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Source: Proceedings of the Entomological Society of Washington, 120(2):308-411.
Published By: Entomological Society of Washington
https://doi.org/10.4289/0013-8797.120.2.308
URL: http://www.bioone.org/doi/full/10.4289/0013-8797.120.2.308

PROC. ENTOMOL. SOC. WASH.
120(2), 2018, pp. 308–411

REVISION OF THE FIRE ANTS OF THE *SOLENOPSIS SAEVISSIMA* SPECIES–GROUP (HYMENOPTERA: FORMICIDAE)

urn:lsid:zoobank.org:pub:F387D696-11D6-4649-A9BC-82D8344F0764

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Abstract.—The fire ants of the *Solenopsis geminata* species-group of Trager (1991) are revised based on the morphology of worker larvae and of adult forms of workers, males, and gynes (winged or dealated members of the queen caste). The amount of intraspecific variation occurring in the adult males and gynes was equivalent to that of workers, making the taxonomic information gained from these castes no better than information from the workers. A new species, *S. metallica*, is described from southern Brazil, based on adult workers, adult gynes, males, and worker larvae. The following classification changes are made: *S. virulens* is placed in the *S. virulens* species-group; *S. tridens* and *S. substituta* are placed in the *S. tridens* species-group; ***S. metallica* new species**, *S. daguerrei, S. electra*, *S. hostilis, S. interrupta, S. invicta, S. macdonaghi, S. megergates, S. pusillignis, S. pythia, S. quinquecuspis, S. richteri, S. saevissima,* and *S. weyrauchi* are placed in the *S. saevissima* species-group; and *S. geminata, S. xyloni, S. amblychila, S. aurea, S. gayi,* and *S. bruesi* are left in the *S. geminata* species-group. The older classification, which designated complexes and subcomplexes, is abandoned. For the *S. saevissima* species-group, adults of males and gynes, as well as worker larvae, are described and diagnosed for each species. Diagnoses and keys (dichotomous and tabular) are provided for adult workers, the most commonly collected material, and distributions of the species are summarized.

Key Words: fire ants, red imported fire ant, black imported fire ant, *Solenopsis geminata* species-group, Myrmicinae, Solenopsidini

DOI: 10.4289/0013-8797.120.2.308

Fire ants are placed in the genus *Solenopsis* Westwood (Hymenoptera: Formicidae) in the subfamily Myrmicinae. There are approximately 190 described species of *Solenopsis* worldwide (Bolton 1995). Most of these species are characterized by small, monomorphic workers that form small colonies and can display a lestobiotic lifestyle, living in the nest walls of other ant species from which they steal food and brood (Thompson 1980, 1989; Pacheco and Mackay 2013). These habits have earned such *Solenopsis* species the name "thief ants." A smaller group composed of five species of *Solenopsis* are considered inquiline social parasites of other ant species. These inquiline social parasites live alongside the host queen, generally lack a worker caste, and their brood is made up only of sexuals (Buschinger 2009). Among the remaining *Solenopsis* are 20 New World species that differ greatly from the thief ants and social parasites in their biology. These species have larger, polymorphic workers, form enormously populous colonies, and are highly aggressive in their foraging and defensive habits. The painful sting wielded by the workers has earned such *Solenopsis* species the name "fire ants." Most fire ant species are Neotropical, although five species are native to North America (Chialvo et al. 2018). One of these (*Solenopsis geminata* (Fabricius), the tropical fire ant) and two of the Neotropical species (*S. invicta* Buren, the red imported fire ant, and *Solenopsis richteri* Forel, the black imported fire ant) have been inadvertently introduced to locations far from their native ranges. *Solenopsis geminata* has been introduced throughout the tropics worldwide (Wetterer 2011, Gotzek et al. 2015), *S. invicta* has been introduced to the United States and several other Pacific Rim countries (Lofgren 1986, Callcott and Collins 1996, Henshaw et al. 2005, Ascunce et al. 2011, Wetterer 2013), and *S. richteri* has been introduced to the United States (Lofgren 1986).

Solenopsis invicta and *S. richteri* have become economically important pests in the United States, where they invade lawns, pastures, and roadsides, attacking and stinging native animals, livestock, and humans when colonies are disturbed, and evidently out-competing native ants for food and nesting habitat (Lofgren et al. 1975, Jouvenaz 1990, Guillebeau et al. 2002, Tschinkel 2006). Annual economic losses in the United States attributable to the imported fire ants are estimated at $6 billion (Lard et al. 2006). Although the pugnacious nature of these exotic ants makes them undesirable inhabitants of areas that they have newly colonized, they nonetheless have become premier objects of study for ecologists and evolutionary biologists. For instance, fire ants offer one of relatively few well-documented cases of the formation of a hybrid zone in historical times (Vander Meer et al. 1985, Ross et al. 1987a, Shoemaker et al. 1996), which makes them a rich source of information for genetic studies of speciation (Baack and Rieseberg 2007, Nolte and Tautz 2010). Fire ants also show variation in the social organization of their colonies, some of which appears to be under simple genetic control (Krieger and Ross 2002, Wang et al.

2013), making them important model systems in the study of social evolution (Gotzek and Ross 2007, Smith et al. 2008, Robinson et al. 2008, Fischman et al. 2011). The flexibility demonstrated by some species in having either a single egg-laying gyne (monogyny) or multiple egg-laying gynes (polygyny) in a single colony has sparked comparative ecological and evolutionary studies about the causes and consequences of such variation (Vargo and Fletcher 1987, Ross and Keller 1995, Porter et al. 1997, Gotzek and Ross 2007, Huang and Wang 2014). *Solenopsis* also includes several social parasites that use various ant species as their hosts (Calcaterra et al. 2000, Davis and Deyrup 2006, Deyrup and Prusak 2008), a characteristic that is of great interest for studies of social evolution as well as integrated pest management. It is remarkable that in spite of the extensive research conducted on fire ants, no thorough taxonomic treatment or phylogenetic analysis of the group has been conducted. Only three phylogenetic analyses have been published, one based on morphology (Pitts et al. 2005), another using mitochondrial DNA (Shoemaker et al. 2006), and the third based on nuclear allozyme markers (Ross and Trager 1990). All suffer from limited taxon and/or character sampling and the appearance of poorly supported clades.

Historically, *Solenopsis* has been a taxonomically difficult group (Creighton 1930, 1950; Wilson 1952; Buren 1972; Trager 1991; Pacheco and Mackay 2013). In South America, where species diversity is highest, distinguishing *Solenopsis* species is exceedingly difficult due to a paucity of reliable characters that are constant within putative species yet differ between them. Frustration with this situation prompted Carlo Emery to call the group the *crux myrmecologorum* (Creighton 1930) and led Wilson (1952) to propose several synonymies, reducing the number of fire ant species to only three. Wilson apparently believed that the South American fire ants comprise nothing more than a large hybrid swarm of unstable variants. Further complicating matters is the fact that several of the species in North America (both native and introduced) hybridize extensively where their ranges overlap (Shoemaker et al. 1996, Helms Cahan and Vinson 2003, Ross and Shoemaker 2005).

Although the fire ants as a group have been revised fairly recently (Trager 1991), some unresolved taxonomic problems remain. Thus, we undertook a systematic study with several specific objectives in mind. The first was to develop additional morphological character systems to aid in the definition and identification of fire ant species by evaluating life stages and castes other than adult workers. Data from the diverse morphological character systems developed for this study also were used to produce a phylogenetic hypothesis for the *S. saevissima* species-group (Pitts et al. 2005). The second objective was to revise the classification of the fire ants following cladistic methodology, whereby only monophyletic groups are designated (sensu Pitts et al. 2005).

We acknowledge the limitations of a purely morphological approach in such a complex and intractable group. It is evident that our current morphological analyses capture only part of the (genetically) diagnosable diversity of the group (Ross and Trager 1990; Ross et al. 2007, 2010), and thus our results almost certainly represent a lower limit to the actual number of species. However, taxonomically and geographically restricted genetic approaches, while uncovering cryptic diversity within a few nominal species (nominal *S. richteri*, *S. invicta*, and *S. saevissima*), have confirmed the distinctiveness of the current morphologically recognized species (Ross and Trager 1990; Ross et al. 2007, 2010; Shoemaker et al. 2006). We caution against the overinterpretation of single locus datasets

(Shoemaker et al. 2006, Gotzek et al. 2007), which can be construed to suggest that some morphologically diagnosed species are not monophyletic and hence not "real" entities. Instead, we suggest using the multi-species coalescent accommodating incomplete lineage sorting and hybridization (Fujita et al. 2012) as a better model to understand genetic patterns in fire ants. We consider our morphological species concept a necessary, important, and invaluably practical first step to continued systematic efforts, which will ultimately require iterative and highly integrative taxonomic approaches and datasets to be utilized to test, refine, and correct our current morphological understanding of species limits in fire ants.

Taxonomic history of *Solenopsis*.—Westwood described the genus *Solenopsis* in 1840 for the type species, *S. geminata*. Creighton (1930) revised the genus and divided it into five subgenera, *Diagyne* Santschi, *Diplorhoptrum* Mayr, *Euophthalma* Creighton, *Oedaleocerus* Creighton, and *Solenopsis*. The subgenus *Solenopsis* included the typical polymorphic fire ants, with the other four subgenera considered the thief ants. Creighton's revision included all *Solenopsis* species except for those in the subgenus *Diplorhoptrum*, which is a large portion of the genus and, to date, these species have not been revised. Creighton based the delineation between the thief ant subgenera mostly on morphology of the gynes. Unfortunately, gynes were unavailable for many of the species included in his study and many remain unknown. There also are cases where the gynes differ substantially between certain species but the workers of these same species do not, and social parasitism cannot be ruled out. In light of these problems, it is undesirable to have a subgeneric classification that is based primarily on the gyne caste.

Ettershank (1966) realized these problems and synonymized the five subgenera. He also synonymized the related "satellite" genera *Lilidris* Kusnezov 1958, *Bisolenopsis* Kusnezov 1953, *Labauchena* Santschi 1930, and *Paranamyrma* Kusnezov 1953 under *Solenopsis*, but gave little explanation for this decision. He recognized three "natural" groups in *Solenopsis*: the fire ants, the social parasites, and the thief ants. The fire ants comprised species previously placed in the subgenus *Solenopsis*, the social parasites were species from the genera *Labauchena* and *Paranamyrma*, and the thief ants were species of all the other synonymized genera and subgenera.

Some higher-level taxonomic work has been done on *Solenopsis* since Ettershank. Baroni-Urbani (1968) resurrected the subgenus *Diplorhoptrum* and elevated it to the generic level, placing all thief ants in this genus. He based his decision on the genitalia of the common European species, *S. fugax* (Latreille), without knowledge of the New World thief ant fauna. Bolton (1987) presented arguments refuting Baroni-Urbani's decision as well as supporting Ettershank's (1966) other synonymies, and again made *Diplorhoptrum* a junior synonym of *Solenopsis*.

The thief ants in *Diplorhoptrum* were separated into five species-groups by Creighton (1930). This system was abandoned shortly afterward due to various shortcomings. For instance, the relationships of the species-groups were never resolved, and many recognized species were never placed in one of Creighton's species-groups. The most serious problem, however, was that subspecies sometimes were classified in different species-groups than their conspecifics. More recently, Trager (1991) placed all species of the old subgenus *Diplorhoptrum* in a single, informal species-group called the *S. fugax* group, but the justification for this change was unclear. He also discussed a *S. tenuis* subcomplex, which presumably belongs

in the *S. fugax* group, however, he did not specify which taxa belonged in the new subcomplex. Based on Trager's discussion of these new groups, one can only surmise that the *S. fugax* group was to contain other subcomplexes as well.

Moreno-Gonzalez (2001) treated the North American species of *Diplorhoptrum* and suggested many species-group changes. She resurrected Creighton's *S. azteca* species complex (sp. com.), and rearranged his remaining species complexes by placing the *S. laeviceps* and *S. basalis-tenuis* species complexes in the *S. molesta* sp. com. She placed Creighton's *S. westwoodi* sp. com. in the *S. fugax* sp. com. of Trager. However, as discussed above, Trager's *S. fugax* sp. com. presumably already contained all thief ants, so we must assume that she intended to place this group in the *S. fugax* subcomplex, which was left undefined by Trager. Moreno-Gonzalez (2001) also erected a new species complex for *S. succinea*—previously the sole member of the subgenus *Diagyne*—called the *S. succinea* sp. com. and erected the *S. minutissima* sp. com. to contain several species, described and undescribed, that were not treated by Creighton. She suggested that the species previously placed in *Euophthalma* should be split into two groups, the *S. globularia* sp. com. and the *S. nigella* sp. com., based on morphology of the postpetiole.

More recently, building on Moreno-Gonzalez' work, Pacheco and Mackay (2013) recognized eight species complexes in their monographic revision of New World *Solenopsis* (excluding the fire ants). While they retained Moreno-Gonzalez' *S. fugax*, *S. nigella*, and *S. globularia* sp. com., they expanded her *S. molesta* sp. com. to include Creighton's subgenus *Oedaleocerus*, subsumed the *S. succinea* sp. com. within the newly erected *S. wasmanni* sp. com., further recognized a *S. stricta* sp. com., and renamed the *S. azteca* and *S. minutissima* sp. com. as the *S. brevicornis* and *S. pygmaea* sp. com., respectively. Pacheco and Mackay further synonymized *Carebarella* with *Solenopsis*, which was subsequently supported by molecular phylogenetic analyses (Ward et al. 2015).

Compared to the New World, the Old World *Solenopsis* fauna has received much less attention. Galkowski et al. (2010) recognized four 'morphological' groups in France: the *S. fugax*, *S. debilior*, *S. lusitanica*, and *S. orbula* groups. It is not clear whether their concept of the *S. fugax* complex matches that of Pacheco and Mackay (2013) and Moreno-Gonzalez (2001) because the works do not reference each other. However, some concordance is expected given that Pacheco and Mackay explicitly state a morphological similarity between members of the New World *S. fugax* species complex and the Holarctic species *S. fugax*.

Recent molecular phylogenetic analyses confirm the placement of *Solenopsis* in the tribe Solenopsidini, its senior synonymy status with *Carebarella*, and identify its sister clade to be composed of *Tropidomyrmex* and *Kempfidris* (Ward et al. 2015), thus disproving previous earlier hypotheses aligning it with *Oxyepoecus* Santschi (Ettershank 1966, Bolton 1987).

The fire ants have been treated taxonomically several times (e.g., Creighton 1930, Wilson 1952, Buren 1972). In the latest revision, Trager (1991) grouped all of the fire ant species in the *Solenopsis geminata* species-group. Trager confirmed that all satellite genera, except *Lilidris*, were synonymous with *Solenopsis*, reaffirming Ettershank's synonymies. His treatment differed from

Ettershank's in proposing two independent derivations of social parasitism (in the former genera *Labauchena* and *Paranamyrma*) rather than a single origin within *Solenopsis*. Trager's revision included the four North American species, two hybrids, and 17 species from South America, three of which were described as new. One of these species, *S. virulens*, Trager considered not a true member of the fire ants, which would render his *S. geminata* species-group paraphyletic. This species was also notably ignored by Moreno-Gonzalez (2001) and Pacheco and Mackay (2013). The species that Trager recognized were distinctive both morphologically and genetically (Ross and Trager 1990), but several studies using genetic data have further complicated the problematic alpha-taxonomy of fire ants by suggesting the presence of cryptic species (Ross and Shoemaker 2005; Ross and Trager 1990; Ross et al. 2007, 2010; Chialvo et al. 2018).

The *Solenopsis* social parasites.—Because *Labauchena* and *Paranamyrma* were synonymized under *Solenopsis* (Ettershank 1966), *Solenopsis* now includes several species of social parasites. Two of these, *S. daguerrei* Santschi and *S. hostilis* Borgmeier, parasitize fire ants, whereas *S. solenopsidis* Kusnezov parasitizes thief ants (formerly *Paranamyrma*; Santschi 1930, Kusnezov 1954, Borgmeier 1959), and *S. phoretica* Davis and Deyrup and *S. enigmatica* Deyrup and Prusak parasitize *Pheidole* Westwood. The social parasites lead an especially interesting life style when compared to other *Solenopsis* species, because the parasitic gyne enters a heterospecific colony and usurps the reproductive role of the host queen, rather than initiating her own colony or joining a conspecific one (as in the case of polygyne fire ants).

Solenopsis daguerrei, S. solenopsidis and, perhaps, *S. hostilis* exhibit permanent social parasitism. *Solenopsis daguerrei* has been reported to kill the host queen in laboratory studies (temporary social parasitism; Bruch 1930), but has been found to allow the host queen to live in field studies (permanent social parasitism; Silveira-Guido et al. 1965). It may be that under certain conditions *S. daguerrei* exhibit either form of social parasitism. This species is known to be a social parasite of *Solenopsis invicta, S. richteri*, *S. macdonaghi*, and *S. quinquecuspis* (Santschi 1930, Briano et al. 1997, Calcaterra et al. 2000). Borgmeier (1959) reported *S. hostilis* as a parasite of *S. saevissima* (Smith), but did not gather any natural history information for the species. *Solenopsis solenopsidis* is reported to be a permanent social parasite of *S. clytemnestra* Emery (Kusnezov 1954). Hölldobler and Wilson (1990) reviewed social parasitism and included the known parasites and hosts of the *Solenopsis* social parasites. However, the host records they listed often disagreed with those of the primary publications (Bruch 1930; Santschi 1930; Borgmeier 1949, 1959; Kusnezov 1954, 1957; Silveira-Guido et al. 1965). *Solenopsis enigmatica* is known from only a single collection from *Pheidole dentata* Mayr and is hypothesized to be a temporary social parasite (Deyrup and Prusak 2008).

Materials and Methods

Loaning institutions and depositories of specimens.—Specimens used in this study were either borrowed from collections at the following institutions or have been deposited in them:

AEIC – American Entomological Institute, Logan, Utah, USA.

AMNH – American Museum of Natural History, New York, USA.

BMNH – The Natural History Museum, London, United Kingdom.
CNCI – Canadian National Collections, Ottawa, Canada.
DZUP – Coleção Entomológica Padre Jesus Santiago Moure, Curitiba, PR, Brazil.
EMUS – Entomological Museum, Department of Biology, Utah State University, Logan, Utah, USA.
FSCA – Florida State Collection of Arthropods, Gainesville, Florida, USA.
ICIB – Museu de Entomologia, Instituto de Biologia, FEIS/UNESP, Ilha Solteira, São Paulo, Brazil.
IMLA – Fundacion e Instituto Miguel Lillo, Tucumán, Argentina.
JPPC – J. P. Pitts Personal Collection, Millville, Utah, USA.
LACM – Los Angeles County Museum of Natural History, Los Angeles, California, USA.
MACN – Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.
MCZ – Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland.
MZSP – Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.
NHMB – Naturhistorisches Museum, Basel, Switzerland.
SDPC – Sanford D. Porter Personal Collection, Gainesville, Florida, USA.
UCDC – University of California, Davis, California, USA.
UGCA – University of Georgia Collection of Arthropods, Athens, Georgia, USA.
USNM – National Museum of Natural History, Washington, D.C., USA.

