

Sicariomorpha, a New Myrmecophilous Goblin Spider Genus (Araneae, Oonopidae) Associated with Asian Army Ants

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ABSTRACT

A new genus of oonopid spider, *Sicariomorpha* Ott and Harvey, is named for the type and only known species, *Gamasomorpha maschwitzi* Wunderlich from Malaysia. The most striking feature of the spider is the eyes, which are arranged in two widely separated triads. Besides taxonomic description, we summarize the biology of *Sicariomorpha maschwitzi*, which is a kleptoparasite of the Southeast Asian army ant *Leptogenys distinguenda* (Emery) and one among only few well-studied myrmecophilous spiders. Its morphology, behavior and life history seem to be well adapted for the life with its predatory army ant host.

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INTRODUCTION

Several different groups of spiders have evolved close associations with ants and can be classified as myrmecomorphs, myrmecophiles, or myrmecophages (Cushing, 1997, 2012), categories that are not mutually exclusive. Myrmecomorphs are Batesian mimics; myrmecophiles show an intimate, symbiotic association with ants by living either in close proximity or within ant colonies; and myrmecophages prey on ants. Considering the immense diversity of myrmecophilous arthropods (Kistner, 1982; Hölldobler and Wilson, 1990; Gotwald, 1995; Rettenmeyer et al., 2011), very few spiders have been described as myrmecophiles. Twelve spider families have been recorded with myrmecophile associations (Cushing, 1997, 2012), including several species of Oonopidae, of which the best studied is *Gamasomorpha maschwitzi* Wunderlich (Witte et al., 1999; Witte et al., 2008; Witte et al., 2009; von Beeren et al., 2012a). This species is a myrmecophile of the army ant *Leptogenys distinguenda* (Emery) in Malaysia. It shows several morphological and behavioral characteristics that seem to be adaptations to the life with army ants. Below, we present a summary of its interesting biology.

Although originally included in the genus *Gamasomorpha* Karsch by Wunderlich (1995), *G. maschwitzi* is an aberrant species that appears to have very few affinities with the type species of *Gamasomorpha*, *G. cataphracta* Karsch, which was redescribed by Brignoli (1974). *Gamasomorpha* currently includes 64 species that are found in various parts of the world, including Asia, Australia, Africa, and South America, as well as various island systems (Platnick, 2014). *Gamasomorpha* is very similar to *Xestaspis* Simon, but *Xestaspis* differs by the presence of a pointed tubercle on the anterolateral face of the epigastric scute (Ott and Harvey, 2008: 338, fig. 1c (Bcp); Eichenberger et al., 2012: 43, fig. 36B, D, E) and females sharing a very similar internal genital sclerite positioned posterior to the epigastric furrow and apparently attached to the ventral scute (see Eichenberger et al., 2012: 7E–G and 37D, E). Despite the work of several authors in removing species from *Gamasomorpha* (e.g., Chickering, 1969; Brignoli, 1974, 1975, 1983; Dumitresco and Georgescu, 1983; Saaristo, 2001; El-Hennawy, 2008; Platnick and Dupérré, 2009; Platnick et al., 2012b), the genus still includes a heterogenous array of species with different morphologies, and it is apparent that many are misplaced and should be reallocated to other genera (R. Ott, unpublished data). The purpose of this paper is to present a redescription of *G. maschwitzi*, which we are convinced is misplaced in *Gamasomorpha*, for which we propose a new genus.

MATERIAL AND METHODS

The specimens examined for this study are lodged in the American Museum of Natural History, New York (AMNH), California Academy of Sciences, San Francisco (CAS), Museu de Ciências Naturais, Porto Alegre, Brazil (MCN), Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC), Senckenberg Naturmuseum, Frankfurt, Germany (SMF) and the Western Australian Museum, Perth, Australia (WAM).

The specimens were studied using a Leica DM2500 compound microscope and Leica MZ16A and M205C stereomicroscopes. Images were produced using Leica DFC 500 digital cameras attached to the microscopes, and the software program AutoMontage Pro Version 5.02

(p). Specimens were prepared for scanning electron microscopy by dehydration through stages of 75% to 100% ethanol and then air-dried.

Descriptions were generated with the aid of the PBI descriptive goblin spider database and shortened where possible. All measurements are in millimeters. The following abbreviations are used in the text: **ALE**, anterior lateral eyes; **ALS**, anterior lateral spinnerets; **PLE**, posterior lateral eyes; **PLS**, posterior lateral spinnerets; **PME**, posterior median eyes; **PMS**, posterior median spinnerets. Male and female genitalia nomenclature follows Burger (2010) with modifications; for the male genitalia the following abbreviations were used: **Co**, conductor; **Cy**, cymbium; **Em**, embolus; **Lf**, long flange of embolus; **Sf**, short flange of embolus; for the female genitalia the following abbreviations were used: **CW**, chitinized wall of receptaculum; **GAp**, globular appendix; **La**, lateral apodemes; **Na**, naillike process; **PSc**, paddle sclerite; **Re**, receptaculum; **SW**, sclerotized wall of receptaculum.

Temporary slide mounts of dissected structures were prepared by immersion of specimens in 50% lactic acid at room temperature for several hours, and mounting them on microscope slides with 10 or 12 mm coverslips supported by small sections of 0.25 mm diameter nylon fishing line. These slide mounts were studied with a Leica DM2500 compound microscope and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study the specimens were rinsed in water and returned to 75% ethanol with the dissected portions placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.).

