinct and partly fused patches at spines on femora and on patellae and proximal tibia, femora ventrally, less so dorsally dotted. Opisthosoma dorsally dark brown, with indistinct light median band especially in anterior half; ventrally pale yellowish, with distinct patch anterior of spinnerets, the latter dorsally and laterally reddish-brown, ventrally pale yellow.

Distribution. Known only from type locality in Kaharian, Kalimantan, Indonesia (Figure 169).

Biology. The holotype female was recorded in a swampy forest in the leaf litter.



Figures 155–157. *Heteropoda uniter* spec. nov., holotype female from Sarawak, Malaysia, copulatory organ (155 epigyne, ventral; 156 vulva, dorsal; 157 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, AB = anterior band, FD = fertilisation duct, GP = glandular pores, PO = epigynal pocket.



Figures 158–168. *Heteropoda* spp., habitus of preserved female specimens. 158–165 *Heteropoda ulna* spec. nov. from Sumatra, Indonesia (158–160 holotype from Bukittinggi, 161–162 specimens from Gunung Leuser, 163–165 specimen from Soekaranda). 166–168 *Heteropoda uniter* spec. nov., holotype female from Sarawak, Malaysia (158, 161, 163, 166 dorsal; 159, 162, 164, 167 ventral; 160, 165, 168 frontal). Photos: P. Jäger.



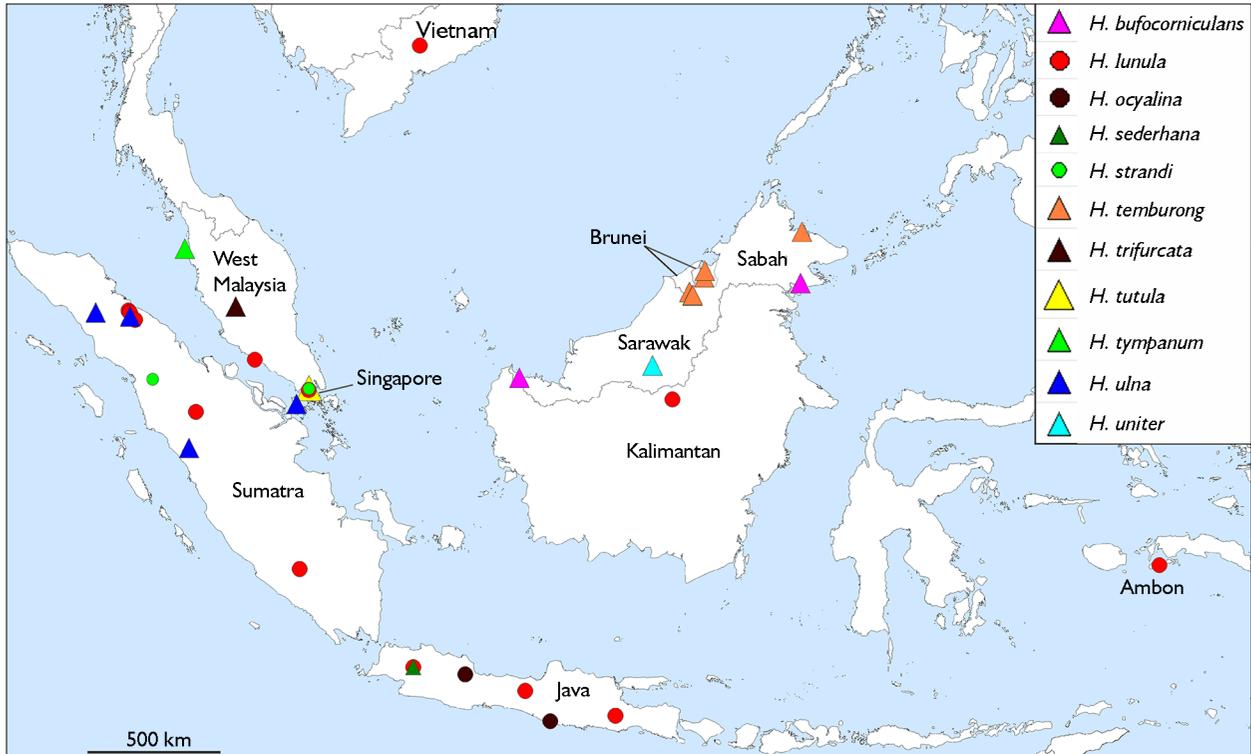


Figure 169. Distribution records of *Heteropoda* spp. in Southeast Asia of new species (triangles) and previously described species (circles).