Sample collection.—Due to the taxonomic difficulties with the *S. saevissima* species-group, it was deemed important to obtain specimens from localities throughout each species' known range in order to infer the extent of geographically-based variation in character states within species. Furthermore, it was necessary to have all relevant castes and life stages available for study of novel character systems, and these specimens needed to be associated with adult workers from the same colony. Unfortunately, such material is not readily available from museums. Therefore, extensive sampling was conducted in South America during trips made by KGR and others in 1988, 1992, and 1998, by KGR and JPP in 2001, and by DG and GPC in 2015. These efforts produced new specimens from more than 1,500 colonies.

Other new material that was utilized for this study includes 118 colonies sampled in South America in 1991 by Sanford D. Porter (SDPC). This material provided adult workers and some alate (winged) gynes for study. The alcohol collection at the FSCA held samples of undetermined South American *Solenopsis* from more than 1,500 colonies that were collected primarily by William F. Buren. Material from the 1988 and 1992 collecting trips made by KGR was identified by James C. Trager and from the 2015 collecting trip was identified by DG and GPC. All other material in the study was identified by JPP.

Material examined.—Although the main focus of this study is the *S. saevissima* species-group, specimens of many other *Solenopsis* species were studied in order to give insight into the usual levels of interspecific variation within the genus and to indicate other possible characters of taxonomic importance in the *S. saevissima* species-group. Listed alphabetically below are all species examined for this study. Four forms of each species (adult males, adult gynes [winged or dealated members of the queen caste], adult workers, and larval workers) were studied unless otherwise indicated: *S. abdita* Thompson, *S. amblychila* Wheeler (adults, all castes), *S. aurea* Wheeler (adults, all castes), *S. bruesi*

Creighton (adult workers), *S. carolinensis* (Forel) (adult gynes and workers), *S. castor* Forel (adult workers), *S. clytemnestra* Emery (adult workers), *S. corticalis* Forel (adult gynes and workers), *S. daguerrei* Santschi (adult males and gynes), *S. electra* Forel (adult gynes and workers), *S. fugax* (Lat.) (adults, all castes), *S. gayi* (Spinola) (adults, all castes), *S. geminata* (Fabricius), *S. globularia littoralis* (Smith), *S. interrupta* Santschi, *S. invicta* Buren, *S. krockowi* Wheeler, *S. macdonaghi* Santschi, *S. megergates* Trager, *S. molesta* (Say), *S. nigella* Emery, *S. pergandei* Forel (adults, all castes), *S. picta* Emery, *S. pusillignis* Trager, *S. pythia* Santschi (adult gynes and workers), *S. quinquecuspis* Forel, *S. richteri* Forel, *S. saevissima* (Smith), *S. substituta* Santschi, *S. succinea* Emery (adult gynes and workers), *S. tennesseensis* Smith (adult males and workers), *S. tenuis* Mayr (adult workers), *S. texana* Emery (adult and larval workers), *S. tonsa* Thompson (adult workers), *S. tridens* Forel, *S. virulens* (adult workers), *S. westwoodi* Forel (adults, all castes), *S. weyrauchi* Trager (adult workers), and *S. xyloni* McCook.

Specimen preparation.—For scanning electron micrographs, the adults and larvae were dehydrated in ethanol and critical point-dried before being sputter-coated with gold. Several attempts were made to prepare specimens using hexamethyldisilazane (HMDS), as described by Nation (1983), but because this approach often caused damage to adult male and larval specimens it was discontinued.

For stereoscopic light microscopy, workers were air-dried after storage in 70%-85% ethanol. Air-drying specimens, especially males, directly from an alcohol solution often causes the head and mesosoma to collapse, resulting in low quality specimens. Therefore, males and gynes were saturated with amyl acetate and allowed to slowly air-dry in a fume hood. This technique prevented fragile specimens from collapsing and also helped to maintain their natural color.

Morphological terminology and measurements for adults.—Several features of the head were used in this study. The positions of the compound eyes (ce) and ocelli (oc) are important and are labeled in Figs. 1, 4, 9, and 10. The apices of the clypeal carinae (cc) (Fig. 1) are called clypeal teeth. Sometimes paracarinal teeth are present lateral to clypeal teeth, as is a small median tooth (mct) between the clypeal teeth (Fig. 1). Often a linear or triangular shaped, darkly pigmented area, called a median frontal streak (fs = frontal median streak), is present on the head (Fig. 50).

The mesosoma of the worker is divided into several well-defined regions. Visible in dorsal view are the pronotum (prn), mesonotum (mes), metanotum (met), and the propodeum (ppm) (Fig. 2). In lateral view, the profiles of these, as well as the mesopleura (msp), are visible (Fig. 3). The mesosoma of males and gynes is divided into additional sclerites. The following are usually visible: pronotum (prn), mesonotum (mes), parapsidal lines (pl), scutellum (sct), axillae (ax), metanotum (met) and propodeum (ppm) (Figs. 2, 5, 9). The mesopleuron is divided into a dorsal sclerite, the anepisternum (an), and a ventral sclerite, the katepisternum (k) (Figs. 5, 9). The wing venation terminology used here (see Fig. 11) is based on the system proposed by Comstock (1918), Ross (1936), and Mason (1986).

The metasoma has a two-segmented petiole. These two segments are referred to as the petiole (pt) and the postpetiole (ppt) (Figs. 5, 9). The dorsal surface of each of the segments is modified as an upwardly directed scale or as a rounded node when viewed laterally.

The remaining portion of the metasoma, the gaster, is comprised of four segments, each bearing a dorsal plate (tergite) and ventral plate (sternite). The tergites and sternites covering these segments are numbered from anterior to posterior as T1, T2, T3, T4, and S1, S2, S3, and S4, respectively.

The male genitalia are composed of several structures. The outermost structures are the parameres. Mesad of the parameres are the volsellae (Fig. 74). Each volsella has a single cuspis (cus) and digitus (dig) (Fig. 74). The innermost organ is the aedeagus, which has an apodeme (ap) projecting dorsally (Fig. 74) (Snodgrass 1941).

Measurements of adult *Solenopsis* were made at 50X or 100X on a stereo dissecting microscope with either an ocular micrometer or a digital micrometer. All measurements are reported in millimeters. Measurements of holotypes are listed separately in parentheses. Head measurements were made with the head held in dorsal view, positioned so that the greatest straight-line distance between the midpoints of the clypeal border and the vertex was achieved. The viewing axis was approximately perpendicular to the surface of the frons. Abbreviations and definitions for measurements and indices are given below:

L Total length of the ant, measured in lateral view with the head in a natural hypognathous position. This measurement is not as accurate as the DML measurement (below) due to distortion of the metasoma that is caused by alcohol preservation and subsequent drying of specimens.

HW Maximum width of the head, including the eyes, measured in full-face, dorsal view (Fig. 6).

VW Width of the posterior portion of the head (vertex), measured along a line drawn through the lateral ocelli, with the head in full-face, dorsal view (Fig. 6).

HL Midline length of head, measured in full-face, dorsal view, from the anterior clypeal margin to the midpoint of a line drawn across the occipital margin (Fig. 6).

EL Maximum length of compound eye, measured with the head in full-face, dorsal view (Fig. 6).

OD Ocellar distance, measured as the distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli. Measured with the head in full-face, dorsal view (Fig. 6).

OOD Ocellocular distance, measured as the distance from the middle of the median ocellus to a line drawn across the posterior margins of the compound eyes (this distance is negative in value if the posterior margin of the compound eye exceeds the median ocellus) (Fig. 6).

LOW Maximum width of the lateral ocelli.

MOW Maximum width of the median ocellus (Fig. 6).

CD Distance from the anterior clypeal margin to a line drawn across the anterior margins of the frontal carinae (Fig. 6).

MFC Minimum distance between the frontal carinae, measured with the head in full-face, dorsal view.

EW Maximum width of compound eye, measured along its short axis, in an oblique dorsolateral view of the head.

SL Length of scape, excluding the radicle (Fig. 6).

SW Maximum width of the scape, measured only for males.

PDL Maximum exposed length of the pedicel, excluding the concealed basal articulating area.

PEW Maximum width of the pedicel, measured only for males.

LFl Maximum exposed length of the first flagellomere.
LF2 Maximum exposed length of the second flagellomere.
LF3 Maximum exposed length of the third flagellomere.
WF1 Maximum width of the first flagellomere.
FL Maximum exposed length of the fore femur, measured in posterior view.
FW Maximum measurable width of the fore femur, measured from the same view as FL, at right angles to the line of measurement of FL.
PW Maximum width of the pronotum in dorsal view, measured only for the major workers.
MW Width of the mesonotum in dorsal view, anterior to tegulae.
DML Diagonal length of the mesosoma, measured in lateral view along a diagonal line drawn from the anterior base of pronotum (exclusive of anterior "cervical flange" which is often concealed) to posterior edge of metapleuron (Fig. 7).
PL Petiole length, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (Fig. 8).
PND Petiolar node distance, distance from the anterior margin of petiole to a vertical line drawn through the petiole at the highest point of the node, measured from the same view as PL (Fig. 8).
PH Maximum height of the petiole, measured in lateral view at right angles to PL, but excluding the anteroventral process (Fig. 8).
PPL Length of the postpetiole, measured in lateral view, from the anterior peduncle of the postpetiole to the point of contact with the fourth abdominal tergite.
DPW Maximum width of the petiole, measured in dorsal view.
PPW Maximum width of the postpetiole, measured in dorsal view.
PHB Height of postpetiole, as measured from attachment of postpetiole to T1.

Indices calculated from the preceding measurements include the following ratios:

CI Cephalic index: HW/HL
OI Ocular index: EW/EL
REL Relative eye length: EL/HL
REL2 Relative eye length, using HW: EL/HW
OOI Ocellocular index: OOD/OD
VI Vertex width index: VW/HW
FCI Frontal carinal index: MFC/HW
CDI Clypeal distance index: CD/HL
SI Scape index: SL/HW
SI2 Scape index, using EL: SL/EL
SI3 Scape index, using LF2: SL/LF2
FI Fore femur index: FW/ FL
NI Petiole node index: PND/PL
PLI Petiole length index: PH/PL
PHI Petiole height index, using PPL: PH/PPL
PWI Petiole width index: DPW/PL
PPWI Postpetiole width index: PPW/PPL
PPWB Postpetiole width index, using PHB: PPW/PHB

The measurements for workers reported here differ from those of Trager (1991) as follows: the abbreviation DML is used instead of AL to denote diagonal length of the mesosoma, REL is used instead of OI for relative eye length, and CI, SI, and REL are not converted to percentages. Measurements of head length reported here include the length of the clypeal teeth.

Morphological terminology and measurements for larvae—Only fourth instar worker larvae or prepupae were used for the study. The fourth instar is discernible by the completely sclerotized mandibles (Petralia and Vinson 1979). Larvae were prepared as outlined in Wheeler (1960). The morphological terminology

follows that of Wheeler and Wheeler (1976) (Fig. 12), however, several rows of setae also were named as follows: occipital setal row (= posterior row of setae on head) (Fig. 13), first setal row of the vertex (Fig. 14), and second setal row of the vertex (Fig. 15). Measurements were made at 400X or 1000X on a compound microscope. Length was measured using the spiracles as in Wheeler and Wheeler (1976).

Standard taxonomic descriptions are provided for adult males, adult gynes and larval workers in the *S. saevissima* species-group. A standard dichotomous key is provided that incorporates useful characters from adult males and gynes. A tabular key is also provided.

Results

Solenopsis saevissima species-group.—Diagnoses for the gynes, males, and larvae of the non-parasitic species of the *S. saevissima* species-group are given below. Due to the drastic modification in body form in the social parasites, descriptions of each species are not provided here. Instead, the description of *S. daguerrei* serves to distinguish all socially parasitic species from the remainder of the species-group. *Solenopsis hostilis* has been included in the key for completeness, although no specimens were found during this study and the species apparently has not been collected since its original description. To avoid repeating the descriptive treatment of the workers by Trager (1991), only diagnostic combinations of characters for the major workers are given here.

Gyne.—*Head:* Usually broader than long, quadrate, wider posterior to eyes than anterior to them, sides weakly convex from eyes to occipital angles, straight to slightly convex ventral to eyes and meeting anterior border of head at a sharp angle (Fig. 1). Occipital angles distinctly defined, occiput flat with narrow, shallow median impression. Occipital furrow clearly to weakly defined. Frontal furrow indistinct. Clypeus projecting, carinal teeth very stout and acute, clypeus with anterior shallow concave impression between carinal teeth (Fig. 1). Paracarinal teeth small (Fig. 20), often poorly defined and, in some cases, absent (Fig. 1). Median carinal tooth well developed (Fig. 1) to indistinct (Fig. 20). Mandibles with outer border convex, masticatory border with four teeth, fourth tooth much smaller than others (Fig. 1). Eyes large, strongly convex, ovate (Figs. 1, 4). Antennal scape in repose reaches or passes lateral ocellus. Antenna with 11 segments (10 segments sometimes in *S. pythia*) with 2-segmented club.

Mesosoma: Robust, elliptical, only slightly narrower than head (Fig. 2). In lateral view, mesonotum with convex anterior portion that overhangs pronotum and with straight posterior half (Fig. 5). Scutellum as high or higher than mesonotum, slightly convex with short perpendicular posterior face, posterior face depressed posteromedially (Fig. 5). Angle of propodeum well defined but obtuse, basal face shorter than declivous face (Fig. 5). Mesosternum large and subglobose ventrally (Fig. 5). Wings hyaline with yellow to brown veins (veins hyaline in *S. daguerrei* and sometimes in *S. electra*).

Metasoma: In lateral view, petiolar node obtusely triangulate, profile of peduncle flattened anteriorly, convex posteriorly (Fig. 5). Petiole with median longitudinal carina on anterior 0.50–0.75 of ventral surface (Fig. 5). Postpetiole evenly convex (Fig. 5). Lateral faces of postpetiole concave to slightly convex. Petiolar and postpetiolar spiracles are tuberculate in some cases. Petiole with basal transverse carina, appears tooth-like

in lateral view. In dorsal view, nodes are very strongly transverse, and postpetiole wider than petiole. In cephalic view, petiole sometimes with distinct median lobe, postpetiole broader than high, highest medially.

Male.—*Head:* Trapezoidal, maximum head width greater than length (Fig. 10). Eyes very large, strongly convex, ovate, occupying more than 0.5X side of head, their anterior border almost reaching insertion of mandible (Fig. 10). Eyes normally with setae protruding from between ommatidia. Ocelli small to large and prominent, elliptical (Fig. 10), lateral ocelli marking boundary of occiput with shallow concave depression between them. Anterior edge of clypeus approximately straight (Fig. 10). Clypeus with blunt, central lobe in lateral view (Fig. 9). Mandibles small, straight, tridentate, third tooth small, sometimes indistinct. Antennal scape longer than broad, roughly cylindrical. Pedicel subglobose, broad or broader than scape or flagellomeres (Fig. 10). First flagellomere >2.0X as long as broad, second flagellomere <1.6X as long as broad, remaining flagellomeres progressively decreasing in width.

Mesosoma: Robust, elliptical, width less than twice that of head. In lateral view, anterior part of mesonotum greatly swollen and overhanging pronotum (Fig. 9). Propodeum rounded, declivous face perpendicular and flat except with distinct to indistinct median longitudinal depression (Fig. 9), basal face strongly convex transversely and longitudinally. Mesosternum large and subglobose ventrally (Fig. 9). Wings hyaline with hyaline to yellow veins.

Metasoma: Node of petiole short in lateral view with acute dorsum (Fig. 9); anterior face not sharply separated from thick peduncle, posterior face perpendicular laterally, gently curving medially (Fig. 9). In cephalic view, dorsum of node with shallow median impression, sometimes bilobate. Postpetiole in lateral view as high as node of petiole, anterior face, dorsum and posterior face rounded (Fig. 9). In dorsal view, both nodes very transverse, postpetiole is approximately 1.0–3.0X as broad as long and as wide as node of petiole. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia strongly retracted (Fig. 74). Cuspis laterally flattened, lobate in lateral view and lacking setae (Fig. 74). Digitus short and cylindrical, with apical setae and sometimes with lateral setae (Fig. 74). Ventral portion of volsellar plate apically produced, clothed with several setae (Fig. 74). Ventral surface minutely dentate with rows of triangular teeth (Fig. 74). Ventral margin of aedeagus with many anteriorly directed triangular teeth (Fig. 74). Aedeagus with anteroventrally directed triangular projection (Fig. 74). Apodeme of aedeagus directed perpendicular to slightly obtuse to ventral surface (Fig. 74).

Sculpture and Pilosity: Punctures fine and numerous, < 0.001mm wide. Antenna covered with dense, short, white pubescence. Pubescence on legs shorter and stouter than on body.

Fourth instar worker larva.—*Head:* Antenna with 2–3 sensilla, each bearing spinule (Fig. 12). Head setae sparse (Fig. 12). Cranial width equal to or slightly broader than long (Fig. 12). Labrum small, short, slightly narrowed medially (Fig. 12). Mandible heavily sclerotized with two parts (Fig. 12): 1) stoutly sickle-shaped body, with three apical teeth not in same plane; 2) straight medial blade forming 0–5 teeth that decrease in size dorsally. Ventral border of labrum weakly concave with ventral corners rounded (Fig. 12). Labrum bearing 2–3 coarse isolated spinules near

each ventrolateral corner. Maxilla with sclerotized band between cardo and stipes. Labium with patch of spinules dorsal to palpus. Labium with small lateral sclerotized bands. Opening of sericteries a long transverse slit (Fig. 12).

Body: Stout. Prothorax bent ventrally at right angles forming very short stout neck. Remainder of body straight. Abdominal diameter greatest at fourth somite. Both ends of body broadly rounded. Dorsal profile of body curved, ventral surface nearly flat. Anus ventral. Leg and wing precursors present. Segmentation indistinct. Integument of ventral surface of thorax and first three abdominal somites with few short transverse rows of minute spinules. Body setae numerous, short, and uniformly distributed. Body setae of two types: 1) simple, slightly curved with alveolus and articular membrane, 4–12 in transverse row on ventral surface of each thoracic somite and anterior abdominal somites; 2) bifid, branches more or less perpendicular to base, tips recurved occurring on various regions of body; often setae posterior to head on thoracic dorsum differ slightly from other setae. Setae on ventral surface with alveolus and articular membrane.

Length: Approximately 2.3–3.8 mm.

Comments.—Indices calculated from adult measurements are provided for gynes and males in Tables 5 and 6, respectively.