SYSTEMATICS

Family Oonopidae Simon, 1890

Subfamily Oonopinae Simon, 1890

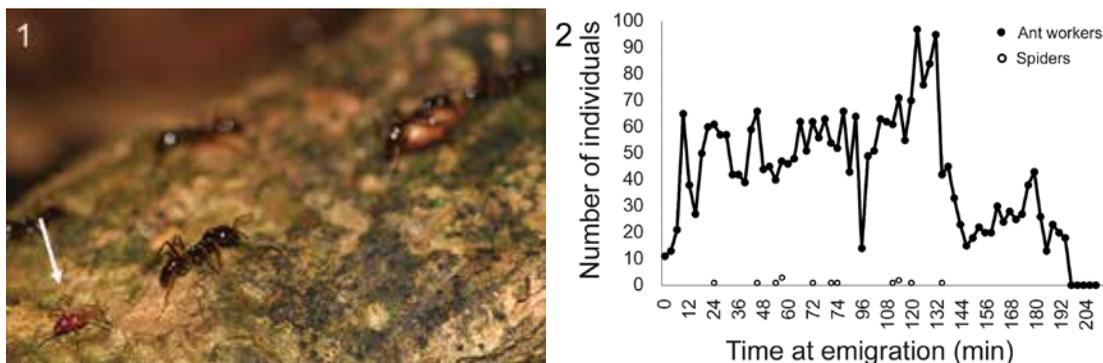
Sicariomorpha Ott and Harvey, new genus

TYPE SPECIES: *Gamasomorpha maschwitz* Wunderlich, 1995.

ETYMOLOGY: The generic name is a contraction of the spider generic names *Sicarius* and *Gamasomorpha* and refers to the unusual carapace shape and eye arrangement, which is reminiscent of the genus *Sicarius*. The gender is feminine.

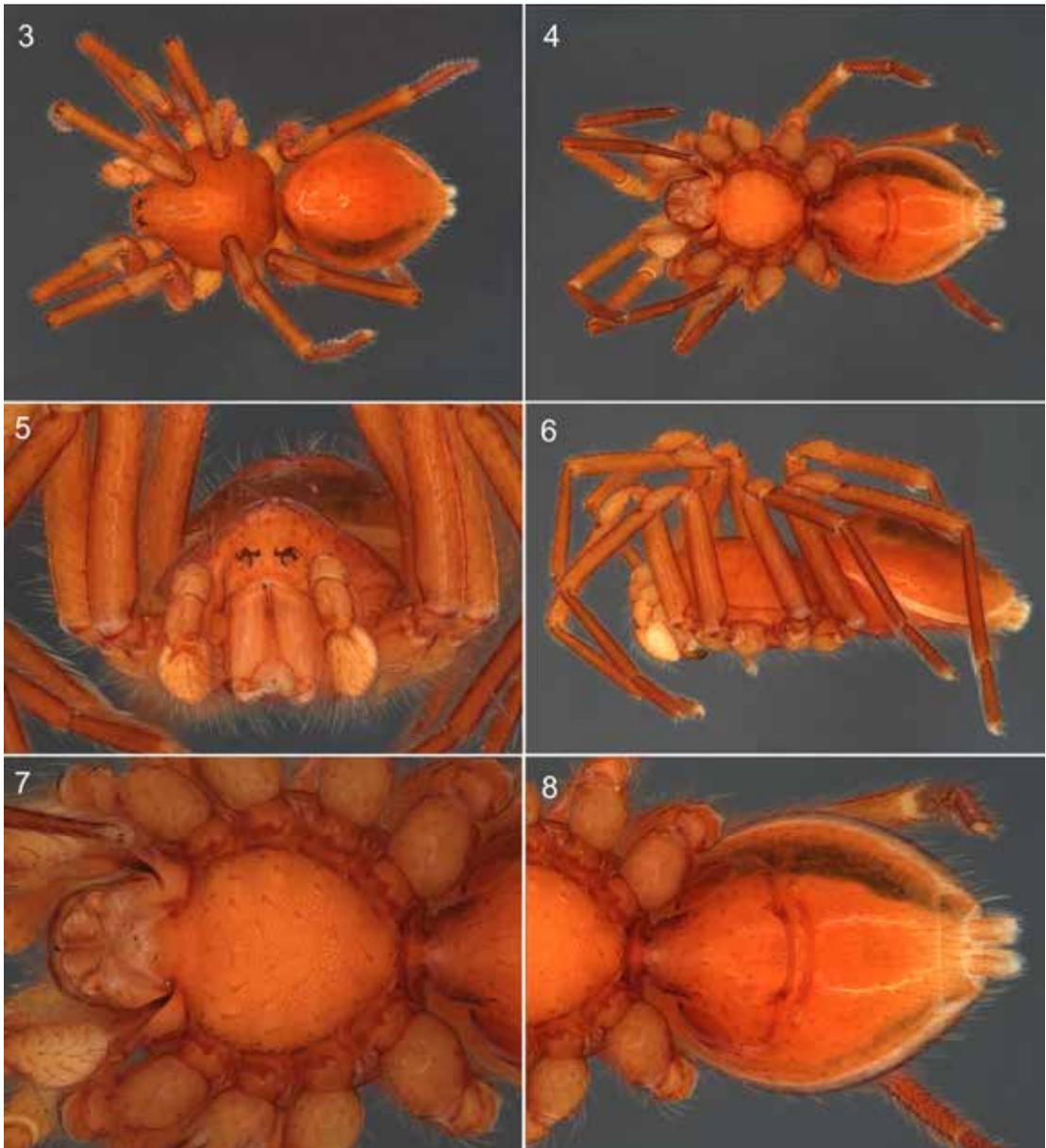
DIAGNOSIS: *Sicariomorpha* differs from all oonopids by the combination of following characters: full set of abdominal scuta (figs. 3, 4, 6, 8, 18, 21); the absence of conspicuous paired spines on metatarsi and tarsi of legs I and II (figs. 6, 20, 25, 26); rounded carapace with strongly narrowed cephalic region (figs. 19); six small eyes in triads and separated from each other by almost twice the diameter of PME (figs. 5, 19, 22); male palpal bulb with strongly sclerotized transverse ridge, which is stronger retrolaterally and weaker prolaterally (figs. 9–13); and female internal genital sclerite totally free and situated anterior to the epigastric furrow (figs. 15).