Heteropoda fasciata (Reimoser, 1927) *nomen dubium*

Parhedrus fasciatus Reimoser, 1927: 1 (description of immature; immature holotype, PJ 1624, label: INDONESIA: Sumatra: Pulau Berhala [ca. 0° 51' 33.37" S, 104° 24' 23.27" E, 24 m], van der Meer Mohr leg., NHMW, examined).

Heteropoda ocyalina,— Jäger & Bayer 2009: 368 (synonymy).

Notes. This species name was considered a junior synonym of *H. ocyalina* by Jäger and Bayer (2009, p. 368) by its elongated opisthosoma and similar colour pattern. At that time, both authors underestimated the diversity within this genus in general and within this species-group in particular. Given the fact that there are much more species of similar appearance described in the present paper and most likely even more undescribed species and that there are various gradual states of elongation in the opisthosoma

in different species in this group, we now no longer consider *H. fasciata* conspecific with *H. ocyalina* because it has a much more slender opisthosoma than all other members of this species-group. The fact that the holotype of *H. fasciata* is immature does not weaken the argument that *H. fasciata* has an exceptionally slender opisthosoma. Immatures of *H. trifurcata* spec. nov., but also of members of other groups, such as *H. boiei*, show the same opisthosomal shape as the adults. Therefore, we remove *H. fasciata* from the synonymy of *H. ocyalina*. Separately, since the holotype of *H. fasciata* is immature and its identity cannot be clarified, we consider it a *nomen dubium*.

DISCUSSION

Considering the many shared diagnostic characters among *H. ocyalina*, *H. asa*, and six of the new species described in the present paper, it seems justifiable to erect a new species-group encompassing all eight species. Jäger and Bayer (2009)

considered *H. ocyalina* a member of the *H. dagmarae*-group based on their similarity of the palpal organs. However, they also highlighted the differences between *H. ocyalina* and the *dagmarae* species-group, such as the elongated opisthosoma with no black venter in *H. ocyalina* (otherwise in the *dagmarae* species-group), and the different positions of their respective conductor apophyses. Whether the *ocyalina* species-group is more closely related to the *H. javana*-group, given their similarities such as having an additional apex on dRTA, should be investigated in the future.

Based on impressions after six years of quarterly field trips in Brunei Darussalam (J.K.H. Koh, unpublished), it may be said that *H. borneensis* is one of the most common *Heteropoda* species in Brunei forests. The species is also notable in that the external appearance of its epigyne is highly variable. The variability is discernible even among population within the same locality. However, the internal duct system in the vulva appears consistent among the specimens collected in Sarawak, Sabah, Brunei, and Singapore. As *H. borneensis* is one of the extraordinary species of huntsman spiders with a unique striking colouration, it was possible to unmistakably assign several records in iNaturalist to that species and gather additional information on its distribution range (among others, the first record for Indonesia: North Kalimantan; Figure 41). However, there are other species of Heteropodinae with similar characteristic white lines on the dorsal side of the legs (e.g., an unidentified *Heteropoda* species from Indonesia, Sumatra; P. Jäger, unpublished data). Even some species of the genus *Pseudopoda* Jäger, 2000 exhibit this remarkable character, which is why an unambiguous identification of *H. borneensis* is valid only after a more holistic check encompassing other diagnostic indicators, including size, the colouration of the male and female bodies, legs and chelicerae, and occurrence on forest floor and only occasional occurrence in ground vegetation (i.e., never arboreal, nor near streams) etc.