Identification of fire ants.—The characters used here for the identification of fire ants are those normally used for myrmecological taxonomic work. The most useful characters for the workers are size, coloration, head shape, and postpetiolar shape. After thorough examination of males and gynes, we feel that the workers are superior to sexuals for distinguishing the various species. The gynes and males of many species are very similar and in some cases are indistinguishable between species without a reference collection. Some gyne characters such as pilosity or sculpturing are highly variable, as they are for workers, but sometimes can be useful. Size, coloration, and head shape are also of some use in identification of the gynes. Coloration and size of males tend to be very similar for many species, making these characters of limited value for identification purposes. Some species, however, have reliable male sculpture characters.

Geographical distribution can be useful for identifying fire ants but can be biased by several factors. As mentioned by Trager (1991), fire ants are easily transported to new regions, which makes geographical information valuable only as a complement to other data. Also, the available distributional data for most species are patchy and are almost certainly incomplete; therefore, some species could have much broader ranges than are reported here. On the other hand, occurrence records for fire ants are often incorrect due to misidentifications or habit of assigning specimens to the most common species (e.g., *S. invicta* or *S. saevissima*) and reported ranges can hence be grossly overestimated. We therefore deliberately omitted use of other sources (Antweb, Antmaps) in the construction of maps to avoid aforementioned errors. Consequently, we present maps as conservative range estimates based mainly on our own collections and, when feasible and sufficiently different from our collections, the type localities. For rarer species (e.g., *S. pythia*, *S. weyrauchi*, or *S. electra*), we also included reliable collection site records from Trager (1991).

In this work, an effort was made to follow the format of the descriptions of prior *Solenopsis* authors to facilitate

future systematic work on the group. As such, adult worker descriptions follow the format of Trager (1991), adult male and gyne descriptions follow the format of Creighton (1930), and larval descriptions follow the format of Wheeler and Wheeler (e.g., Wheeler and Wheeler 1976, 1986).

KEY TO THE *SOLENOPSIS SAEVISSIMA* SPECIES-GROUP

(Modified from Trager 1991)

This key is not intended for the identification of minor workers. To fully utilize all of the available information and to obtain an accurate identification, one should take a sizeable sample of workers, males, gynes and larvae from a colony. Special effort should be made to obtain major workers. A positive identification may be impossible for colonies lacking such individuals, such as those sampled soon after founding. Tabular keys to the major workers, gynes, and males are presented in Tables 1, 2, and 3, respectively. These should be consulted especially when a colony sample does not include representatives of all forms.

1. Gyne and male: small, 5.0 mm or less in length; sculpture reduced, body polished; metapleuron fused to propodeum. Gyne: parapsidal lines absent; clypeus lacking longitudinal carinae and apical teeth (Fig. 196); posterior margin of head broadly emarginated with posterolateral corners angulate (see below and Fig. 195) (social parasites lacking workers) 2

Photo of casent0911238 by Alexandra Westrich. From www.antweb.org [Accessed 20 July 2017].

– Gyne and male: larger, greater than 5.0 mm in length; sculpture not reduced, present at least on propodeum, petiole and postpetiole; metapleuron not fused to propodeum. Gyne: parapsidal lines present; clypeus with longitudinal carinae terminating in teeth apically (Figs. 20, 22, 24, etc.); posterior margin of head narrowly emarginated medially with posterolateral corners rounded (see below and Figs. 20, 22, 24, etc.) (free living with workers) 3

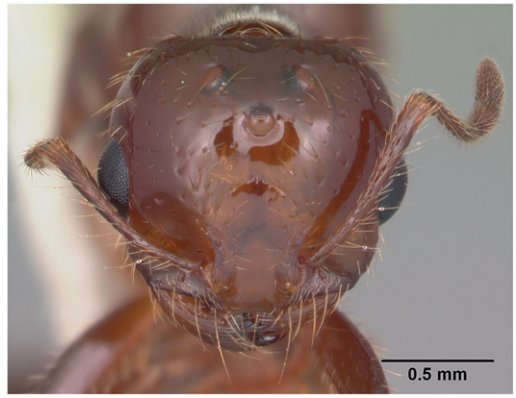
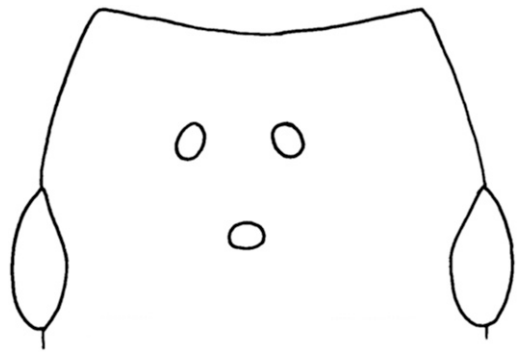


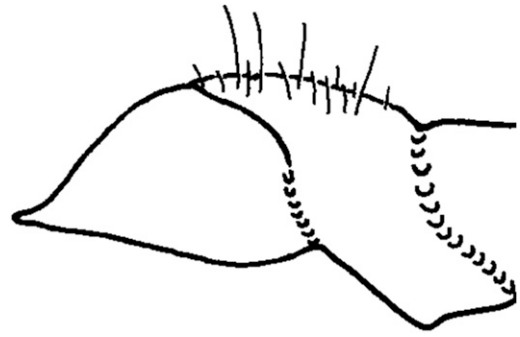
Photo of casent0104504 by April Nobile. From www.antweb.org [Accessed 20 July 2017].

2(1). Gyne: posterior margin of head angulate (see below and Fig. 195), lobate in lateral view (Fig. 196). Distribution: south from Mato Grosso do Sul, Brazil to Buenos Aires Province, Argentina (Fig. 203) . . . . . *S. daguerrei*



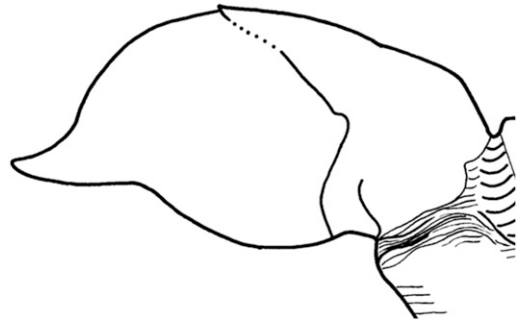
– Gyne: posterior margin of head rounded, not lobate in lateral view. Distribution: Jacarepaguá, Rio de Janeiro, Brazil southwest to Rolândia, Paraná, Brazil . . . . . *S. hostilis*

3(1). Major worker: pronotum low and nearly flat or weakly convex in profile (see below); metasoma black, legs yellow (yellowish brown in darker specimens), head and mesosoma ranging from clear yellowish red with some black or brownish black markings in the occipital area to uniformly brownish black (especially in vicinity of Cochabamba, Bolivia). Distribution: northwestern Argentina to Bolivia in Andean foothills (Fig. 201) . . . . *S. electra*

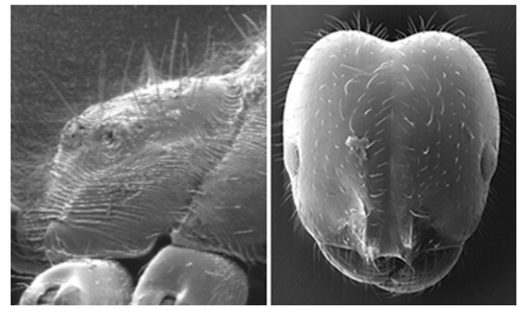


Drawing by James Trager. From Trager 1991 J. New York Entomol. Soc. (Fig. 42).

– Major worker: pronotum higher, angular or strongly convex in profile (see below); color variable but never with metasoma completely black and with yellow legs 4

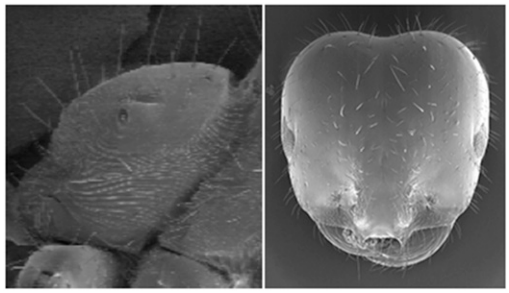


4(3). Major worker: area immediately posterior and dorsal to metapleural spiracle finely punctate or striato–punctate (see below and Fig. 140); largest major workers with head strongly cordate (see below and Fig. 141). Male: weak to distinct mesonotal maculations present; ocelli moderate to large, OOI 0.80–1.26, normally OOI<1.00 (Fig. 65). Distribution: southern half of Mato Grosso, western Mato Grosso du Sul, Brazil (Fig. 203) . . . . . *S. pusillignis*

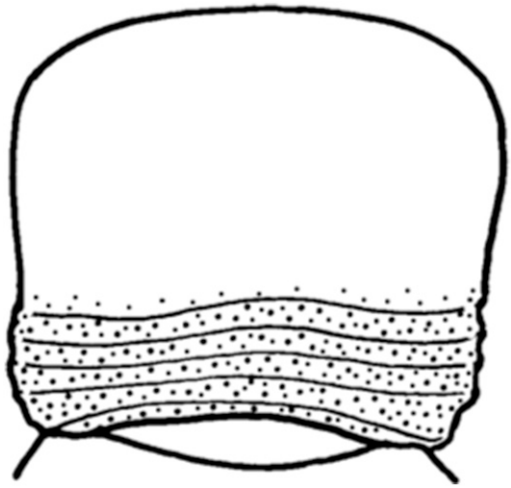


– Major worker: area surrounding metapleural spiracle shiny and smooth (see below and Figs. 130, 132, 134, 136, 138, 142, 144, 146); largest major workers with head moderately

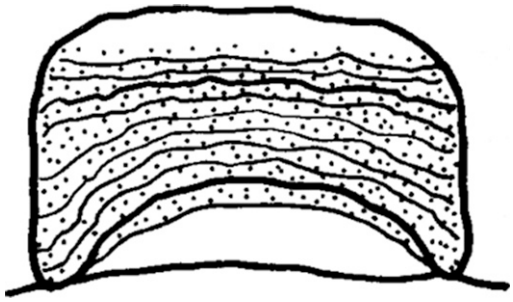
(see below and Figs. 131, 133, 137, 139) to weakly cordate (Figs. 135, 143, 145, 147). Male: mesonotal maculations absent; male ocelli moderate to small, OOI > 1.00 (Figs. 57, 59, 61, 63, 67, 69, 71) 5



5(4). Major worker: posterior face of postpetiole as high or higher than broad (see below) 6



– Major worker: posterior face of postpetiole broader than high (see below) 11

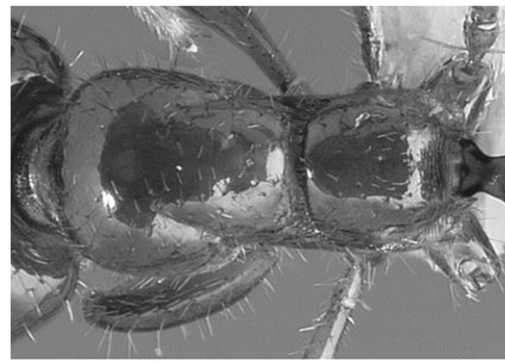


6(5). Major worker: pronotal dorsum in posterodorsal view medially concave; anterolateral bosses giving squared-off appearance to anterodorsal rim of pronotum (see below); head uniformly

brownish black; mandibles usually brownish yellow; frons without dark median streak or this barely distinct from remainder of frons. Male: often with distinct tuberculate postpetiole, tubercle height ≥ 1.5X width at base, tubercles glabrous; OOI < 1.35. Distribution: southeastern Brazil to central eastern Argentina (Fig. 203); introduced into southeastern United States . . . . . *S. richteri*

Photo of casent0103101 by April Nobile. From www.antweb.org [Accessed 20 July 2017].

– Major worker: pronotal dorsum in posterodorsal view usually flat or weakly convex; pronotum lacking anterolateral bosses (see below); or if bosses present, head yellowish, at least near mandibular bases and clypeus and often more extensively yellowish; Male: often lacking distinct tuberculate postpetiole, tubercle height ≤ 1.5X width at base, tubercles granulate or rugose; OOI > 1.4 7



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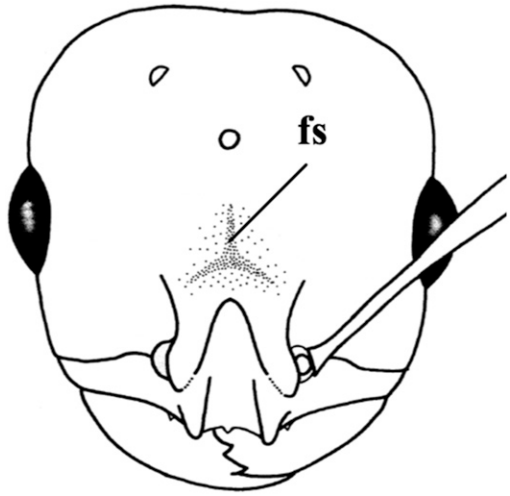
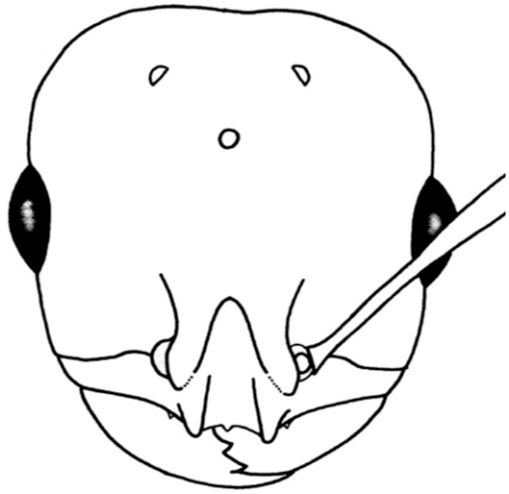
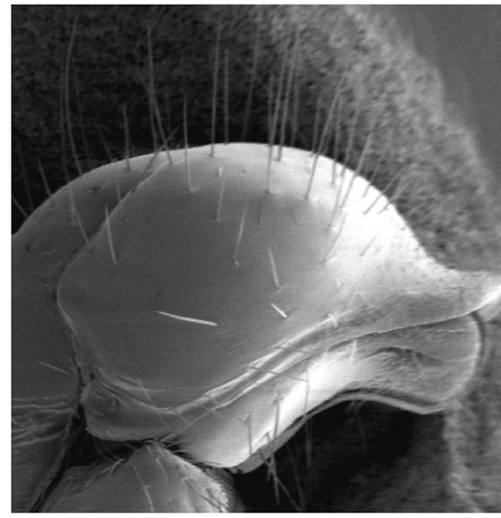
7(6). Major worker: median streak (frontal streak, fs) usually present (see below and Fig. 50). Gyne: mesonotal maculations present (Fig. 52) (gyne of *S. weyrauchi* was not examined) 8



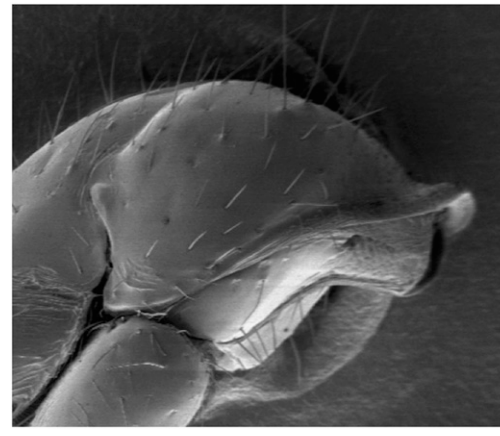
– Major worker: median frontal streak usually absent (see below). Gyne: mesonotal maculations usually absent 10



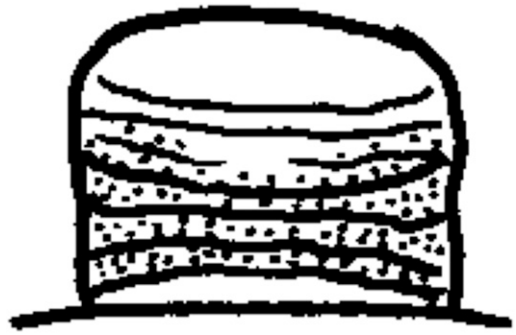
8(7). Major worker: large with DML exceeding 1.75 mm (sometimes over 2.0 mm) in largest workers of most series; piligerous foveolae small (<0.01 mm, see below). Gyne: if T1 maculation present, it sometimes has distinctly defined posterior margin. Distribution: normally lowlands species in western Argentina and Bolivia (Fig. 202) . . . . . *S. interrupta*



– Major worker: small with DML rarely in excess of 1.7 mm in even largest workers of most series (rarely up to 1.80 mm); piligerous foveolae large (0.005–0.03 mm, see below); Gyne: if T1 maculation present, it lacks a distinctly defined posterior margin (gyne of *S. weyrauchi* was not examined). Distribution: normally high elevation species 9

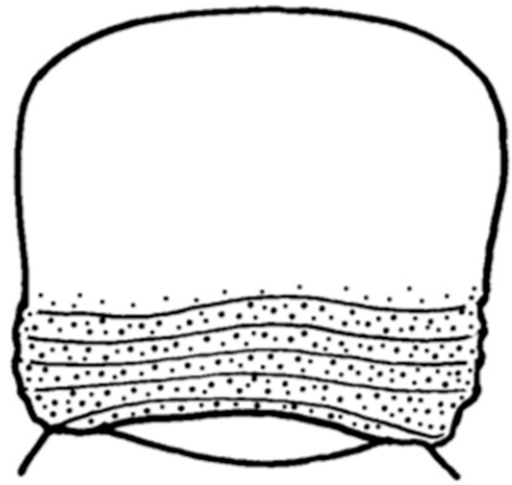


9(8). Major worker: cephalic piligerous foveolae small (<0.01 mm); rear face of postpetiole with striae present on lower 0.50–0.75 (see below); mandibles with 5–6 costulae; katepisternum of mesopleuron not or only weakly defined dorsally by finely striate furrow. Gyne unknown. Distribution: Peruvian, Bolivian, and Argentinian Andes, 2,000–3,500 m elevation (Fig. 201) . . . . . *S. weyrauchi*



Drawing by James Trager. From Trager 1991. J. New York Entomol. Soc. (Fig. 81).