DESCRIPTION: MALE (figs. 3–8, 9–14, 23–33, 42–46): **Cephalothorax**: Carapace orange-brown, without any pattern, broadly oval in dorsal view (fig. 3), pars cephalica slightly elevated in lateral view, anteriorly narrowed to 0.49 times its maximum width or less, with rounded posterolateral corners, posterolateral edge without pits, posterior margin not bulging below posterior rim, anterolateral corners without extension or projections, posterolateral surface without spikes, surface of



FIGURES 1–2. 1, *Sicariomorpha maschwitzi*, comb. nov., participates in ant emigrations by performing a “tandem-running”-like behavior. 2, Participation of *S. maschwitzi* in host migrations. *Leptogenys distinguenda* workers heading toward the new nest were counted periodically for 90 sec, followed by a 90 sec break. Additionally, the presence of spiders was counted throughout the entire emigration.

elevated portion of pars cephalica finely reticulate, sides granulate, thorax without depressions, fovea absent, without radiating rows of pits; lateral margin undulate, rebordered, without denticles; plumose setae near posterior margin of pars thoracica absent; nonmarginal pars cephalica setae light, needlelike, present, scattered; nonmarginal pars thoracica setae light, needlelike; marginal setae light, needlelike. Clypeus margin unmodified, curved downward in front view (fig. 5), sloping forward in lateral view, high, ALE separated from edge of carapace by their radius or more, median projection absent; setae present, light, needlelike. Chilum absent. Six eyes, reduced, tiny, ALE largest, all eyes circular; posterior eye row recurved from above, straight from front; ALE separated by more than their diameter, ALE-PLE touching, PME separated by more than their diameter, PLE-PME touching (fig. 5). Sternum (fig. 7) as long as wide, orange-brown, uniform, fused to carapace, median concavity absent, without radial furrows between coxae I-II, II-III, III-IV, radial furrow opposite coxae III absent, surface finely reticulate, without pits, microsculpture covering entire surface, sickle-shaped structures absent, anterior margin unmodified, posterior margin not extending posteriorly of coxae IV, anterior corner unmodified, lateral margin with infracoxal grooves and anterior and posterior openings, distance between coxae approximately equal, extensions of precoxal triangles present, lateral margins unmodified, without posterior hump; setae sparse, light, needlelike, evenly scattered, originating from small pits, without hair tufts. Mouthparts: chelicerae, endites and labium orange-brown (fig. 7). Chelicerae straight, anterior face unmodified; without teeth on both promargin and retromargin (fig. 28); fangs without toothlike projections, directed medially, shape normal, without prominent basal process, tip unmodified (figs. 30, 31); setae light, needlelike, densest medially; paturon inner margin with scattered setae, distal region abruptly narrowed, posterior surface unmodified, promargin unmodified, inner margin with medial denticles, laminate groove absent. Labium (figs. 7, 27) triangular, fused to sternum, anterior margin indented at middle, same as sternum in sclerotization; with 3–5 setae on anterior margin, subdistal portion with unmodified setae. Endites distally not excavated (figs. 7, 27), serrula present in single row, anteromedian tip unmodified, posteromedian part unmodified, same as sternum in sclerotization. **Abdomen:** Ovoid, without long posterior extension, rounded posteriorly, interscutal membrane rows of small sclerotized plate-



FIGURES 3–8. *Sicariomorpha maschwitzi*, comb. nov., male. 3, Dorsal; 4, ventral; 5, frontal; 6, lateral; 7, sternum, ventral; 8, abdomen, ventral.

lets absent posteriorly; dorsum soft portions white, without color pattern (figs. 3, 8). Book lung covers large, ovoid, without setae, anterolateral edge unmodified (fig. 8). Posterior spiracles connected by groove. Pedicel tube medium, ribbed (fig. 8), scutopedicel region unmodified, scutum extending far dorsal of pedicel, plumose hairs absent, matted setae on anterior ventral abdomen in pedicel area absent, cuticular outgrowths near pedicel absent. Dorsal scutum strongly sclerotized, orange-brown, without color pattern, covering full length of abdomen, no soft tissue visible from