The wide distribution pattern of *Heteropoda borneensis* is reminiscent of that of *H. davidbowie* Jäger, 2008, also occurring in northern Borneo, peninsular Malaysia and

Singapore, in addition to Indonesia (Sumatra) and southern Thailand. Further studies are required to explain the wide distribution of *H. borneensis*. There are two questions that need to be addressed: first, why it is more frequently sighted in Borneo and less so in Singapore and peninsular Malaysia by iNaturalist contributors; second, whether its presence in Singapore and peninsular Malaysia could have been introduced through the exports of plants. In the context of the first question, it should be noted that the species has often been seen and photographed in Singapore, but not posted on the iNaturalist platform. In the context of the latter question, while *H. davidbowie* has been observed on ornamental plants at Bukit Fraser in peninsular Malaysia (P. Jäger, unpublished data), *H. borneensis* has never been seen in gardens or other artificially cultivated habitats in Singapore. On the other hand, the latter species has been photographed on the forest floor in forest reserves in Johor and Selangor in peninsular Malaysia, and in the more pristine forest patches in nature reserves in Singapore, including the Bukit Timah Nature Reserve which has been protected since 1883 (J.K.H. Koh, from unpublished records of other nature photographers).

Some morphological characters in *Heteropoda bufocorniculans* spec. nov. are unique not only in the genus *Heteropoda*, but also in the entire family. Striking features are the erect femoral spines and the absence of spines in many positions of some leg segments. Apparently, both characters evolved together, since erect spines in retrolateral positions, e.g. in femora would disturb a smooth movement of the legs. A similar reduction is known from femur IV in almost all Sparassidae: retrolateral proximal spines are reduced because they would interfere with the antero-lateral part of the opisthosoma during locomotion. While it cannot be explained easily how these modifications (erect spines) occurred, the tufted body could be explained by a selective advantage in certain habitats, where the spider is better camouflaged. Similar colour and setal modifications are known, e.g., from *Pandercetes* L. Koch, 1875 (lichen huntsmen) or *Barylestis saaristoi* Jäger 2008, all living also on bark of tree trunks.



A more general remark concerns the usage of photos posted on platforms like iNaturalist or Flickr: it is clear that only a small fraction of spider species with unmistakably recognisable morphological characters can be identified accurately purely from photos. On the other hand, for this small group, these platforms offer an added avenue to ascertain the full extent of their distribution range, and even provide information on their ecology or biology. In the present paper we used only data for one species, *H. borneensis*, but there are more candidates, like *H. bufocorniculans* spec. nov. and *H. lunula*, identifiable by their unique shape or colour pattern. Another example shows that unknown sexes can be found on such platforms: after the species *H. dede* Jäger, 2024 was described, a photo of a male Sparassidae from Tawau Hill, Sabah, ca. 50 km south of the type locality, Danum Valley, Sabah, posted in 2021 by Wong Tsu Shi was identified as being conspecific. However, a critical recheck should be done when photos are used as lone base for identification.

ACKNOWLEDGEMENTS

We thank Maria Tavano (MCSN) for sending the type material of *H. borneensis*, and Ondřej Machač (Prague) for providing additional material. We are grateful to all persons who contributed with photos on the internet platform iNaturalist (listed here with their names or aliases: albertkang, andrea349, andrewblayney, arlo7, astyring, Bruce Teo, carol_kwok, cclborneo, desertnaturalis, dolceamore, filee14, Frank DeschandoI, hw0529649, janusolajuanboediman, Christian Langner, littlebrownskink, matuty, nickvolpe, roeyo, shia_a, talibzuo, tony_robillard). Faiz Bustami (Singapore) and Guek Hock Ping (Kuala Lumpur) gave detailed locality information on their photographic records provided on Flickr. We thank cordially Chris Ang and Nicky Bay (both Singapore) for providing photos of live spiders. Finally, we are grateful to Antonio D. Brescovit (São Paulo) and Alexandre B. Bonaldo (Belém) for their comments which helped to improve the manuscript.

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AUTHORS' CONTRIBUTION

P. Jäger contributed to conceptualization, data curation, formal analysis, investigation, methodology, visualization, and writing (original draft, review and editing); and J. K. H. Koh contributed to data curation, investigation, visualization, and writing (original draft).