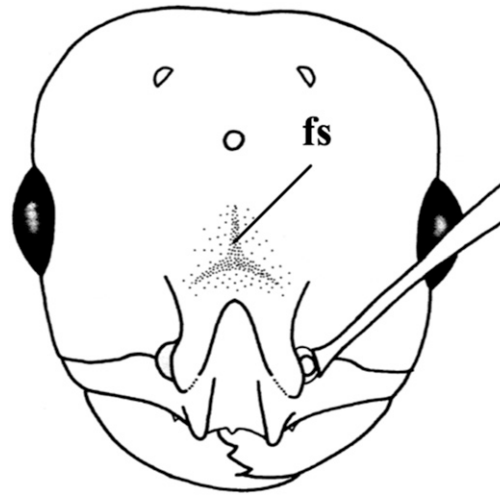
– Major worker: cephalic piligerous foveolae large (0.01–0.03 mm); scape long, almost reaching the vertex of the head; rear face of postpetiole with striae present on lower 0.25–0.33 and smooth and shiny upper (see below and Fig. 19); mandibles with 10–12 costulae, weak to obsolescent medially; katepisternum of mesopleuron weakly to distinctly defined dorsally by finely striate furrow (Fig. 18); promesonotal suture angulate medially, sometimes projecting upward (Fig. 18); first sternite of gaster with anterior projections, visible in dorsal view. Gyne: large piligerous foveolae (0.01–0.03 mm) present on head; interfoveolar areas of head striate; ocellar triangle striate (Fig. 20); median cell open by loss of m-cu cross vein (Fig. 89); postpetiole glabrous on upper 0.75 (Fig. 44). Distribution: southern and southeastern Brazil, northeastern Argentina (Fig. 201) . . . . . *S. metallica* n. sp.



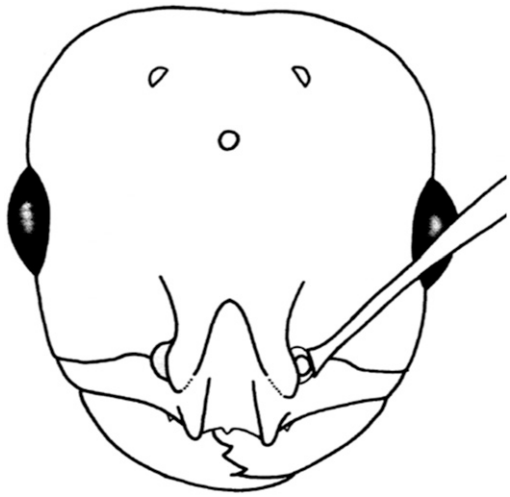
10(7). Major worker: larger, DML 1.4–l .6 mm (rarely 1.7 mm) in large workers; piligerous foveolae usually very small, inconspicuous. Gyne: cephalic pilosity approximately 0.30–0.33 mm long; metasoma pilosity arising from small, inconspicuous foveolae; median furrow on posterior 0.33 or less of mesonotum; bidentate metasternal process present. Larger species. Distribution: Orinoco drainage, Guianas, Amazonia and along rivers in bordering regions, also southeastern and eastern Brazil (Fig. 201) . . . . . *S. saevissima*

– Major worker: smaller, DML < 1.4 mm in even the largest workers; piligerous foveolae on head and pronotum sometimes conspicuous, 5–l0X as wide as base of seta. Gyne: cephalic pilosity about 0.15–0.20 mm long (Fig. 53); metasoma pilosity arising from conspicuous piligerous foveolae nearly or actually as large as those of head and mesosoma (Fig. 51); median furrow on posterior 0.33–0.50 of mesonotum (Fig. 51); bidentate metasternal process absent. Smaller and much rarer species. Distribution: Mato Grosso do Sul to southeastern Brazil and Misiones, Argentina (Fig. 202) . . . . . *S. pythia*

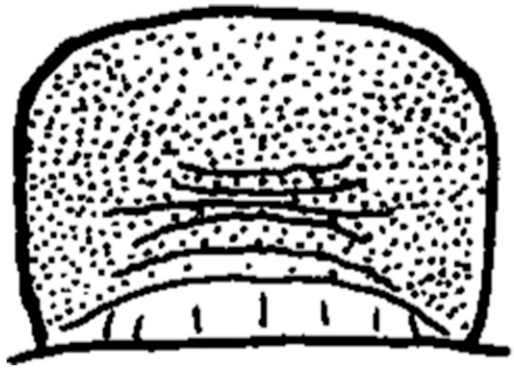
11(5). Major worker: smaller, DML rarely in excess of 1.70 mm in even largest workers of most series; median (frontal) streak (fs) present (see below). Gyne: frontal streak present (as in Fig. 50), sometimes faint; postpetiole usually completely sculptured, only extreme dorsum lacking striae (Fig. 42). Male: head usually completely granulate, shagreened; gena moderately to coarsely rugose. Distribution: lowland species, western Amazonia, south through Mato Grosso, eastern Bolivia, Paraguay and southeastern Brazil to Santa Fe Province, Argentina (Fig. 203); introduced into Southern United States . . . . . *S. invicta*



– Major worker: larger, DML exceeding 1.75 mm (up to over 2.0 mm) in largest workers of most series; median frontal streak usually absent (see below). Gyne: median frontal streak usually absent; postpetiole usually completely sculptured, only highest portion lacking striae (Figs. 41, 43). Male: head usually incompletely granulate, glabrous anterolaterally of median ocellus, not shagreened; gena striate to granulate 12

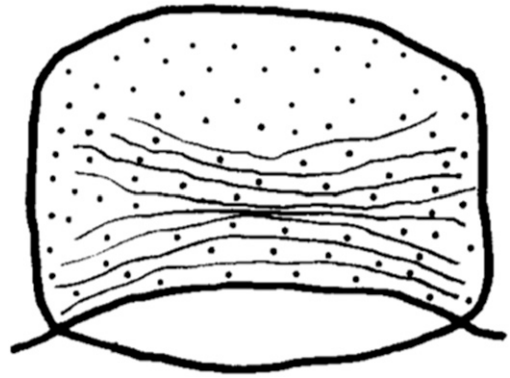


12(11). Major worker: color mainly red to orange; mesosoma pilosity usually decumbent, not curved; transverse striae or rugae on rear face of postpetiole usually lacking, or faint, punctate or shagreened (see below); outer surface of mandible usually shining medially, costulae obsolescent. Distribution: Uruguay, Entre Rios Province and adjacent parts of bordering provinces in Argentina; apparently introduced at Cochabamba, Bolivia (Fig. 202) . . . *S. macdonaghi*



Drawing by JamesTrager. From Trager 1991 from J. New York Entomol. Soc. (Fig. 63).

– Major worker: color brown to nearly black; mesosoma pilosity erect, longest setae usually curved; sculpture on rear face of postpetiole with conspicuous transverse striae or rugae on lower 0.66–0.75, punctate or shagreened (see below); outer surface of mandible with costulae, sometimes obsolescent medially 13



13(12). Major worker: small with HL 1.45–l .55 mm; eye of largest workers relatively (and often absolutely) larger, REL 0.18–0.20 in large majors; head mostly dark brown to brownish black; in contrast, distal portion of clypeus, head near base of mandible, and (usually) area around dark median frontal sulcus distinctly lighter yellowish brown. Male: lateral faces of scutellum weakly to distinctly striate. Distribution: Buenos Aires and La Pampa Provinces, Argentina, Uruguay, north to Santa Catarina, Brazil (Fig. 202) . . . . . *S. quinquecuspis*

– Major worker: large with HL 1.6–1.75 mm in largest workers; eye of largest workers relatively (and often absolutely) smaller than above species, REL 0.16–0.18 in large majors; head uniform reddish brown or gradually fading anteriorly to a slightly lighter reddish brown; distal portion of clypeus, sides of head anterior to eye, and frons faintly or not at all chromatically distinct from posterior portions of head, median frontal streak absent or very faint. Male: lateral faces of scutellum glabrous. Distribution: Southern Brazil (Fig. 202) . . . . . *S. megergates*

Descriptions

Solenopsis metallica Pitts, Camacho, Gotzek, McHugh, and Ross, new species

urn:lsid:zoobank.org:act:D0AC4A84-95B8-4E9D-9FA9-FBB76636ABDA

(Figs. 16–20, 44, 89)

Solenopsis altipunctata Pitts, 2002: 63. *Nomen nudum.*

Solenopsis species 'A': Krieger and Ross 2005; Shoemaker et al. 2006.

Solenopsis altipunctata Gotzek et al. 2007. *Nomen nudum.*

Solenopsis saevissima 'southern highlands': Ross et al. 2010.

Holotype.—Brazil: Santa Catarina State, Rt.166 ca 22 km north of Santa Cecilia, Serra Geral, 1200 m, .xi.1998, K. G. Ross, M. C. Mescher, D. D. Shoemaker, and L. Keller, n. G-84 [USNM: 1 worker, USNMENT01126728].

Paratypes.—Brazil: Santa Catarina State, Rt.166 ca 22 km north of Santa Cecilia, Serra Geral, 1200 m, .xi.1998, K. G. Ross, M. C. Mescher, D. D. Shoemaker, and L. Keller [MZSP: 1 worker, G-83, USNMENT01126729], [DZUP: 1 worker, G-84, USNMENT01126730], [EMUS: 1 worker, G-84, USNMENT-01126731], [UGCA: 1 worker, G-83, USNMENT01126732]. Brazil: Paraná State, Edge of Ponto Grossa, median of Rt.PR-513, 20.xi.2015, G. Camacho and

D. Gotzek, n. PR15-084 [USNM: 1 male, USNMENT01126733; 1 gyne, USNMENT01126734].

Diagnosis of major worker.—Head broad, cordate (Fig. 16). Head sculpture with large piligerous foveolae, 0.01–0.03 mm in diameter. Median frontal streak present. Median ocellus absent (Fig. 16). Scape long, almost reaching the vertex of the head. Mandibular costulae well developed throughout entire length. Mesonotum with 30–36 setae. Promesonotal suture in largest major workers angulate medially, sometimes projecting upward (Fig. 18). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 18). Postpetiole shape as high as or higher than broad (Fig. 19). Postpetiole sculpture in posterior view with lower 0.25–0.33 transversely rugose, upper surface glabrous and shiny (Fig. 19); first gaster sternite with anterior projections, visible in dorsal view.

Major worker.—*Head:* Cordate, slightly longer than broad, widest posterior to eyes, sides weakly convex (Fig. 16). Posterior border of head with concave median impression, concavity 0.5X as wide as distance between apices of frontal lobes. Lower edge of anterior border of clypeus bearing large median seta borne on weakly developed median tooth, tooth is absent in some specimens (Fig. 16). Clypeal carinae, strongly developed, divergent distally, projecting as triangular teeth that are notably larger than median tooth and much larger than paracarinal teeth (Fig. 16). Paracarinal teeth reduced in some specimens. Carinal and paracarinal teeth more dorsally on clypeal border than median tooth (Fig. 16). Mandible with normal curvature (Fig. 16), four teeth (Fig. 16), and 10–12 fine costulae, weakly developed or obsolescent medially, apically becoming broader with shallower intercostular furrows on upper surface. Eye ovate, with maximum diameter 10–12 ommatidia, and minimum diameter 6–7 ommatidia. Scape curved basally, thickest subapically. Apex of scape in repose not surpassing posterior border of head.

Mesosoma: Anterodorsal pronotal border, weakly convex (Fig. 18). Anterolateral pronotal corners variously rounded, never distinctly angulate and bearing slight humeral bosses. Promesonotal suture angulate medially with small dorsal projection at apex (Fig. 18). Pronotum with steep anterior declivity distinguished from dorsum with slight break in outline at point of anterior mesonotal projection. Metanotal impression conspicuous, set off by steep, coarsely striate, posterior mesonotal and anterior propodeal declivities (Fig. 18). Propodeum with dorsal face slightly convex, curving evenly into declivous face. Propodeum angulate posterolaterally due to slight longitudinal, posterolateral bosses. Mesopleural katepisternum defined dorsally by finely striate impression (Fig. 18), weakly defined in some specimens.

Metasoma: Petiolar peduncle notably to slightly shorter than base of node. Postpetiolar node globular to subrectangular with dorsum convex, lateral faces straight, parallel to convergent ventrally. Postpetiole, as seen from behind, with height greater than width.

Pilosity: Composed of yellow setae. Longer setae curved. Mesonotum usually with 30–36 erect setae. Mesopleuron with several dorsal setae. Longest setae on metasomal dorsum usually at least 3–4X length of shortest. Suberect pubescence present on cervical flange of pronotum, on anterior face of petiolar nodes, and on propodeal dorsum.

Sculpturing: Integument with distinct piligerous foveolae present on head, mesosoma and petiole, 0.01–0.03 mm in diameter (conspicuous even in minors). Piligerous foveolae conspicuous but smaller on legs. Interstitial area smooth, shiny. Sculpture of metapleuron consisting of longitudinal

striae. Posterior face of petiole with striae on basal 0.25. Posterior face of postpetiole with transverse striae on basal 0.25, upper 0.75 glabrous with several conspicuous piligerous foveolae (Fig. 19).

Coloration: Color varies from yellow-orange with brown metasoma and with T1-T4 lighter anteriorly to brown-red dorsally with ventral portion of head and legs orange, and T1 with apical margin orange. Some specimens with darker medial portions of leg segments. Median streak present, but faint in some specimens.

Morphometric Measurements: HL 1.14–1.31, HW 1.00–1.24, SL 0.91–1.06, EL 0.17–0.20, PW 0.59–0.70, DML 1.48–1.70, CI 0.90–0.95, SI 0.80–0.86, REL 0.14–0.16, N=21, (HL 1.21, HW 1.14, SL 0.94, EL 0.18, PW 0.62, DML 1.61, CI 0.94, SI 0.83, REL 0.15).

Gyne.—*Head:* Broader than long, quadrate, wider dorsal to eyes than ventrally, sides of head convex from eyes to occipital angles, curving inwards to mandibular base (Fig. 20). Eye sometimes with 1–4 setae protruding from between ommatidia, setae ≤ 3X length of ommatidium. Ocelli small (Fig. 20). Median ocellus circular to slightly elliptical; lateral ocelli ovate, smaller than median ocellus (Fig. 20). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, less so dorsally, greatly divergent ventrally (Fig. 20). Paracarinal teeth small, sometimes poorly defined. Median clypeal tooth poorly developed to absent (Fig. 20). Approximately 0.33% of eye dorsal to midpoint of head (Fig. 20).

Mesosoma. Narrower than head, robust, ovate. Parapsidal lines present on posterior 0.50 to 0.75 of disk. Mesonotum without posteromedian furrow. Median bidentate process present on metasternum. Wing venation as in Fig. 89, m-cu cross vein absent, medial cell open.

Metasoma. Lateral faces of postpetiole strongly to slightly concave. Petiolar spiracle tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae large, width 0.01–0.03 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, yellow and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length >0.30 mm) 2X longer than shortest pubescence. Mandible with 7–8 coarse, distinct costulae present throughout entire length. Propodeum with fine striae posteriorly, anterior 0.25% polished. Petiolar node with 0.25 coarsely striate, remainder polished. Lower 0.25 of posterior face of postpetiole granulate to striato-granulate, upper 0.75% of surface polished (Fig. 44). Area between ocelli coarsely striate, sometimes drastically so. Interfoveolar spaces on head finely striate. Remaining integument smooth and polished. Color orange with black mesonotal maculations present anteromedially and around parapsidal lines. Dorsal transverse band dark brown on pronotum and mesopleuron. Metasoma dark brown, except petiole ventrally and basal 0.25% of T1 and S1 orange blending to dark brown apically. Leg segments orange, brown medially. Sometimes T1 base completely dark brown. Internal margins of ocelli dark brown.

Morphometric Measurements. L ~6.1–6.4, HW 1.30–1.40, VW 0.80–0.85, HL 1.10–1.15, EL 0.31–0.36, OD 0.19–0.22, OOD 0.16, LOW 0.04–0.06, MOW 0.07–0.09, CD 0.19–0.22, MFC 0.13–0.15, EW 0.29–0.36, SL 0.90–1.01, PDL 0.14–0.16, LF1 0.08–0.11, LF2 0.07–0.10, LF3 0.07–0.10, WF1 0.05–0.08, FL 1.10–1.20, FW 0.19–0.30, MW 1.15–1.31, DLM 2.34–2.51, PRH 0.93–1.10, PL 0.60–0.70, PND 0.55–0.65, PH 0.55–0.65, PPL 0.25–0.35, DPW 0.50–0.65, PPW 0.66–0.74, PHB 0.34–0.44, N=2.

Male.—*Head.* Trapezoidal. Eye very large, strongly convex, ovate, occupying

more than 0.5X side of head, anterior border not reaching insertion of mandible. Ocelli large, prominent. Anterior edge of clypeus convex. In lateral view, clypeus shows small, blunt, beak-like central lobe directed anteriorly. Mandible linear, with two large teeth. Antennal scape ~1.3X as long as broad, cylindrical. Pedicel subglobose, broader than scape or following flagellomere.

Mesosoma. Robust, elliptical. In lateral view, mesonotum flat, at the same level as the pronotum. Scutellum swollen and strongly convex, higher than mesonotum. Propodeum rounded, basal face strongly convex transversely, only slightly convex longitudinally, declivous face flat and perpendicular. Posterior margin of metapleuron separated from propodeum by a suture and ventral margins of metapleuron fused to propodeum. Wing venation similar to the male of *S. invicta*, as in Fig. 95.

Metasoma. Anterior face of petiole gently sloping, posterior face parallel. In lateral view, postpetiole globulose, wider than petiole. Dorsum of petiole with a strong median longitudinal impression, forming two lateral lobes. Petiole anteroposteriorly flattened, bilobate. Postpetiole wider than petiole, ventral surface flat. Postpetiolar spiracles high, strongly projected laterally. Genitalia as in *S. invicta* (e.g. Fig. 75).

Coloration, Sculpturing, and Pilosity. All sculpture lacking except for basal 0.25 of petiole and postpetiole, metapleuron and sides of propodeum finely striate and punctuated. Body smooth and polished. Setae golden, suberect, distributed all over the body. Mesonotal pubescence absent. Color black except legs and gaster brown. Wings and veins light brown.

Morphometric Measurements. L ~5.44, HW 1.02, VW 0.52, HL 0.8, EL 0.44, OD 0.11, OOD 0.12, LOW 0.11, MOW 0.12, CD 0.29, MFC 0.26, EW 0.35, SL 0.12, SW 0.11, PDL 0.08, PEW 0.14, LF1 0.21, LF2 0.15, LF3 0.17, WF1 0.08, FL 0.41, FW 0.23, MW 0.96, DML 2.4, PL 0.6, PND 0.5, PH 0.43, PPL 0.48, DPW 0.62, PPW 0.72, PHB 0.51, CI 1.28, OI 0.79, REL 0.55, OOI 1.09, VI 0.52, FCI 0.25, CDI 0.36, SI 0.12, SI2 0.27, SI3 0.8, FI 0.56, NI 0.83, PLI 0.72, PHI 0.89, PWI 1.03, PPWI 1.5, PPWB 1.41.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.43 mm, width 0.45 mm) (Figs. 148, 151). Cranium slightly broader than long (Figs. 148, 151). Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 148, 151). Occipital setal row with 7–8 bifid setae, base 0.5–0.8X total length of seta, setae 0.07–0.16 mm long (Figs. 148, 150, 151). First setal row on vertex with 2 bifid setae, base ~0.66X total length of seta, 0.10 mm long (Figs. 148, 151). Second setal row on vertex with 4 setae, inner 2 setae simple, outer 2 setae with bifid apices (base ~0.66X length), 0.10–0.15 mm long (Figs. 148, 151). Setae ventral to antenna level simple, 0.15–0.17 mm long (Figs. 148, 151). Clypeus with row of 3–4 setae, inner setae shorter than outer setae, 0.05–0.10 mm long (Fig. 148). Labrum small, short (width 2X length) (Figs. 148, 151). Labrum with 4–5 minute sensilla and 2 setae on dorsal surface of each half and apical border with 3–6 sensilla on each half. Labrum with 2–3 coarse isolated spinules near each ventrolateral corner. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 149). Maxilla with apex conical, palpus peg-like with 5 sensilla, each bearing one spinule. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with patch of spinules dorsal to each palpus, spinules coarse and isolated or in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types.