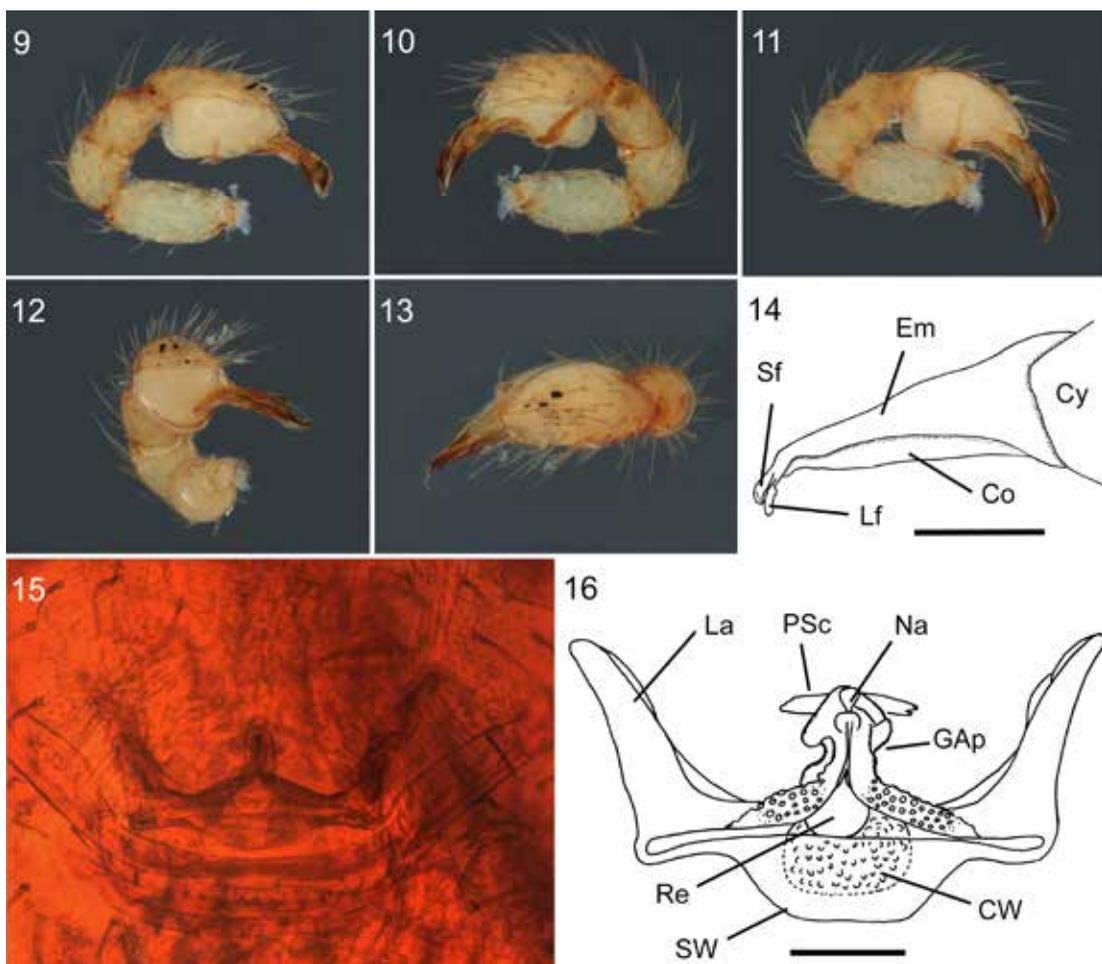
above, not fused to epigastric scutum, middle surface finely reticulate, sides finely reticulate, anterior half without projecting denticles (fig. 3). Epigastric scutum strongly sclerotized, surrounding pedicel, slightly protruding, small lateral sclerites absent (fig. 8). Postepigastric scutum strongly sclerotized, orange-brown, almost semicircular, covering nearly full length of abdominal length, fused to epigastric scutum, anterior margin unmodified, without posteriorly directed lateral apodemes (fig. 8). Spinneret scutum present, enlarged into platelet (fig. 8). Supraanal scutum absent (fig. 8). Dorsum setae present, light, needlelike. Epigastric area setae uniform, light, needlelike. Postepigastric area setae present, light, needlelike. Spinneret scutum without fringe of setae. Dense patch of setae anterior to spinnerets absent. ALS with one major ampullate and three minor ampullate glands; PMS with 14–15 aciniform glands; PLS with 24–25 aciniform glands (fig. 33). Interscutal membrane with setae. Colulus represented only by setae. **Legs:** Orange-brown, without color pattern (fig. 6); femur IV not thickened, same size as femora I–III (fig. 6), patella plus tibia I longer than carapace, tibia I unmodified, tibia I Emerit's glands absent, tibia IV specialized hairs on ventral apex present, tibia IV ventral scopula absent, metatarsi I and II mesoapical comb absent, metatarsi III and IV weak ventral scopula absent. Leg spines absent (fig. 6). **Genitalia:** Male with epigastric region with sperm pore small, circular, situated at level of anterior spiracles, unmodified (fig. 8); furrow without Ω -shaped insertions, without setae. Palp (figs. 9–13) normal size, not strongly sclerotized, right and left palps symmetrical, proximal segments yellow; embolus dark, prolateral excavation absent; trochanter normal size, unmodified; femur normal size, two or more times as long as trochanter, without posteriorly rounded lateral dilation, attaching to patella basally; patella shorter than femur, not enlarged, without prolateral row of ridges, setae unmodified; tibia trichobothria not examined; cymbium pale orange, ovoid in dorsal view, fused with bulb but with clearly defined seam between, not extending beyond distal tip of bulb, plumose setae absent, without stout setae, without distal patch of setae; bulb yellow, 1 to 1.5 times as long as cymbium, stout, spherical. Female (figs. 14–22, 28, 34–41), as in male except as noted. Palp: claws absent; spines absent; tarsus unmodified, patella without prolateral row of ridges.