Simple setae (0.05–0.10 mm long) arranged in transverse row of 6–9 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.06–0.09 mm long) occur elsewhere, base 0.5X length.

Length. Approximately 2.6–2.8 mm.

Material examined.—Argentina: Missiones, Aristóbulo del Valle, 23.v.2015, 27°05.235′, 54°57.168′ (19 w). Brazil: Paraná: "Pinhais, R. Rod. Dep. Joao Leopoldo Jacomel", 18.xi.2015, -25.43045098, -49.20909698, G. Camacho and D. Gotzek, PR15-036, (4 w); "Curitiba, Barigui Park", 19.xi.2015, -25.42987799, -49.31599097, G. Camacho and D. Gotzek, PR15-039, (18 w); "Rt.BR-277, Campo Largo, Metalurgica Gans factory, field and roadside by factory", 19.xi.2015, -25.43349998, -49.41256902, G. Camacho and D. Gotzek, PR15-051, (10 w); "Rt.BR-277, Campo Largo, Metalurgica Gans factory, on hillside next to road; ~3m from PR15-067", 19.xi.2015, -25.43395202, -49.41203199, G. Camacho and D. Gotzek, PR15-066, (4 w); "S. Luis do Purunã, open gravel field behind truck stop on Rt.BR-277", 20.xi.2015, -25.47302401, -49.70426696, G. Camacho and D. Gotzek, PR15-075, (4 w); "S. Luis do Purunã, open gravel field behind truck stop on Rt.BR-277", 20.xi.2015, -25.47300699, -49.70436101, G. Camacho and D. Gotzek, PR15-076, (2 w); "Edge of Ponto Grossa, median of Rt.PR-513", 20.xi.2015, -25.14492497, -50.14723303, G. Camacho and D. Gotzek, PR15-082, (6 w); "Vila Velha N.P., Campos Gerais open shrubland", 21.xi.2015, -25.25196397, -50.008018, G. Camacho and D. Gotzek, PR15-086, (6 w); "Rt.BR-376, side of road", 21.xi.2015, -24.87010701, -50.44417997, G. Camacho and D. Gotzek, PR15-093, (2 w); "Cascavel (Guarapuava, southeastern suburb to Rt.PR-170)", 24.xi.2015, -25.392934, -51.49619398, G. Camacho and D. Gotzek, PR15-153, (4 w); "Candoi, empty lot in town center", 24.xi.2015, -25.56748403, -52.05006, G. Camacho and D. Gotzek, PR15-161, (2 w); "Pinhao, town park", 24.xi.2015, -25.69448998, -51.660301, G. Camacho and D. Gotzek, PR15-165, (8 w); Rt.BR-277 btwn Guarapuava + Irati, 25.xi.2015, -25.31583399, -51.19612, G. Camacho and D. Gotzek, PR15-194, (6 w); National Forest Irati, 26.xi.2015, -25.40887697, -50.57687396, G. Camacho and D. Gotzek, PR15-211, (26 w); "Pinheiros, edge of soccer field", 26.xi.2015, -25.42351797, -50.55518403, G. Camacho and D. Gotzek, PR15-224, (2 w); Rt.BR-153 btwn Irati + União d. Vitoria, 26.xi.2015, -25.68580499, -50.76397598, G. Camacho and D. Gotzek, PR15-226, (4 w); Rt.BR-153 exit to Rio Azul, 26.xi.2015, -25.70675304, -50.78334597, G. Camacho and D. Gotzek, PR15-228, (10 w); "Mallet, town center, recently mowed field", 26.xi.2015, -25.88597297, -50.83851499, G. Camacho and D. Gotzek, PR15-233, (16 w); "Paula Freitas, in front of medical center", 26.xi.2015, -26.11710403, -50.82043698, G. Camacho and D. Gotzek, PR15-240, (4 w); Rondinha, 26.xi.2015, -26.171502, -50.91157199, G. Camacho and D. Gotzek, PR15-242, (2 w); União da Vitoria, 26.xi.2015, -26.20269299, -51.06220803, G. Camacho and D. Gotzek, PR15-249, (2 w); "Palmeira, Rt.BR-277", 27.xi.2015, -25.43500604, -49.991854, G. Camacho and D. Gotzek, PR15-255, (4 w); Colonîa Johannesdorf on Rt.BR-476, 27.xi.2015, -25.742842, -49.76574504, G. Camacho and D. Gotzek, PR15-264, (2 w), Rt.BR-476 btwn Lapa + Sao Mateus do Sul, 27.xi.2015, -25.85078599, -49.94710797, G. Camacho and D. Gotzek, PR15-268, (10 w); "Rio Negro, Rt.BR-116", 28.xi.2015, -26.070288, -49.73545603, G. Camacho and D. Gotzek, PR15-275, (4 w);

"Campo do Tenente, town center", 28. xi.2015, -25.97824599, -49.68351698, G. Camacho and D. Gotzek, PR15-282, (6 w); "Colombo, Rt.BR-476 to Tunas", 29. xi.2015, -25.32895703, -49.15940403, G. Camacho and D. Gotzek, PR15-308, (12 w); "Rt.BR-476, edge of Bocaiuva do Sul", 29.xi.2015, -25.19912797, -49.11631904, G. Camacho and D. Gotzek, PR15-317, (2 w); "Rt.BR-476, btwn Bocaiuva do Sul + Tunas", 29.xi.2015, -25.18001899, -49.12016901, G. Camacho and D. Gotzek, PR15-318, (6 w); "Tunas, town center", 29.xi.2015, -24.97498498, -49.08486804, G. Camacho and D. Gotzek, PR15-321, (14 w); "Rt.BR-476, btwn Tunas + Bocaiuva do Sul", 29.xi.2015, -25.01404096, -49.07943397, G. Camacho and D. Gotzek, PR15-330, (18 w); "Colombo, town center, along Rt.BR-476", 29.xi.2015, -25.30889997, -49.14433798, G. Camacho and D. Gotzek, PR15-341, (2 w); Rt 277 @ KM 493; near Guaraniacu, 1998, -25.107, -52.867, G-72, (1 w); Rt 116 at Rio Negro, 1998, -26.10583333, -49.7975, G-80, (2 w); Rt 277 @ KM 317; at junction with Rt 373, 1998, -25.46, -51.958, G-74, (1 w); Palmas, 2009, -26.484151, -51.991450, E. Fox, Bra09-22, (2 w). Brazil: Rio de Janeiro: Três Rios, 2009, -22.118277, -43.209538, E. Fox, Bra09-15, (1 w); Itaipava, 2009, -22.383333, -43.133333, E. Fox, Bra09-31, (2 w); Rio de Janeiro University campus, 2009, -22.911267, -43.236059, E. Fox, Bra09-68, (1 w).

Nomenclatural notes.—An unpublished manuscript name, "*S. altipunctata*" (Pitts 2002), was used by Gotzek et al. (2007) in reference to this species. Since that usage occurred without the species being formally described in a publication satisfying the requirements of ICZN Article 8, the name was rendered unavailable as a nomen nudum following Article 13 of the Code (ICZN, 1999). Here we formally describe this species as *Solenopsis metallica*.

Etymology.—This species is named for one of its most common and conspicuous color morphs, the bright, metallic orange phase. It is also one of several authors' favorite rock bands. The specific epithet is a noun in apposition.

Distribution.—The type series of the species was originally collected in the highlands of Santa Catarina state, southern Brazil. Further examination of material collected in Rio de Janeiro State in 2008 and Misiones Province in 2015 also proved to be *S. metallica*, suggesting a southeastern Atlantic Forest range for the species. In 2015, extensive collections in Paraná State showed that the species is widely distributed in subtropical humid forest in the region. See Fig. 201.

Comments.—The major workers of this species are easily distinguished from others in this species-group by the long scape failing to reach the vertexal margin of the head, postpetiole sculpture in posterior view with lower 0.25–0.33 transversely rugose, upper surface glabrous and shiny and the anterior projection on the first gaster sternite visible in dorsal view. Other distinguishing characters are present on the gyne, including the greatly diverging clypeal carinae, the large piligerous foveolae on the head and mesosoma, the strongly to weakly defined striae between the ocelli, the lack of a median cell due to the loss of the m-cu cross vein, and the reduction in postpetiolar sculpturing.

The major workers of *S. metallica* can be easily differentiated from their putative sister species, *S. weyrauchi*. *Solenopsis metallica* have 10–12 costulae on the mandible that are obsolescent medially and have larger piligerous foveolae on the head and mesosoma. In comparison, the major workers of *S. weyrauchi* have 5–6 complete mandibular costulae and their cephalic foveolae are smaller. The shape of the postpetiole of the workers is most similar to that of *S. saevissima*, but is more coarsely

sculptured. The darker colored workers appear bicolored, which is similar to the color pattern of *S. electra*. The minor workers (Fig. 17) of this species are usually lighter than the majors, but can sometimes have similar coloration. They also have large, distinct foveolae on the head and mesosoma, which is easily noticed. As with the other fire ant species, however, the minors are difficult to identify. The larvae of this species are unremarkable and are similar to *S. saevissima* and *S. invicta* by having bifid setae on the head capsule. The setae on the head capsule are longer in this species, however, than in *S. invicta* or *S. saevissima*.

In addition to the morphological characters that define the species, *S. metallica* can be differentiated in the field by ecological and behavior characteristics that are different from sympatric fire ant species. During collections in Paraná state in 2015, we observed that *S. metallica* presents a less aggressive response and sting to nest disturbance than *S. invicta* and other fire ants, apart from its usual bright orange or goldish appearance to the naked eye. It appears much more shade tolerant than *S. invicta* as it builds nests underneath closed canopy.

The taxonomic distinctiveness of *S. metallica* is also circumstantially supported by genetic data. DNA sequence data (mitochondrial: Shoemaker et al. 2006; Ross et al. 2010; nuclear: Gotzek et al. 2007; Krieger and Ross 2005) and a large panel of microsatellite and allozyme data (Ross et al. 2010) clearly distinguish individuals of this species (alternately termed *S.* sp. "A", "southern highlands", or "*S. altipunctata*" in those studies) from other fire ant species.

Solenopsis daguerrei (Santschi)

(Figs. 86, 106, 108, 195–200)

Labauchena daguerrei Santschi 1930: 81. [Holotype (?) gyne, males. ARGENTINA. Buenos Aires Province. Rosas. F. C. Sud. MACN]

Labauchena acuminata Borgmeier 1949: 208. [IMLA]

Solenopsis daguerrei: Ettershank 1966: 140.

Gyne.—*Head:* broader than long, quadrate, wider anterior to eyes, sides of head weakly convex from eyes to occipital angles, nearly straight anterior to eyes. Occipital angles well defined (Fig. 195), lobate in lateral view (Fig. 196). Vertex flattened posteriorly with narrow, transverse impression just anterior to occipital carina. Occipital furrow lacking (Fig. 195). Frontal furrow lacking (Fig. 195). Ocelli small, median ocellus ventral to posterior margin of eyes (Fig. 195). Clypeus not projecting, lacking carinae or carinal teeth, anterior margin straight. Mandible gently curving, masticatory border with one large tooth and usually rudiments of two more teeth, with dorsal lobe dorsal to teeth rudiments (Fig. 197). Eye convex, ovate, midpoint of head reaches posterior 0.33 of eye. Antennal scape in repose surpasses lateral ocellus. Antenna 11-segmented. Pedicel ≥ 2X length of second flagellomere. First and second flagellomere length each >1.5X their width.

Mesosoma. Elliptical, narrower than head. In lateral view, mesonotum convex anterior portion that greatly overhangs pronotum, lobate (Fig. 196), posterior half straight. Pronotum wider than mesonotum. Scutellum as high as mesonotum, flattened with short, perpendicular posterior face. Angle of propodeum well-defined, obtuse, differentiation between basal and declivous faces indistinct (Fig. 198). Mesosternum small, slightly rounded beneath. Parapsidal lines absent. Posterior and ventral margin of metapleuron fused to pronotum. Propodeal spiracle much reduced in size (Fig. 198). Metasternal bidentate median process present. Wing

venation reduced (Fig. 106), medial cell lacking or barely discernable as such.

Metasoma. Petiolar node thick, dorsum somewhat flattened at obtuse angle, appearing to have anterior median boss on dorsum. Petiole ventrally with median carina on anterior 0.50. Postpetiole lacking ventral transverse carina, only slightly convex.

Coloration, Sculpturing, and Pilosity. Sculpture lacking, body polished, except posterior 0.25 of petiole finely striate. Setae long (0.10–0.28 mm), golden, semi-erect, somewhat longer on mesosoma than elsewhere. Color yellow with apex of mandibles and apices of metasoma segments 3–6 brown. Internal margins of ocelli yellow.

Male.—*Head.* Trapezoidal (Fig. 199). Eye very large, strongly convex, ovate, occupying more than 0.5X side of head, anterior border reaching insertion of mandible (Fig. 199). Ocelli large, prominent (Fig. 199). Anterior edge of clypeus straight (Fig. 199). In lateral view, clypeus shows small, blunt, beak-like central lobe. Mandible linear, with single apical tooth, lobe present dorsal to tooth (Fig. 199). Antennal scape ~1.7X as long as broad, cylindrical (Fig. 200). Pedicel subglobose, broader than scape or following flagellomere (Fig. 200).

Mesosoma. Robust, elliptical. In lateral view, mesonotum swollen anteriorly, overhanging pronotum. Scutellum convex, slightly higher than mesonotum. Propodeum rounded, basal face strongly convex transversely, only slightly convex longitudinally, declivous face flat and perpendicular. Posterior and ventral margins of metapleuron fused to propodeum. Wing venation reduced (Fig 108), many veins being nebulous.

Metasoma. Anterior face of petiole gently sloping, posterior face abruptly curved. In lateral view, postpetiole elongate, slightly shorter than petiole. Dorsum of both with slight median longitudinal impression. Petiole dorsolaterally rounded, not bilobate. Postpetiole wider than petiole, ventral surface flat. Genitalia reduced in form, digitus lacking setae, aedeagus with few ventral teeth (Fig. 86).

Coloration, Sculpturing, and Pilosity. All sculpture lacking except for basal 0.25 of petiole and postpetiole finely striate. Body smooth and polished. Setae golden, suberect, length 0.10–0.16 mm, mesonotum and petiolar nodes sparsely pubescent. Mesonotal pubescence sparse (as in Fig. 72). Color yellow except vertex of head and gaster brown. Wings and veins hyaline.

Material Examined.—See Appendix A.

Distribution.—The known range of *S. daguerrei* extends from Buenos Aires Province, Argentina northward, including Uruguay, to Campo Grande, Brazil and eastward to São Paulo, Brazil (Fig. 203) (Briano et al. 1997). *Solenopsis daguerrei* seems to be generally sparse over most of its range. They appear to be concentrated in colonies only in certain areas (Briano et al. 1997).

Comments.—The males and gynes of this species are distinct from the other members of the group by their coloration, and the reduction in size, sculpturing, and wing venation associated with their socially parasitic existence. The genitalia of the male are also distinct from the other species by lacking setae on the digitus, having a reduced number of ventral setae on the volsella, and having a reduced number of ventral teeth on the aedeagus (Fig. 86).

Solenopsis daguerrei has been reported to either kill the host gyne in laboratory studies (Bruch 1930) or to be an inquiline, allowing the host gyne to live (Silveira-Guido et al. 1965). Regardless of the outcome for the host gyne, the parasite lowers the egg

production of the host colony and some speculation has been made regarding its use as a biological control agent (Jouvenaz 1990; Wojcik 1990). Regarding hosts, it is reported to parasitize *S. invicta, S. richteri*, *S. macdonaghi*, and *S. quinquecuspis* (Santschi 1930; Briano et al. 1997; Calcaterra et al. 2000). We found *S. daguerrei* only in *S. invicta* colonies during our extensive sampling in Brazil and Argentina (see Appendix A).

Solenopsis electra Forel

(Figs. 39, 40, 107)

Solenopsis pylades electra Forel 1914: 397. [Syntype workers. ARGENTINA. Salta. Jujuy. XI-913 (=1913). Schuer. #129. MHNG.]

S. saevissima electra: Santschi 1916: 381.

S. (*Solenopsis*) *saevissima electra*: Creighton 1930: 92. Worker, gyne.

S. saevissima saevissima cline *S. saevissima richteri* (Bolivian variant): Wilson 1952: 65. [MCZ.]

S. saevissima saevissima cline *S. saevissima richteri* subsp. *electra*: Wilson 1952: 65. [MCZ.]

S. electra: Trager 1991: 192.

Worker.—Head subovate. Head sculpture with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak absent. Median ocellus in largest major workers present. Mandibular costulae well developed throughout entire length. In lateral view, pronotum low and nearly flat to weakly convex. Mesonotum with 20–25 setae. Promesonotal suture in largest major workers gently curved medially, never projecting upward. Mesonotum weakly convex in lateral view. Propodeum sculpture granulate posteroventral to spiracle. Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view with lower 0.66 transversely rugose, granulate, upper surface glabrous and shiny. Color of head, legs, antennae generally red yellow. Mesosoma and gaster dark brown. T1 yellow anteriorly. Mandibles brown. Some specimens darker brown black, with appendages slightly lighter.

Gyne.—*Head.* Slightly broader to as broad as long, quadrate, sides of head convex from eyes to occipital angles, straight anterior to eyes (Fig. 40). Eye sometimes with 2–4 long setae protruding from between ommatidia, setal length >4X width of ommatidium. Ocelli large, prominent (Fig. 40). Median ocellus circular, lateral ocelli slightly ovate (Fig. 40). Ocelli in more anterior position on head (Fig. 40). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, prominent between antennal scrobes, slightly divergent ventrally (Fig. 40). Paracarinal teeth small, indistinct to absent (Fig. 40). Median clypeal tooth well developed (Fig. 40). Approximately 0.50 of eye basal to midlength of head (Fig. 40).

Mesosoma. Parapsidal lines present on posterior half of disk (Fig. 39). Mesonotum without posteromedian furrow. Metasternum with bidentate median process. Wing venation as in Fig. 107.

Metasoma. Lateral faces of postpetiole weakly concave. Petiolar spiracle normally not tuberculate. Postpetiolar spiracles normally tuberculate.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesonotum pubescence 0.16–0.25 mm, longest pubescence on mesonotum 2X

longer than shortest pubescence. Mandible with 5–8 coarse, distinct costulae present throughout entire length. Propodeum with fine striae throughout (Fig. 39). Petiolar node basal 0.75 with striate, dorsum polished. Postpetiolar node basal 0.50 with fine striae, dorsum polished. Remaining integument smooth and polished. Color yellow with gaster red brown. T1 with basal 0.50 yellow, remaining segments yellow anterolaterally. Internal margins of ocelli dark brown.

Morphometric Measurements. L ~6.2–6.5, HW 1.15–1.28, VW 1.09–1.15, HL 1.20–1.30, EL 0.36–0.44, OD 0.15–0.21, OOD 0.09–0.12, LOW 0.10–0.15, MOW 0.10–0.16, CD 0.15–0.19, MFC 0.18–0.21, EW 0.25–0.34, SL 0.78–0.91, PDL 0.14–0.19, LF1 0.07–0.11, LF2 0.05–0.10, LF3 0.07–0.10, WF1 0.04–0.07, FL 0.92–1.05, FW 0.21–0.29, MW 1.21–1.33, DLM 2.15–2.31, PRH 0.88–1.04, PL 0.56–0.68, PND 0.45–0.56, PH 0.55–0.64, PPL 0.31–0.36, DPW 0.50–0.68, PPW 0.56–0.64, PHB 0.32–0.45, N=2.

Male.—Unknown.

Fourth instar worker larva.—Unknown.

Material Examined.—Various specimens (FSCA).

Distribution.—The currently known range of *S. electra* extends northward from Santiago del Estero Province of Argentina to Santa Cruz, Bolivia (Fig. 201). Trager (1991) lists a sample examined from Asunción, Paraguay. Sampling efforts between the known range and Asunción, Paraguay have not produced any specimens of *S. electra*, so this record may represent an introduction.

Comments.—The gyne of *S. electra* is similar to *S. pusillignis, S. saevissima,* and *S. macdonaghi* in coloration and in the lack of mesonotal maculae. The gyne of this species has a thinner petiolar node, a smaller OOI, and a smaller body size than those of *S. saevissima* and *S. macdonaghi*. The gynes of *S. electra* differ from the gynes of the sister species, *S. pusillignis*, by having a smaller OI, a more developed median clypeal tooth, and a darker coloration of the gaster.

The northern populations of *S. electra* have much larger workers than the southern populations, but the gynes of these populations remain unchanged in size. Males were not available for examination for this study, but Trager (1991) describes them as being relatively small compared to males of the rest of the species-group.

Solenopsis interrupta Santschi

(Figs. 21, 22, 47, 52, 56, 57, 73, 74, 92, 93, 132, 133, 152–154, 157)

Solenopsis saevissima var. *interrupta* Santschi 1916: 397. [Syntype (?) workers. ARGENTINA. La Rioja. Bajo Hondo. NHMB.]

S. (*Solenopsis*) *saevissima interrupta*: Creighton 1930: 89 (In part.).

S. interrupta Wilson 1952: 61 (In part.).

Worker.—Head weakly to strongly cordate (Fig. 132). Head and mesosomal sculpture with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak mostly absent, but sometimes distinctly darkened. Median ocellus in largest major workers absent (Fig. 133). Mandibular costulae dense, present throughout, rarely partially obsolescent. Mesonotum with 20–25 setae (Fig. 132). Promesonotal suture in largest major workers gently curved medially, never projecting upward (Fig. 132). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 132). Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view weakly transversely rugose, weakly granulate,

reaches dorsum only in largest workers. Color generally red yellow to brown yellow, with head and mesosoma dorsum darker. Gaster dark brown. T1 with maculation red yellow to brown yellow.

Gyne.—*Head:* broader than long, quadrate, slightly wider dorsal to eyes than ventral to them, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 22). Eyes sometimes with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large, prominent (Fig. 22). Median ocellus circular, lateral ocelli slightly ovate (Fig. 22). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, less so dorsally, slightly divergent ventrally, edge of clypeus between carinae with shallow concave depression, depression deepest between carinal teeth (Fig. 22). Paracarinal teeth poorly defined to absent (Fig. 22). Median clypeal tooth usually well developed; sometimes less developed (Fig. 22). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 22).

Mesosoma. Parapsidal lines present on posterior half of disk (Fig. 21). Mesonotum with indistinct to distinct median furrow, usually on posterior 0.25–0.33 of disk. Propodeum sometimes with median longitudinal depression. Median bidentate process present on metasternum. Wing venation as in Fig. 92.

Metasoma. Lateral faces of postpetiole weakly concave to straight sided. Petiolar spiracle tuberculate in some cases. Postpetiolar spiracle usually not tuberculate.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae moderate to small, sparse, width 0.01–0.03 mm in diameter on head, smaller on meso- and metasoma. Pubescence golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Pubescence darker on darkly maculated areas. Mesosoma with longest pubescence (length 0.30 mm or greater) 3X longer than shortest pubescence. Mandible with several coarse, 6–8, distinct costulae present throughout. Propodeum with fine striae posteriorly, anterior 0.25 polished to finely striate. Petiolar node posterior surface with lower 0.75 coarsely striate, dorsum finely striate. Postpetiolar node posterior surface with middle 0.50 striate (with 7–10 striae), finely granulate, lower 0.25 coarsely granulate (Fig. 47). Interfoveolar spaces on head finely striate when piligerous foveolae are large. Remaining integument smooth and polished. Two color varieties exist. Dark form brown with katepisternum, metasoma and medial area of legs dark brown. Light form orange to yellow orange, except vertex and T2-4, T1 laterally and apically and sternites apically dark brown. Light form also with posterior margin of orange maculation of T1 distinct. Both color forms with dark brown maculations anteriorly on pronotum, anteromedian area of mesonotum, area around parapsidal lines, sometimes on median area of axillae, anteromedian and triangular posteromedian area of scutellum, medially on anepisternum, and medially and laterally on propodeum (Fig. 52). Internal margins of ocelli dark brown. Median frontal streak present (as in Fig 50). Wings hyaline with pale yellow to hyaline veins.

Morphometric Measurements. L ~7.8–8.4, HW 1.35–1.60, VW 0.89–1.01, HL 1.20–1.35, EL 0.40–0.51, OD 0.10–0.15, OOD 0.15–0.20, LOW 0.10–0.12, MOW 0.10–0.12, CD 0.15–0.20, MFC 0.18–0.23, EW 0.30–0.35, SL 0.90–1.10, PDL 0.15–0.20, LF1 0.10–0.12, LF2 0.08–0.11, LF3 0.08–0.10, WF1 0.06–0.08, FL 1.10–1.21, FW 0.21–0.31, MW 1.30–1.40, DLM

2.49–2.62, PRH 1.00–1.11, PL 0.59–0.75, PND 0.55–0.65, PH 0.60–0.72, PPL 0.30–0.40, DPW 0.61–0.82, PPW 0.59–0.73, PHB 0.41–0.50, N=5.

Male.—*Head.* Eyes sometimes with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large and prominent, median ocellus circular, lateral ocelli elliptical (Fig. 57). In lateral view, clypeus with blunt, central lobe with indistinct anterior transverse carina.

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally (Fig. 56). Metapleuron broad almost 0.66 as wide as high (Fig. 56). Wing venation as in Fig. 93.

Metasoma. In cephalic view, dorsum of node transverse to having weak median depression and weakly bilobate. Petiolar and postpetiolar spiracles slightly tuberculate to not tuberculate. Genitalia as in Fig. 74.

Coloration, Sculpturing, and Pilosity. Pubescence sparse, yellow to yellow orange, erect to suberect, not of uniform length over body (0.10–0.35 mm long), longer on gena and vertex. Mesonotal pubescence dense (Fig. 73). Base of propodeum striato-granulate. Propodeum with anteromedial area glabrous. Area between eye and insertion of antenna (Fig. 57), and lateral faces of scutellum finely striate. Area between ocelli granulate. Remainder of head weakly to coarsely granulate throughout, shagreened in some cases (Fig. 57). Lower surface of petiolar nodes coarsely striato-granulate, dorsum finely striato-granulate. Postpetiole often with fine striations present dorsomedially. Metapleuron with dorsal longitudinal region finely striate. Gena granulate. Remaining integument smooth and polished. Color red brown to dark brown. Mandible brown anteriorly changing to yellow brown at apex. Flagellum yellow brown and legs segments brown medially grading to yellow towards base and apex.

Morphometric Measurements. L ~5.6–6.0, HW 1.00–1.10, VW 0.30–0.55, HL 0.81–0.92, EL 0.40–0.51, OD 0.10–0.15, OOD 0.15–0.20, LOW 0.11–0.14, MOW 0.11–0.15, CD 0.15–0.25, MFC 0.15–0.21, EW 0.32–0.40, SL 0.15–0.20, SW 0.10–0.15, PDL 0.05–0.10, PEW 0.11–0.15, LF1 0.20–0.25, LF2 0.13–0.16, LF3 0.16–0.22, WF1 0.08–0.10, FL 1.09–1.22, FW 0.20–0.30, MW 1.35–1.50, DLM 2.30–2.51, PRH 0.90–1.00, PL 0.60–0.75, PND 0.50–0.65, PH 0.39–0.52, PPL 0.29–0.41, DPW 0.60–0.71, PPW 0.55–0.75, PHB 0.18–0.30, N=6.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.44 mm, width 0.51 mm) (Figs. 152, 157). Cranium slightly broader than long (Figs. 152, 157). Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 152, 157). Occipital setal row with 8–12 bifid setae, base 0.5 to 0.8X total length of seta, 0.067–0.010 mm long (Figs. 152, 157). First setal row on vertex with 1–2 bifid setae, base ~0.66X total length of seta, 0.07–0.09 mm long (Figs. 152, 157). Second setal row on vertex with 4 simple setae, 0.13 mm long. Setae ventral to antenna level simple, 0.15–0.21 mm long (Figs. 152, 157). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.07–0.12 mm long (Figs. 152, 157). Labrum small, short (breadth 2X length) (Fig. 152). Labrum with 4–6 minute sensilla and 2 setae on dorsal surface of each half and apical margin with 5–6 sensilla on each half. Each half of epipharynx with 2–4 isolated sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size

dorsally (Fig. 154). Maxilla with apex conical, palpus peg-like with 5 sensilla, each bearing one spinule. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with patch of spinules dorsal to each palpus, spinules in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.05–0.11 mm long) arranged in transverse row of 5–10 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.07–0.10 mm long) occur elsewhere, base 0.5–0.75X length (Fig. 153). Some bifid setae on thoracic dorsum with base 0.33X length of seta.

Length. 3.2–3.4 mm.

Material examined.—Various specimens (FSCA). Also, see Appendix A.

Distribution.—There is some question concerning the exact type locality for *S. interrupta.* Santschi (1916) merely lists the type locality as "Argentine: Bajo Hondo, Monte Hermeso". But there are at least two locations in Argentina called Bajo Hondo. Buren (1972) placed the type locality in Buenos Aires Province and he considered the nominal *S. interrupta* range to span Uruguay and Buenos Aires, Entre Rios, Santa Fe Provinces, Argentina. He excluded the northwestern Argentinian and Bolivian forms from the species. Trager (1991) placed the type locality in La Rioja Province, since he considered Buenos Aires to be well outside the range of his concept of the species (Cordoba and Mendoza Provinces in Argentina northward into Bolivia (Fig. 202)) and he considered Santschi's description to fit well within his image of *S. interrupta*. Here, we follow Trager's (1991) interpretation.

Comments.—The gynes of *S. interrupta* superficially resemble *S. pythia* and *S. metallica* in both coloration and sculpture of the head. Both *S. pythia* and *S. metallica* have other derived characters, however, and thus are easily distinguished from *S. interrupta*.

The gynes of *S. interrupta* and *S. richteri* are similar in coloration and both sometimes have a distinct orange tergal maculation with a demarcated posterior margin. In many cases, the gynes of these two species are difficult to differentiate, but they may be separated by the sculpture of the postpetiole. The gynes of *S. interrupta* are typically slightly lighter in coloration. In addition, the OOI of *S. interrupta* gynes is much greater than that of the *S. richteri* gynes. The workers of these species, however, are relatively easy to separate from the other members of this species-group.

The male is dark in coloration as are males of most species in this group. The pubescence of the males is longer and denser than that of *S. saevissima* males. Often, the head of the male is shagreened as it is in *S. invicta* males.

The larvae of *S. interrupta* are similar to those of *S. invicta* and *S. saevissima*. They differ, however, in the size and shape of the body setae. Also, the setae ventral to the antennal level are typically longer in *S. interrupta* than in *S. invicta* or *S. saevissima*.

Solenopsis invicta Buren

(Figs. 23, 24, 42, 58, 59, 75, 94, 95, 134, 135, 167, 160–164)

Solenopsis saevissima var. *wagneri* Santschi 1916: 380. [Syntype workers. ARGENTINA. Santiago de Estero. Near Icano. Wagner. NHMB.] (Name suppressed in accord with ICZN 1976 (2001) as proposed by Shattuck, Porter, and Wojcik (1999).)

S. saevissima saevissima cline *S. saevissima richteri*: Wilson 1952: 65. [MCZ.]

S. invicta Buren 1972: 9. Worker, gyne, male. [NMNH.] (Name conserved (ICZN 2001)).

Worker.—Head subquadrate to weakly cordate (Fig. 135). Head of largest specimens cordate. Sculpture of head and mesosomal dorsum with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak present. Median ocellus in largest major workers absent (Fig. 135). Mandibular costulae absent medially, distinct apically and basally along outer border. Mesonotum with 20–25 setae. Mesonotum with anteromedian margin in largest major workers gently curved. Mesonotum in lateral view convex (Fig. 134). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 134). Postpetiole shape in posterior view width greater than height. Postpetiole in posterior view with lower 0.66 or greater transversely rugose to punctate-rugose, extreme dorsum nitid, granulate. Color generally with head and mesosoma yellow red to dark red brown, gaster brown, T1 with maculation yellow red to concolorous with surrounding integument.

Gyne.—*Head.* Slightly broader than long, quadrate, wider dorsal to eyes than ventral to them, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 24). Eyes sometimes with 2–10 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Median ocellus large, prominent, circular (Fig. 24). Lateral ocelli moderate to large, slightly ovate (Fig. 24). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, less so dorsally, slightly divergent ventrally (Fig. 24). Paracarinal teeth small, sometimes poorly defined. Median clypeal tooth well developed (Fig. 24). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 24). Antennal scape in repose surpasses lateral ocellus.

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 23). Mesonotum with indistinct, median furrow on posterior one-sixth or less. Bidentate median process present on metasternum (Fig. 23). Wing venation as in Fig. 94.

Metasoma. Lateral faces of postpetiole slightly concave to wider ventrally. Petiolar and postpetiolar spiracles slightly tuberculate to not tuberculate.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length ≤0.25 mm) 2X longer than shortest pubescence (Fig. 23). Mandible with 9–11 fine, distinct, costulae, sometimes costulae obsolescent medially. Propodeum with fine striae throughout (Fig. 23). Petiolar nodes with lower 0.75 finely striate; granulate throughout. Postpetiole usually with 12–18 striations, often transverse (Fig. 41), other times appearing to create swirling or circular patterns. Remaining integument smooth and polished. Color varies from red brown to brown red on dorsum of head, dorsum of thorax, and katepisternum of mesopleuron. Gaster brown. Sometimes on lighter colored individuals, bases of T1 and S1 are somewhat orange blending to brown apically. Brown maculations sometimes present anteromedially and on parapsidal lines (as in Fig. 52). Median streak present (as in Fig. 50), weak, sometimes indistinct or absent. Internal margins of ocelli often dark brown.

Morphometric Measurements. L ~5.9–8.3, HW 1.30–1.46, VW 0.66–0.88, HL 1.18–1.43, EL 0.38–0.49, OD 0.10–0.18, OOD 0.19–0.26, LOW 0.08–0.15, MOW 0.16–0.24, CD 0.15–0.22,

MFC 0.15–0.25, EW 0.25–0.48, SL 0.78–1.11, PDL 0.13–0.25, LF1 0.08–0.14, LF2 0.07–0.10, LF3 0.07–0.12, WF1 0.06–0.11, FL 0.94–1.26, FW 0.22–0.36, MW 1.14–1.48, DLM 2.42–2.73, PRH 0.88–1.19, PL 0.72–0.83, PND 0.56–0.84, PH 0.57–0.78, PPL 0.24–0.42, DPW 0.51–0.74, PPW 0.71–0.77, PHB 0.26–0.48, N=25.

Male.—*Head.* Eyes sometimes with 2–10 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large and prominent, elliptical (Fig. 59).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron not broad, ~0.33 as wide as high, sometimes with transverse posterior carina (Fig. 58). Wing venation as in Fig. 95.

Metasoma. In cephalic view, dorsum of node with shallow to deep median impression and weakly to strongly bilobate. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia Fig. 75.

Coloration, Sculpturing, and Pilosity. Pubescence short, sparse, yellow to brown, erect to suberect (0.20–0.30 mm), longest on gena and vertex. Mesonotal pubescence dense (as in Fig. 73). Propodeum with base striato-granulate, medially finely granulate (Fig. 58). Area between eye and insertion of antenna, posterior portion of metapleuron, lateral faces of scutellum, and base of petiolar node granulate to striato-granulate (Fig. 58). Posterior surface of postpetiolar node granulate throughout, rugae present dorsomedially. Area between ocelli weakly to coarsely striato-granulate (Fig. 58). Gena coarsely rugose to coarsely striato-granulate. Head often completely granulate, shagreened, dull. Remaining integument smooth and polished. Color red brown to black with antenna completely yellow, sometimes scape and pedicel brown. Mandibles brown to light brown.

Morphometric Measurements. L ~5.4–6.3, HW 0.91–1.08, VW 0.30–0.40, HL 0.67–0.83, EL 0.37–0.53, OD 0.06–0.11, OOD 0.18–0.26, LOW 0.09–0.18, MOW 0.10–0.17, CD 0.16–0.24, MFC 0.13–0.18, EW 0.28–0.39, SL 0.16–0.20, SW 0.09–0.14, PDL 0.06–0.10, PEW 0.10–0.15, LF1 0.10–0.17, LF2 0.13–0.15, LF3 0.12–0.16, WF1 0.07–0.10, FL 1.00–1.15, FW 0.15–0.20, MW 1.20–1.68, DLM 2.27–2.64, PRH 0.78–1.04, PL 0.62–0.69, PND 0.54–0.61, PH 0.44–0.56, PPL 0.20–0.28, DPW 0.55–0.71, PPW 0.58–0.69, PHB 0.14–0.28, N=25.