REMARKS: *Sicariomorpha* can be included in the Oonopidae due the presence of a proximal longitudinal ridge on the tarsal organ, which is very round and open, with a similar pattern to *Triaeris stenaspis* Simon (Platnick et al., 2012a). Judging by the eyes, which are not arranged in a H-shaped pattern, the spider belongs to the subfamily Oonopinae. This group is characterized by dimorphic 3-3-2-2 tarsal organ receptor pattern, a feature found in all oonopines except *Kapitia* Forster, from New Zealand (Platnick et al., 2012a). The tarsal organ pattern was not clearly visible in *S. maschwitzi* due to a fine layer of some type of exudate (figs. 37–46). It seem to belong to the “gamasomorphoid” suite of oonopine genera defined by Álvarez-Padilla et al. (2012), which can be recognized by an embolic complex that is “fairly evenly curved and composed of three elongate, subequal divisions” (considered herein as in Burger, 2010: 25, fig. 5G as: conductor, long flange of embolus and short flange of embolus; fig. 14), and female genitalia with a round to longitudinally elongate receptaculum composed of transparent components and with posterior apodemes that are relatively short. The full composition of this complex remains to be verified, but Álvarez-Padilla et al. (2012) suggest that gamasomorphoids are primarily present in Asia and the New World. The presence of a free internal genital sclerite of females in *S. mas-*

chwitzi also suggests an affinity with the “pelicinoids” (sensu Saucedo et al., 2015), but this characteristic, along with a narrower receptaculum, suggests a closer relationship with *Grymeus* Harvey from Australia and some Neotropical species of *Gamasomorpha* (e.g., *G. puberula* (Simon), *G. silvestris* (Simon), *G. simplex* (Simon)), *Lutecia* (*L. distincta* Dumitrescu and Georgescu, 1983; see Dumitrescu and Georgescu, 1983: 111, figs. 6, 7), and *Yumates* Chamberlin (e.g., *Yumates nesophila* Chamberlin).

BIOLOGY: *Sicariomorpha maschwitzi* is one of the best-studied myrmecophilous spiders. It inhabits colonies of the Southeast Asian army ant *Leptogenys distinguenda* (Witte et al., 1999; Witte, 2001; Witte et al., 2009; von Beeren et al., 2012a) with a high prevalence at the Ulu Gombak study site (46 colonies colonized out of 50). Its host spectrum is unknown as host records have not been studied systematically. Even though it shows a high prevalence with *L. distinguenda*, these spiders presumably have only a low negative impact on the host population, which seems to be a common phenomenon in ant-nest inhabiting spiders such as *Cosmophasis bitaeniata* Keyserling and *Attacobius attarum* Roewer (Cushing 2012). In *S. maschwitzi*, this is indicated by the spider’s kleptoparasitic habit by feeding on dead host prey items (Witte et al., 2008; Witte et al., 2009) and the low number of individuals per colony (range = 0–30 spiders per colony, median = 4 spiders per colony, $N_{\text{host colonies}} = 50$). In contrast to *C. bitaeniata* and *A. attarum*, *S. maschwitzi* does not prey on immatures of the host and has instead lost its predatory behavior, a plesiomorphic trait in spiders (Riechert and Luczak, 1982). In species-rich host-myrmecophile communities, low-cost parasites like *S. maschwitzi* are supposedly more likely to achieve high levels of integration due to lower selection pressure on the host to evolve counterdefenses (Witte et al., 2008; von Beeren et al., 2011). Indeed, *S. maschwitzi* is very well integrated into the social system of its predatory host *L. distinguenda* (“integrated species” sensu Kistner, 1979). Most interactions between spiders and workers are peaceful in nature and spiders are even sometimes groomed by host ants (von Beeren et al., 2012a). This might be in part due to the fact that *S. maschwitzi* acquires nestmate recognition cues from ant workers (“acquired chemical mimicry” sensu von Beeren et al., 2012b), thus duping workers to be colony members (von Beeren et al., 2012a). A chemical mimicry strategy was also found in the salticid spider *C. bitaeniata*, a guest of the weaver ant *Oecophylla smaragdina* Fabricius (Allan et al., 2002), and might generally constitute a good strategy to avoid ant attacks in nest-inhabiting myrmecophiles (Lenoir et al., 2001). Interestingly, the nestmate-recognition cues were acquired differently: *S. maschwitzi* acquired them from host workers, while *C. bitaeniata* acquired them by feeding on host larvae (Elgar and Allan, 2004). It should not be forgotten, though, that additional behavioral and morphological adaptations might play important roles in interspecific interactions between spiders and ants. A detailed experimental study revealed, for example, that *S. maschwitzi* does not entirely depend on chemical mimicry for social integration (von Beeren et al., 2012a). In laboratory nests they primarily rested on top of ants, which might help to avoid constant confrontations with ant workers (see video footage at <http://www.evolution-of-life.com/en/observe/video/fiche/an-evolutionary-arms-race.html>).

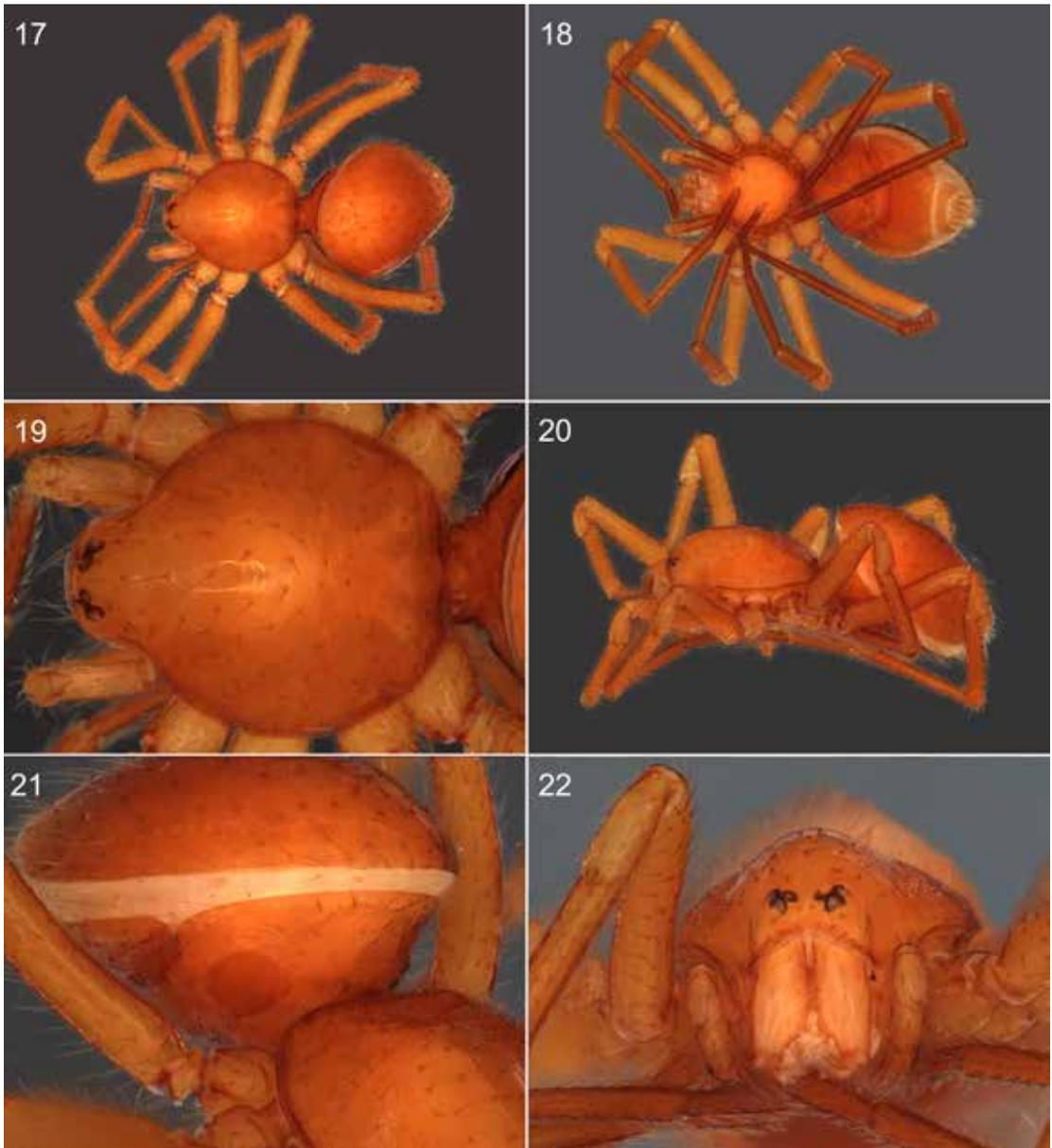
Adaptations to the nomadic life style of its army ant host are apparent. *Sicariomorpha maschwitzi* participates in the frequent host emigrations to new nest sites by using a combina-



FIGURES 9–16. *Sicariomorpha maschwitzi*, comb. nov., 9–14, male palp; 13–16, female genitalia, ventral view. 9, Retrolateral; 10, prolateral; 11, ventral; 12, frontal; 13, dorsal; 14, Palp distal (embolus and conductor), dorsal view; 15, cleared; 16, internal genital sclerite. Scale bars = 0.10 mm.

tion of tactile and chemical stimuli (Witte et al., 1999). Spiders were found primarily when ant traffic flow on trails was high (see fig. 2).

Very little is known about the reproduction of *S. maschwitzi*. Spiders were regularly observed to mate in laboratory nests among ant workers (sex ratio is 1:1, $N_{\text{spiders}} = 95$). Unfortunately, egg-laying was never observed. Histological sections of female opisthosomas revealed unusually large eggs indicating high investment in offspring (Witte et al., 1999; Witte, 2001). This requires further investigation, but we speculate that spiderlings hatch shortly after egg-laying in order to avoid a free-living phase and immediately track the frequent colony migrations. In summary, *S. maschwitzi* shows several characteristics that seem to be specific adaptations to the life with its army ant host, a life style that is generally assumed to be a favorable niche by providing a predator-free space and richly laden tables of high-quality food (Hölldobler and Wilson 1990).