Fourth instar worker larva.—*Head.* Large, subpyriform in anterior view (height 0.50 mm, width 0.54 mm) (Figs. 160, 162). Cranium slightly wider than long (Figs. 160, 162). Antenna with 2 or 3 sensilla, each with 1 spinule. Integument of head with minute spinules. Occipital setal row normally with 6–8 bifid setae, base ~0.66X total length of seta, setae 0.08–0.10 mm long (Figs. 160, 162). First setal row on vertex with 2 bifid setae, base ~0.66X total length of seta, 0.05–0.07 mm long (Figs. 160, 162). Second setal row on vertex with 4–6 simple setae, ~0.10 mm long (Figs. 160, 162). Setae anterior to antenna level simple, 0.08–0.14 mm long (Figs. 160, 162). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.06–0.08 mm long (Figs. 160, 162). Labrum small, short (width 2.5X length). Labrum with 4–6 minute sensilla and 2 setae on dorsal surface of each half and apex with 4–6 sensilla on each half. Each half of the epipharynx with 2–3 isolated and 2 contiguous sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 160). Maxilla with apex

conical, palpus peg-like with 5 sensilla, each bearing one spinule (Fig. 160). Galea conical with 2 apical sensilla bearing spinules (Fig. 160). Maxilla with sclerotized band between cardo and stipes. Labium with patches of spinules dorsal to each palpus, in 2–3 rows. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Stout. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.06–0.11 mm long) arranged in transverse row of 6–12 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.06–0.09 mm long) occur elsewhere, base ~0.5X length (Fig. 161).

Length. About 3.1 mm (Fig. 164).

Material examined.—Various specimens (FSCA). Also, see Appendices A and B.

Distribution.—The range of *Solenopsis invicta* in South America currently extends from as far north as Porto Velho, Rondônia State, Brazil and eastward from Peru and Bolivia to Cuiabá, Mato Grosso State, Brazil, southward to Santiago del Estero Province of Argentina, through Uruguay to São Paulo State, Brazil (Fig. 203). Its range in North America includes the Gulf States west to Texas. It is found sporadically in New Mexico and Arizona and apparently is well established in California. It recently has been introduced to Australia, Taiwan, China, and Japan (Henshaw et al. 2005; Ascunce et al. 2011). A comprehensive assessment of genetic variation for colonies sampled from 75 geographic sites worldwide revealed that at least nine separate introductions of *S. invicta* occurred into newly invaded areas and that the main southern U.S. population is probably the source of these secondary introductions (Ascunce et al. 2011).

Comments.—Although it was discovered that the name *S. wagneri* has priority over *S. invicta* (Bolton 1995), the International Commission of Zoological Nomenclature ruled that the name *S. invicta* is to be conserved in order to maintain stability and continuity (ICZN 2001).

As noted with the workers (Trager 1991; J. Pitts and K. R. Ross, pers. obs.), the gynes are highly variable in color. The darker variants of gynes are found in southeastern Brazil to Uruguay and Argentina and are associated with the darker workers. A lighter variant occurs in the northern area of the species' range. The gynes and workers of these colonies are also similar in coloration. A third variant, a light orange form, is found in the Pantanal region of Brazil. This form has larger workers and gynes. No morphological differences could be found between these forms, other than size and coloration.

The darker colored gynes of *S. invicta* look most similar to *S. megergates* and *S. quinquecuspis*. However, the CI and OI of *S. invicta* gynes are normally smaller than those of *S. megergates* and the OI of *S. invicta* is normally smaller than that of *S. quinquecuspis*. The lighter gynes of *S. invicta* look similar to *S. richteri* and *S. interrupta*. The gynes of *S. interrupta* normally are lighter in coloration than *S. invicta*, have larger cephalic foveolae, and sometimes have distinct striations between the foveolae. The OOI of *S. invicta* gynes is normally greater than that of *S. richteri*, and the postpetiole of *S. invicta* gynes has straight sides, unlike the concave sides of *S. richteri*. In many cases, the sculpture of the mandible and postpetiole can help separate *S. invicta* gynes from similar species. The gynes of *S. invicta* normally have the most densely sculptured postpetiole compared to the other species.

The male of *S. invicta* is dark in coloration and is similar to most of the other darker species. The pubescence of the *S. invicta* male is longer and denser than that of *S. saevissima*. Sometimes the head of the *S. invicta* male is shagreened as in *S. interrupta*. The gena of the male is much more sculptured than in other species. In moderate to extreme forms, this feature is easily recognized and it may be autapomorphic for *S. invicta*.

Allozyme, microsatellite, and mitochondrial DNA data suggest that the current concept of *S. invicta* might actually represent a group of several cryptic species (Ross and Shoemaker 2005; Shoemaker et al. 2006; Ross et al. 2007). A thorough examination of *S. invicta* adults from genetically distinct populations revealed no apparent morphological differences. In one colony of *S. invicta* (colony O-18, see Appendix A), the larvae differed from typical *S. invicta* both in size and setal type. This colony was collected in close proximity to typical *S. invicta* and the adults do not differ from typical *S. invicta.*

Fourth instar worker larva (O-18).—*Head*. Large, subpyriform in anterior view. Cranium slightly broader than long. Antenna with 2 or 3 sensilla, each bearing spinule. Integument of head with minute spinules. Occipital setal row with 4–6 setae (0.06–0.08 mm long), median pair simple, other setae bifid with base 0.66–0.75X total length of seta. First setal row on vertex with 2 simple setae, ~0.09 mm long. Second setal row on vertex with 2 simple setae, 0.10–0.12 mm long. Setae ventral to antenna level simple, 0.09–0.12 mm long. Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.05–0.10 mm long. Labrum small, short (width 1.8X length), slightly narrowed medially. Labrum with 5 minute sensilla and 2 setae on anterior surface of each half and ventral border with 6 sensilla on each half. Each half of posterior surface of labrum with 2–3 isolated sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size basally. Maxilla with apex conical, palpus peg-like with 5 sensilla, each bears one spinule. Galea conical with 2 apical sensilla. Labium with patch of spinules dorsal to each palpus, spinules coarse and isolated or in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.07–0.12 mm long) arranged in transverse rows of 6–9 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.08–0.12 mm long) occur elsewhere, base ~0.33X length, branches more or less perpendicular to base, tips recurved.

Length. 2.7–2.9 mm.

Solenopsis macdonaghi Santschi

(Figs. 25, 26, 60, 61, 76, 77, 96, 97, 136, 137, 165–169)

Solenopsis saevissima var. *macdonaghi* Santschi 1916: 379. [Syntype workers, gynes. ARGENTINA. Entre Rios. Estación Sosa. MacDonagh. NHMB.]
S. geminata pylades: Bruch 1916: 313.
S. (*Solenopsis*) *saevissima interrupta*: Creighton 1930: 89.
S. macdonaghi: Trager 1991: 179.

Worker.—Head broad, cordate (Fig. 137). Head sculpture with small piligerous foveolae, approximately 0.01 mm in diameter. Median frontal streak absent. Median ocellus in largest major workers present. Mandibular costulae obsolescent, except apically, rarely complete. Mesonotum with 20–25 setae (Fig. 136).

Promesonotal suture in largest major workers angulate medially, sometimes projecting upward (Fig. 136). Mesonotum in lateral view weakly convex. Propodeum sculpture glabrous posteroventral to spiracle (Fig. 136). Propodeum in largest major workers curves upward from metanotal groove higher than flattened posterior portion, appearing as anterior raised portion in lateral view. Postpetiole shape much broader than high. Postpetiole in posterior view lacking transverse rugae or with rugae medially, normally granulate to dorsum. Color generally red yellow to brown yellow, gaster dark brown, T1 with red yellow to brown yellow maculation.

Gyne.—*Head.* Slightly wider than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 26). Eyes sometimes with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large, prominent (Fig. 26). Median ocellus circular, lateral ocelli slightly ovate (Fig. 26). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, slightly divergent ventrally, edge of clypeus between carinae with shallow concave depression, depression deepest between carinal teeth (Fig. 26). Paracarinal teeth small, indistinct (Fig. 26). Median clypeal tooth poorly developed, usually absent (Fig. 26). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 26).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 25). Mesonotum with indistinct, median furrow present on posterior 0.25 or less. Bidentate median process present on metasternum. Wing venation as in Fig. 96.

Metasoma. Lateral faces of postpetiole straight to weakly convex. Petiolar and postpetiolar spiracles tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter. Pubescence simple, golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length >0.30 mm) 3X longer than shortest pubescence (Fig. 25). Mandible with 10–12 fine, distinct costulae present throughout. Propodeum with fine striae throughout (Fig. 25). Petiolar node with lower 0.75 of surface finely striate, dorsum polished. Postpetiole node with striations on lower 0.75 of surface somewhat coarser, 7–9 striae, finely granulate, dorsum polished (Fig. 41). Remaining integument smooth and polished. Color varies from orange to dark orange and legs orange to yellow orange with T1-T4 brown laterally and apically. Basal orange coloration of T1 blends evenly to brown apically. Mesonotum maculations absent on parapsidal lines, although sometimes present anteromedially. Internal margins of ocelli not dark brown. Median frontal streak absent.

Morphometric Measurements. L ~6.9–7.5, HW 1.42–1.46, VW 0.85–0.92, HL 1.22–1.34, EL 0.41–0.46, OD 0.12–0.15, OOD 0.23–0.25, LOW 0.08–0.11, MOW 0.10–0.14, CD 0.15–0.17, MFC 0.18–0.20, EW 0.30–0.34, SL 0.95–1.05, PDL 0.21–0.25, LF1 0.10–0.14, LF2 0.07–0.11, LF3 0.07–0.09, WF1 0.07–0.09, FL 1.20–1.25, FW 0.26–0.27, MW 1.35–1.45, DLM 2.48–2.84, PRH 1.02–1.09, PL 0.73–0.82, PND 0.54–0.70, PH 0.65–0.70, PPL 0.32–0.38, DPW 0.65–0.70, PPW 0.70–0.75, PHB 0.35–0.40, N=7.

Male.—*Head.* Eyes normally with 2–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli moderate to large, prominent, elliptical (Fig. 61).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except

with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron not broad, ~0.66 as wide as high (Fig. 60). Wing venation as in Fig. 97.

Metasoma: In cephalic view, dorsum of node with deep median depression, bilobate. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia as in Figs. 76 and 77.

Coloration, Sculpturing, and Pilosity. Pubescence short, thin, yellow, erect to suberect and of uniform length over body (0.25–0.30 mm), longest on gena and vertex. Mesonotal pubescence dense (as in Fig. 73). Propodeum with base striato-granulate, medially finely granulate. Area between eye and insertion of antenna, pronotum posteriorly and base of petiolar node coarsely granulate. Posterior surface of postpetiolar node granulate throughout. Area between ocelli and vertex finely striato-granulate to granulate (Fig. 61). Areas anterolateral to median ocellus usually glabrous (Fig. 61). Gena coarsely granulate, less often rugose anterior to occipital carina, never rugose throughout. Metapleuron and lateral faces of scutellum striato-granulate. Remaining integument smooth and polished. Color red brown to black, antennae and legs yellow brown. Mandibles yellow, extreme apex brown.

Morphometric Measurements. L ~5.7–6.6, HW 1.00–1.20, VW 0.34–0.39, HL 0.74–0.89, EL 0.40–0.52, OD 0.08–0.11, OOD 0.15–0.28, LOW 0.10–0.18, MOW 0.13–0.16, CD 0.16–0.22, MFC 0.13–0.18, EW 0.34–0.41, SL 0.14–0.18, SW 0.09–0.11, PDL 0.05–0.08, PEW 0.12–0.15, LF1 0.20–0.24, LF2 0.12–0.15, LF3 0.14–0.18, WF1 0.07–0.10, FL 0.95–1.30, FW 0.15–0.22, MW 1.35–1.62, DLM 2.28–2.80, PRH 0.80–1.10, PL 0.55–0.65, PND 0.50–0.60, PH 0.43–0.63, PPL 0.25–0.34, DPW 0.50–0.74, PPW 0.54–0.79, PHB 0.20–0.29, N=10.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.47 mm, width 0.54 mm) (Figs. 165, 169). Cranium slightly wider than long. Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 165, 169). Occipital setal row with 6–8 setae, median pair simple (Fig. 171) otherwise bifid, base 0.5–0.66X total length of seta, 0.06–0.10 mm long (Figs. 165, 169). First setal row on vertex with 2 denticulate to simple setae, 0.10–0.11 mm long. Second setal row on vertex with 4 simple setae, 0.10–0.13 mm long (Figs. 165, 169), rarely denticulate. Setae ventral to antenna level simple, 0.12–0.16 mm long (Figs. 165, 169). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.10–0.11 mm long (Figs. 165, 169). Labrum small, short (breadth 2X length). Labrum with 4–6 sensilla and 2 setae on dorsal surface of each half. Apex with 4–6 sensilla on each half. Each half of epipharynx with 2–3 isolated sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 168). Maxilla with apex conical, palpus peg-like with 5 sensilla, 1 bears spinule. Galea conical with 2 apical sensilla bearing spinules. Labium with patch of spinules dorsal to each palpus, spinules in rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.06–0.12 mm long) arranged in transverse row of 6–10 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.09–0.14 mm long) occur elsewhere, base 0.66X length (Fig. 166). Bifid setae on thoracic dorsum with shorter bases.

Length. 3.4–3.5 mm.

Material examined.—Various specimens (FSCA). Also, see Appendix A.

Distribution.—*Solenopsis macdonaghi* is found throughout the floodplains of eastern Argentina and western Uruguay (Fig. 202). Several records exist for Paraguay. Trager (1991) reports a population at Cochabamba, Bolivia but this is far removed from the known range of *S. macdonaghi* and, in fact, may represent an introduction.

Comments.—Superficially, the lighter gynes of *S. macdonaghi* look most similar to *S. interrupta* and *S. metallica* in coloration. However, the coloration does differ by being a somewhat duller yellow orange in *S. macdonaghi*. Also, the *S. macdonaghi* gynes lack the large piligerous foveolae on the head and mesosoma, along with interfoveolar striae, which are characters present in *S. interrupta* and *S. metallica.* The gynes of these three species also differ slightly to greatly in sculpturing of the postpetiole and can be normally distinguished by this character.

Trager (1991) reported that the heads of *S. macdonaghi* gynes are typically broader than other species, but this observation was based on a limited number of specimens. Additional measurements have shown this not to be the case (Table 5).

The males of *S. macdonaghi* closely resemble other species, but they, along with *S. saevissima*, are among the largest males. The males of *S. macdonaghi* look most similar to *S. quinquecuspis* in size, shape and coloration. Although males of *S. macdonaghi* are normally less coarsely sculptured than *S. quinquecuspis,* the males of these two species are not easily distinguished. Males of *S. macdonaghi* are also very similar to *S. megergates*, but the CI for males of *S. macdonaghi* is somewhat smaller than for *S. megergates*.

The larva of *S. macdonaghi* is distinct from that of *S. saevissima* in that it has bifid setae on the head capsule. The larva of *S. macdonaghi* is virtually indistinguishable from that of *S. megergates* and *S. quinquecuspis,* despite the smaller body size and the longer base of the body setae in *S. macdonaghi.*

Solenopsis megergates Trager

(Figs. 27, 28, 62, 63, 78, 79, 98, 99, 138, 139, 170–175)

Solenopsis megergates Trager 1991: 181–182. [Holotype worker. BRAZIL. Paraná State. 4 km North of Curitiba. Trager. MZSP.]

Worker.—Head broad, cordate (Fig. 139). Head sculpture with small piligerous foveolae, approximately 0.01 mm in diameter. Median frontal streak absent or faint. Median ocellus in largest major workers present (absent in Fig. 139). Mandibular costulae usually present throughout, sometimes obsolescent. Mesonotum with 20–25 setae (Fig. 138). Mesonotum weakly convex, in lateral view (Fig. 138). Promesonotal suture in largest major workers angulate, sometimes projecting upward (Fig. 138). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 138). In largest major workers, propodeum curves directly to flattened posterior portion (Fig. 138). Postpetiole shape much broader than high. Postpetiole in posterior view transversely rugose on lower 0.50–0.75, weakly granulate, sculpture not extending to dorsum. Color red brown on head, mesosoma, legs and T1 maculation. Color dark brown on metasoma excluding maculation.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 28). Eye sometimes with 3–4 setae protruding from between ommatidia, length most setae <3X length of ommatidium, sometimes setae longer, ~4X length of

ommatidium. Ocelli large, prominent (Fig. 28). Median ocellus circular, lateral ocelli slightly ovate (Fig. 28). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, less so dorsally, slightly divergent ventrally (Fig. 28). Paracarinal teeth small, sometimes poorly defined (Fig. 28). Median clypeal tooth well developed, infrequently indistinct (Fig. 28). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 28).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 27). Mesonotum with indistinct, posteromedian furrow. Wing venation as in Fig. 98.

Metasoma. Lateral faces of postpetiole straight to weakly concave. Petiolar and postpetiolar spiracles tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae moderate, width 0.005–0.03 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length >0.30 mm) 2X longer than shortest pubescence (Fig. 27). Sometimes fine striae present between ocelli. Mandible with 5–7 coarse, distinct costulae present, sometimes obsolescent medially. Propodeum with fine striae posteriorly, anterior 0.25 polished (Fig. 27). Petiolar nodes with lower 0.50 of posterior surface finely striate to granulate, dorsum polished. Postpetiole with 12–16 striations, dorsum finely granulate to polished. Remaining integument smooth and polished. Color varies from red brown to brown orange. Ocellar triangle sometimes darkly pigmented. Legs usually red brown, sometimes becoming lighter than body (yellow brown). Mesonotal maculations present anteromedially and parapsidal lines, usually black to dark brown, sometimes only slightly discernable from surrounding integument. Integument along internal margins of ocelli usually brown. Median frontal streak absent, sometimes area is slightly darker than surrounding integument.

Morphometric Measurements. L ~7.4–8.9, HW 1.35–1.68, VW 0.90–1.02, HL 1.22–1.42, EL 0.40–0.48, OD 0.14–0.20, OOD 0.20–0.28, LOW 0.10–0.12, MOW 0.10–0.12, CD 0.16–0.26, MFC 0.16–0.28, EW 0.30–0.42, SL 0.95–1.15, PDL 0.21–0.25, LF1 0.10–0.14, LF2 0.08–0.11, LF3 0.07–0.11, WF1 0.05–0.08, FL 1.15–1.32, FW 0.25–0.30, MW 1.46–1.54, DLM 2.51–2.82, PRH 0.90–1.25, PL 0.71–0.79, PND 0.55–0.68, PH 0.65–0.75, PPL 0.30–0.41, DPW 0.56–0.68, PPW 0.74–0.79, PHB 0.38–0.45, N=6.

Male.—*Head.* Eye normally with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli moderate to small, elliptical (Fig. 63).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron not broad, ~0.33 as wide as high (Fig. 62). Wing venation as in Fig. 99.

Metasoma. In anterior view, dorsum of node with deep median impression, bilobate. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia as in Figs. 78 and 79.