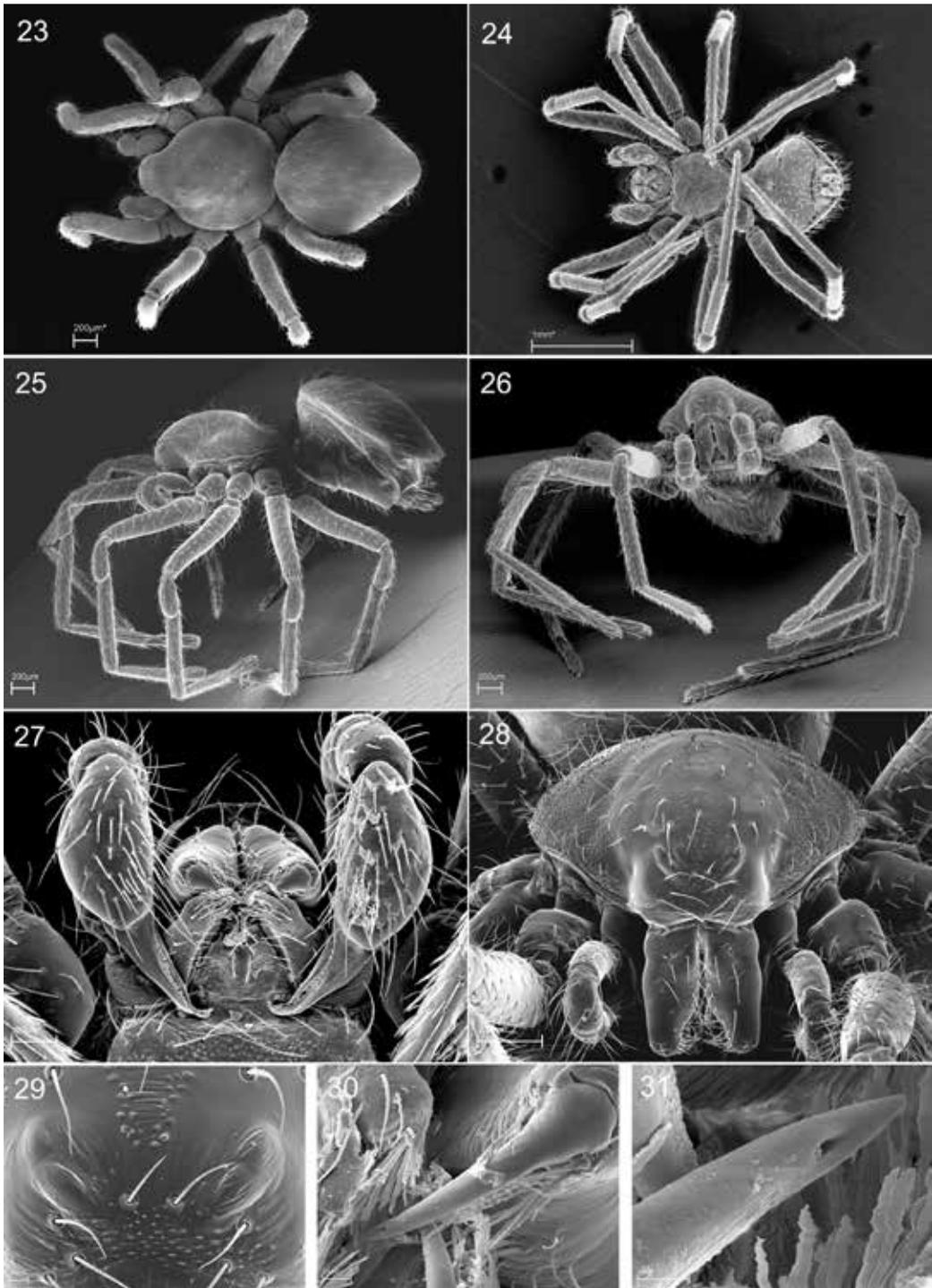
FIGURES 17–22. *Sicariomorpha maschwitzi*, comb. nov., female. 17, Dorsal; 18, ventral; 19, carapace, dorsal; 20, lateral; 21, abdomen, anterolateral; 22, carapace, anterior.

Sicariomorpha maschwitzi (Wunderlich), comb. nov.

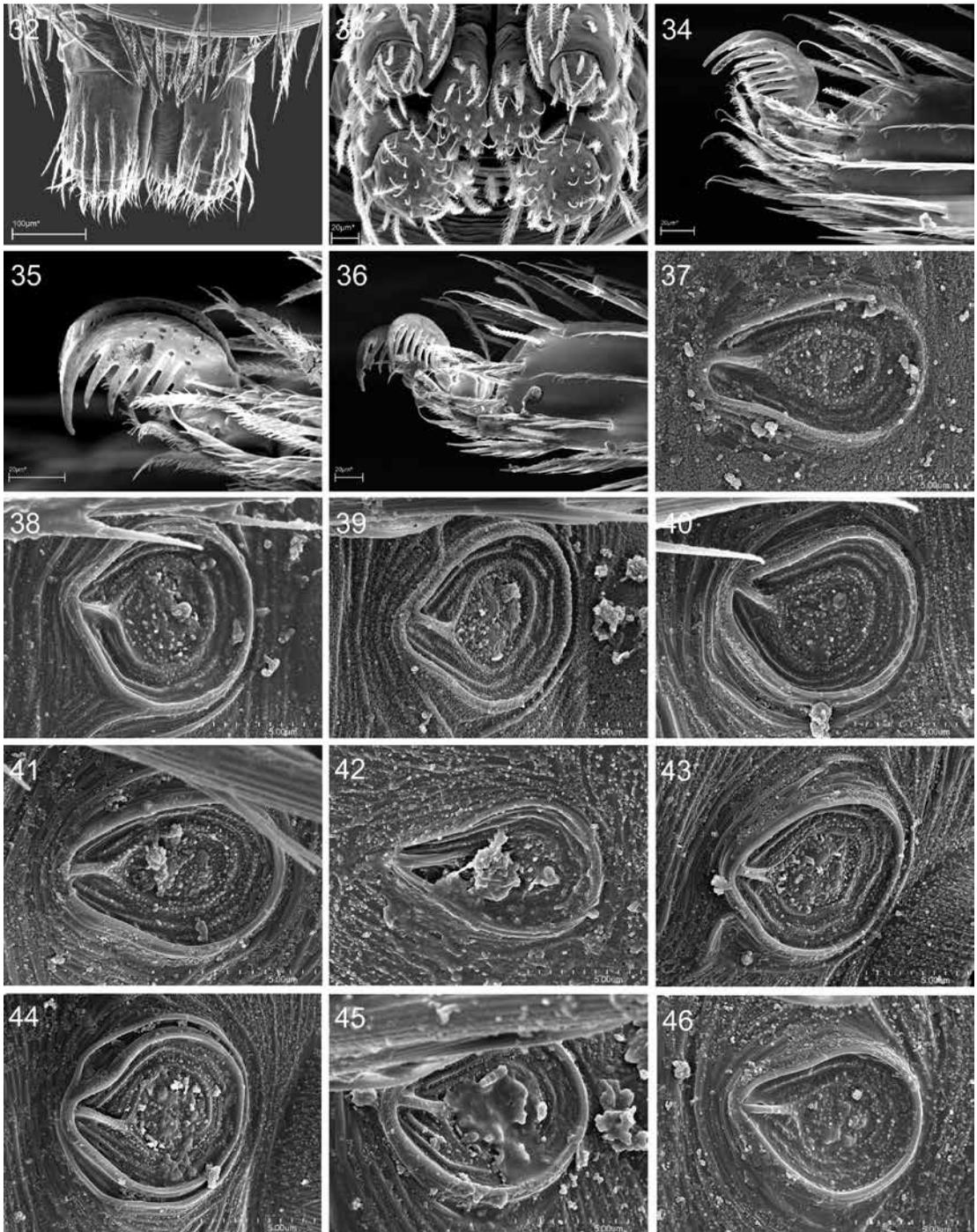
Figures 1–46

Gamasomorpha maschwitzi Wunderlich, 1995: 560, figs. 1–5.

TYPES: MALAYSIA: **Selangor**: holotype male, from Gombak valley, near Kuala Lumpur; secondary rain forest, forest ground with *Leptogenys distinguenda* ants (Nov. 1982, H. Hänel), deposited in SMF (37191, PBI_OON 25587) (examined). Paratypes: 1 male, 2 females, collected



FIGURES 23–31. *Sicariomorpha maschwitzi*, comb. nov., 23–27, 29–31, male. 23, Dorsal; 24, ventral; 25, lateral; 26, anterior; 27, anterior portion of carapace, ventral; 28, female carapace, anterior; 29, eyes, anterior; 30, chelicera fang, ventral; 31, chelicera fang venom duct opening.



FIGURES 32–46. *Sicariomorpha maschwitzi*, comb. nov., 32, 33, 42–46, male; 34–41, female. 32–33, spinnerets. 34, leg I, lateral; 35, leg III, lateral; 36, leg IV, lateral. 37–46, tarsal organ, dorsal view. 37, 42, palp; 38, 43, leg I; 39, 44, leg II; 40, 45, leg III; 41, 46, leg IV.

with holotype, deposited in SMF (37192, PBI_OON 25588) (examined); 1 male, 1 female, collected with holotype, deposited in J. Wunderlich private collection (not examined).

DIAGNOSIS: *Sicariomorpha maschwitzi* can be recognized by the generic characters and also by the shape of male palp and female genitalia (figs. 9–16).

MALE (PBI_OON 25587): Total length 2.71. **Cephalothorax:** Carapace very broad, anteriorly narrowed by less than 1/3 of its width (fig. 3); nonmarginal pars thoracica setae scattered over all pars thoracica. Clypeus twice the ALE diameter (fig. 5). Eyes in triads (fig. 5). **Legs:** Tarsi I–IV superior claws inner face smooth; tarsi I–IV with four teeth on lateral surface and five teeth on median surface (figs. 34–36). **Genitalia:** Palp: embolus distally enlarged, gull-beak shaped, with distal translucent area (fig. 9–14); bulb with prolateral sclerotized ridge (duct?).

FEMALE (PBI_OON 25588): Total length 2.81. As in male except as noted. **Palp:** Spines absent. **Genitalia:** With free internal genital sclerite placed anteriorly to the epigastric furrow (fig. 15). Genital sclerite crown shaped, with stout medial portion; receptacle rounded; lateral apodemes directed and narrowing anteriorly, slightly outward directed, with curved tip and posteriorly with angular corner (figs. 15–16).

OTHER MATERIAL EXAMINED: MALAYSIA: **Selangor:** 4 ♂, 3 ♀, Ulu Gombak, 03°19.4796'N, 101°45.1630'E, 2008, ex ant colony, lowland dipterocarp rainforest, C. von Beeren (WAM T108254, PBI_OON 46565); 2 ♂, 2 ♀, same data (AMNH); 3 ♂, 5 ♀, same data except 2008 (WAM T108259, PBI_OON 46570); 1 ♂, 3 ♀, same data except 2009 (WAM T108260, PBI_OON 46571); 1 ♂, 2 ♀, same data except 2010 (WAM T108255, PBI_OON 46566); 3 ♂, 3 ♀, same data (WAM T108256, PBI_OON 46567); 1 ♂, 1 ♀, same data (CAS); 1 ♂, 1 ♀, same data (MRAC); 1 ♂, 1 ♀, same data (MCN); 16 ♀, same data except 2007 (WAM T108257, PBI_OON 46568); 2 ♂, 5 ♀, same data (WAM T108258, PBI_OON 46569); **Pahang:** 3 ♂, 7 ♀, Pahang, Bukit Rengit, 03°35.779'N, 102°10.814'E, 2010, ex ant colony, lowland dipterocarp rainforest, C. von Beeren (WAM T108261, PBI_OON 46572).

DISTRIBUTION: *Sicariomorpha maschwitzi* is known only from lowland dipterocarp forest in the states of Selangor and Pahang where it is closely associated with the army ant *Leptogenys distinguenda*. MSH visited Ulu Gombak in 2010, but did not locate any specimens of this spider in forest leaf litter, although representatives of several other oonopid genera were present.

ACKNOWLEDGMENTS

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