Coloration, Sculpturing, and Pilosity. Pubescence short, thin, yellow, erect to suberect and of uniform length over body (0.25–0.30 mm), longest on gena and vertex. Mesonotal pubescence dense (as in Fig. 73). Propodeum with base striato-granulate (Fig. 62). Area between eye and insertion of antenna (Fig. 63), posterior portion of metapleuron, and

base of petiolar node granulate. Sometimes, base of petiolar node rugose to striato-granulate. Area between ocelli (Fig. 63) and gena striato-granulate. Vertex granulate (Fig. 63). Areas anterolateral to median ocellus usually glabrous (Fig. 63). Lower 0.25 of postpetiole finely striato-granulate to granulate, remaining surface granulate. Lateral faces of scutellum glabrous (Fig. 62). Remaining integument smooth and polished. Color red brown to brown, antennae and legs brown yellow. Mandibles yellow to yellow brown.

Morphometric Measurements. L ~5.0–6.7, HW 0.97–1.10, VW 0.30–0.38, HL 0.66–0.80, EL 0.40–0.49, OD 0.06–0.09, OOD 0.12–0.18, LOW 0.09–0.12, MOW 0.10–0.15, CD 0.15–0.18, MFC 0.13–0.16, EW 0.30–0.38, SL 0.16–0.18, SW 0.09–0.10, PDL 0.05–0.06, PEW 0.10–0.15, LF1 0.14–0.21, LF2 0.10–0.15, LF3 0.13–0.16, WF1 0.06–0.09, FL 1.04–1.11, FW 0.16–0.21, MW 1.40–1.54, DLM 2.35–2.44, PRH 0.81–1.05, PL 0.61–0.66, PND 0.56–0.61, PH 0.46–0.54, PPL 0.22–0.31, DPW 0.56–0.63, PPW 0.65–0.69, PHB 0.21–0.28, N=8.

Fourth instar worker larva.—*Head.* Large, subpyriform in anterior view (height 0.46 mm, width 0.50 mm) (Figs. 170, 173). Cranium slightly broader than long (Figs. 170, 173). Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 170, 171, 173). Occipital setal row with 4–6 setae (0.06–0.08 mm long) (Figs. 170, 173); inner and outer setae simple to denticulate, otherwise bifid, base ~0.75 length of seta (Figs. 170, 173, 174). First setal row on vertex with 2 simple to denticulate setae, 0.07–0.08 mm long (Figs. 170, 173, 174). Second setal row on vertex with 4 simple setae, 0.09–0.13 mm long (Figs. 170, 173, 174). Setae ventral to antenna level simple, 0.08–0.14 mm long (Figs. 170, 173, 174). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.06–0.10 mm long (Figs. 170, 173, 174). Labrum small, short (breadth ~2X length). Labrum with 4 sensilla and 2 setae on dorsal surface of each half and apex with 6 sensilla on each half. Each half of epipharynx with 3–5 isolated. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 172). Maxilla with apex conical, palpus peg-like with 5 sensilla, each bearing one spinule. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with patch of spinules dorsal to palpus, in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Integument with fine rugae throughout. Body setae of 2 types (Fig. 175). Simple setae (0.04–0.14 mm long) arranged in transverse row of 6–10 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.06–0.11 mm long) occur elsewhere, base ~0.5X length (Figs. 174, 175), some with bases ~0.75X (0.08–0.10 mm long) on thoracic dorsum posterior to head capsule.

Length. 3.7–3.8 mm.

Material examined.—Various specimens (FSCA). Also, see Appendix A.

Distribution.—The type specimens were unavailable for study. The type series locality is Curitiba, Paraná, Brazil (Trager 1991). *Solenopsis megergates* is currently known only from the three southern Brazilian states of Paraná, Santa Catarina, and Rio Grande do Sul (Fig. 202).

Comments.—Gynes and workers of *S. megergates* are similar in coloration. The workers of this species are the largest of any of the fire ants. The gynes, along with those of *S. macdonaghi* and *S. saevissima*, are the largest gynes in

this group. The darker-colored gynes of *S. megergates* could be confused with *S. invicta,* but the CI and OI of *S. megergates* are normally larger than those of *S. invicta.* In many cases, the sculpture of the mandible and postpetiole for workers can help separate *S. megergates* from similar species.

The males of *S. megergates* are distinct from all other species by lacking sculpture on the lateral faces of the scutellum; the males of the other species have weakly to strongly striate lateral faces. Also, the males of *S. megergates* usually have smaller ocelli than their closest relatives (Pitts et al. 2005), *S. macdonaghi* and *S. quinquecuspis*.

The larvae of *S. megergates* are distinct from the *S. saevissima* type by having simple setae on the head capsule. The larvae are virtually identical to *S. macdonaghi* and *S. quinquecuspis*. The *S. megergates* larvae have bifid setae on the body that differ slightly from *S. macdonaghi* and *S. quinquecuspis* by having a slightly longer base.

Solenopsis pusillignis Trager

(Figs. 29, 30, 45, 64, 65, 80, 87, 88, 140, 141, 190–194)

Solenopsis pusillignis Trager 1991: 194. [Holotype worker. BRAZIL. Mato Grosso State. Cuiabá. Trager. MZSP.]

Worker.—Head subovate to cordate (Fig. 141). Head sculpture with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak absent. Median ocellus in largest major workers absent. Mandibular costulae well developed throughout entire length at least medially. Mesonotum with 20–25 setae (Fig. 140). Promesonotal suture in largest major workers gently curved medially, never projecting upward (Fig. 140). Propodeum sculpture granulate posteroventral to spiracle (Fig. 140). Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view with lower 0.75 transversely rugose, granulate, weakly granulate to glabrous and shiny. Color generally brown yellow to darker yellow brown with brown gaster.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight anterior to eyes (Fig. 30). Eye sometimes with 6–10 long setae protruding from between ommatidia, setal length >4X length of ommatidia. Ocelli large, prominent (Fig. 30). Median ocellus circular, lateral ocelli slightly ovate (Fig. 30). Ocelli placed in more anterior position on head (Fig. 30). Clypeus projecting, carinal teeth stout and sharp, carinae well defined, prominent between antennal scrobes, slightly divergent ventrally, edge of clypeus between carinae with shallow concave depression, depression deepest between carinal teeth (Fig. 30). Paracarinal teeth small, well defined (Fig. 30). Median clypeal tooth well developed (Fig. 30). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 30).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 29). Mesonotum with median furrow on posterior 0.25. Metasternum with bidentate median process. Wing venation as in Fig. 87.

Metasoma. Lateral faces of postpetiole weakly to strongly concave. In lateral view, petiolar node obtusely triangular, profile of peduncle flattened anteriorly, convex posteriorly. Postpetiole evenly convex. Postpetiolar spiracles weakly tuberculate.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, golden and erect, longer and denser on head than elsewhere,

longest on anterior edge of clypeus. Mesonotum pubescence 0.06–0.25 mm, longest pubescence on mesonotum 3–4X longer than shortest pubescence (Fig. 29). Mandible with 9–11 fine, distinct costulae present throughout. Propodeum with fine striae throughout (Fig. 29). Petiolar node basal 0.75 with striato-granulate, dorsum polished. Posterior face of postpetiolar node with lower 0.50–0.75 finely striate, lower 0.75 granulate, dorsum polished (Fig. 45). Remaining integument smooth and polished. Color generally orange with mandibles and antennae orange brown, apical and lateral margins of metasoma segments 3–6 brown, and internal margins of ocelli dark brown.

Morphometric Measurements. L ~6.6, HW 1.20, VW 0.80, HL 1.14, EL 0.29, OD 0.12, OOD 0.16, LOW 0.11, MOW 0.13, CD 0.13, MFC 0.16, EW 0.28, SL 0.83, PDL 0.17, LF1 0.09, LF2 0.07, LF3 0.08, WF1 0.06, FL 0.96, FW 0.23, MW 1.25, DLM 2.20, PRH 0.43, PL 0.61, PND 0.51, PH 0.60, PPL 0.34, DPW 0.50, PPW 0.62, PHB 0.36, N=1.

Male.—*Head.* Eye normally with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli very large and prominent, elliptical (Fig. 65).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron not broad, ~0.50 as wide as high (Fig. 64). Wing venation as in Fig. 88.

Metasoma. In cephalic view, dorsum of node with shallow median impression, weakly bilobate. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia as in Fig. 80.

Coloration, Sculpturing, and Pilosity. Pubescence short (0.15–0.20 mm), dense, yellow, erect to suberect and of uniform length over mesonotum, longest on gena and vertex. Mesonotal pubescence sparse (as in Fig. 72). Propodeum striato-granulate, medially finely granulate (Fig. 64). Lateral faces of scutellum striato-granulate (Fig. 64). Surface granulate in area between eye and insertion of antenna (Fig. 65), posterior portion of metapleuron, and base of petiolar node. Posterior surface of postpetiolar node with lower 0.25 finely striato-granulate, sometimes with lower 0.50 finely striato-granulate but glabrous medially, dorsum polished. Area between ocelli rugose to granulate (Fig. 65). Vertex glabrous posterior to ocelli. Several striae present anterior to occipital carina. Area posterior to eyes and antennal scrobes weakly granulate. Remaining integument smooth and polished. Head and gaster red brown. Clypeus, mandibles, petiole and postpetiole lighter yellow. Antennae and legs yellow. Mesosoma yellow to brown with median longitudinal stripe, area around parapsidal lines and scutellum red brown. Sometimes mesosoma yellow and parapsidal lines only slightly darker than surround integument.

Morphometric Measurements. L ~4.9–5.4, HW 0.95–1.0, VW 0.35–0.42, HL 0.74–0.80, EL 0.44–0.48, OD 0.10–0.14, OOD 0.10–0.13, LOW 0.16–0.17, MOW 0.16–0.19, CD 0.10–0.12, MFC 0.33–0.36, EW 0.3–0.40, SL 0.14–0.18, SW 0.07–0.10, PDL 0.05–0.08, PEW 0.10–0.12, LF1 0.17–0.19, LF2 0.13–0.15, LF3 0.13–0.14, WF1 0.09–0.10, FL 0.98–1.05, FW 0.15–0.19, MW 1.20–1.30, DLM 2.15–2.30, PRH 0.80–0.88, PL 0.65–0.66, PND 0.58–0.61, PH 0.40–0.42, PPL 0.26–0.30, DPW 0.49–0.55, PPW 0.55–0.64, PHB 0.14–0.16, N=8.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.44 mm, length 0.44 mm) (Figs.

190, 193). Cranium as broad as long (Figs. 190, 193). Antenna with 2 or 3 sensilla, each bears spinule (Figs. 190, 193). Occipital setal row with 10–12 bifid setae (less often 8), base ~0.3–0.5X total length of seta (Fig. 191), setae 0.05–0.10 mm long (Figs. 190, 193, 194). First setal row on vertex with 2 bifid setae, base ~0.5X total length of seta, ~0.07 mm long (Figs. 190, 193, 194). Second setal row on vertex with 4 setae, inner 2 setae simple to denticulate, outer 2 setae bifid (base ~0.5X length), 0.08–0.11 mm long (Figs. 190, 193, 194). Setae ventral to antenna level simple, 0.08–0.18 mm long (Figs. 190, 193, 194). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.08–0.11 mm long. Labrum small, short (breadth 2.4X length). Labrum with 5 minute sensilla and 2 setae on anterior surface of each half and ventral border with 4–6 sensilla on each half. Each half of posterior surface of labrum with 3–4 isolated and 2 contiguous sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 192). Maxilla with apex conical, palpus peg-like with 5 sensilla, 1 bears spinule. Galea conical, smaller than maxillary palpus, with 2 apical sensilla, each bearing one spinule. Labium with patch of spinules dorsal to each palpus, spinules coarse and isolated or in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.06–0.10 mm long) arranged in transverse row of 4–5 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.05–0.09 mm long) occur elsewhere, base varying between 0.2–0.5X length.

Length. 2.6–2.7 mm.

Material examined.—See Appendix A. (Holotype was unavailable for study.)

Distribution.—Currently, *S. pusillignis* is known from the type locality and the vicinity of Corumbá, Mato Grosso do Sul, Brazil (Fig. 203).

Variation.—Trager (1991) considered this to be a small species, but also reported measurements from one series of specimens that he thought were atypically large. All of the newly collected colonies reported here have larger workers that fall into the atypical ranges noted in parenthesis by Trager (1991). Thus, this species is larger than first thought. In addition, some of the major workers have their heads deeply emarginate posteriorly (Fig. 141), a distinctive feature that was not mentioned previously.

Comments.—The gynes and workers of *S. pusillignis* superficially look like small *S. macdonaghi*. This species is easily distinguished from *S. macdonaghi* and others, however, by having yellow workers with the posterodorsal and posteroventral area of the propodeal spiracle granulate, and by having the heads of the largest workers deeply emarginate (Fig. 141). This species also has small gynes with small OOI measurements and large OI measurements and light-colored males with mesonotal maculae. The gynes of *S. pusillignis* differ from *S. electra* in coloration of the gaster (*S. pusillignis* has a lighter gaster and has a weakly developed T1 maculation), and *S. pusillignis* has a less developed median clypeal tooth.

The males of *S. pusillignis* normally have relatively large ocelli. This suggests that they may be nocturnally active.

The larvae of this species are also distinct in having more setae on the head capsule (10–12) than other species

(normally 8 or less). Also, some have denticulate setae on the body, which differ from those found in some *S. saevissima* by being denticulate only at the extreme apex.

Solenopsis pythia Santschi

(Figs. 31, 32, 46, 51, 53)

Solenopsis pythia Santschi 1934: 30. [Holotype gyne. ARGENTINA. Misiones Province. Lorento. A. A. Oglobin. NHMB.]

S. (*Solenopsis*) *pythia* Wilson 1952: 61.

Worker.—Head weakly ovate to subquadrate. Head sculpture with small piligerous foveolae, approximately 0.01 mm in diameter. Median frontal streak absent. Median ocellus absent in largest major workers. Mandibular costulae present throughout. Mesonotum with 20–25 setae. Promesonotal suture in largest major workers gently curved medially. Mesonotum weakly convex in lateral view. Propodeum sculpture glabrous posteroventral to spiracle. Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view with lower 0.33–0.50 transversely rugose, upper surface glabrous and shiny. Color generally orange brown, with frons, clypeus and venter yellow brown.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 32). Eye normally with 2–4 several short setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large, prominent (Fig. 32). Median ocellus circular, lateral ocelli slightly ovate (Fig. 32). Clypeus projecting, carinal teeth stout and sharp, carinae weakly to moderately defined, less so dorsally, slightly divergent ventrally (Fig. 32). Paracarinal teeth usually absent, or more rarely poorly defined (Fig. 32). Median clypeal tooth poorly developed, usually absent (Fig. 32). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 32). Antenna usually 11-segmented, sometimes 10-segmented.

Mesosoma. Parapsidal lines present on posterior half of disk (Fig. 31). Mesonotum with distinct, median furrow on posterior 0.50 to 0.33 on disk. Posterior margin of mesonotum angulate medially, bent anteriorly. Posterior margin of scutellum sometimes angulate medially. Metasternum lacking median bidentate process. Wings not examined.

Metasoma. Lateral faces of postpetiole strongly to slightly concave. Petiolar spiracle weakly tuberculate. Postpetiolar spiracle not tuberculate.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae large, conspicuous, width 0.010–0.020 mm in diameter (Fig. 32), slightly larger on head than on thorax and abdomen (Fig. 32). Dorsum of mesosoma with distinctly piligerous foveolae (Fig. 51). Pubescence simple, golden and erect, of uniform length (0.15–0.20 mm) (Fig. 53), longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mandible with several coarse, distinct costulae present throughout. Propodeum and petiole postpetiole striato-rugulose throughout (Fig. 31). Postpetiole striato-rugulose throughout, sometimes extreme dorsum glabrous (Fig. 46). In some cases, sculpture of postpetiole tuberculate and dorsum finely granulate. Interfoveolar spaces of head and pronotum finely striate; striae distinct to indistinct (Fig. 32). Remaining interfoveolar spaces smooth and polished. Color yellow orange with medial area of mesonotum, parapsidal lines, lateral margins of T1 and preapical transverse areas on gaster segments brown (Fig. 53). Internal margins of ocelli sometimes brown.

Morphometric Measurements. L ~5.3–6.2, HW 1.3, VW 0.7–0.8, HL 1.0–1.1, EL 0.4–0.5, OD 0.1–0.15, OOD 0.15–0.25, LOW 0.08–0.12, MOW 0.10–0.12, CD 0.14–0.16, MFC 0.15–0.18, EW 0.35–0.40, SL 0.69–0.82, PDL 0.16–0.18, LF1 0.1, LF2 0.1, LF3 0.1, WF1 0.06–0.07, FL 0.91–1.02, FW 0.19–0.25, MW 1.18–1.32, DLM 2.28–2.44, PRH 0.90–1.03, PL 0.72–0.83, PND 0.61–0.73, PH 0.62–0.72, PPL 0.32–0.43, DPW 0.49–0.84, PPW 0.48–0.61, PHB 0.58–0.71, N=7.

Male.—Unknown.

Fourth instar worker larva.—Unknown.

Material examined.—Specimens examined were from Campo Grande, Mato Grosso do Sul, Brazil, Boctucatua, São Paulo State, Brazil (FSCA), and Posadas, Misiones Province, Argentina (JPPC, SDPC).

Distribution.—Currently, this species is known from the material listed above and the type locality of Loreto, Misiones Province, Argentina (Fig. 202).

Comments.—The major workers of *S. pythia* look like small workers of *S. saevissima*. The gynes, however, are easily recognized by having acute occipital angles, large piligerous foveolae of the head and mesosoma, coarse costulae on the mandibles, a small OI, a distinct median furrow on the posterior 0.33 to 0.50 of the mesonotum, and a thick coarsely sculptured petiolar node. Trager (1991) lists piligerous foveolae size as 0.01–0.15 mm: this must be a misprint and should read "0.010–0.015 mm." The petiolar node is shorter and subquadrate and the posterior angles of propodeum are more defined than in *S. saevissima*. This is the only species in the *S. saevissima* species-group that lacks the bidentate metasternal process.

Solenopsis pythia has been suggested by some (e.g., Trager 1991) to be so unique that it is suspected to be a social parasite. Many of the gyne characters may actually be sympleisomorphic, as they are shared with the gynes in the *S. molesta* species-group. These characters include a quadrate first flagellomere, large and conspicuous piligerous foveolae on the head and mesosoma, coarse costulae of the mandibles, thick and coarsely sculptured petiolar node, short and subquadrate petiolar node, well demarcated posterior angles of propodeum, and absent bidentate process of the metasternum. There are obvious synapomorphic *S. saevissima* species-group characters in *S. pythia*, however, such as the lack of a ventral petiolar process in gynes and workers.

Several dealated (wingless) gynes were collected from a single nest, suggesting that polygyny may occur in this species.

Solenopsis quinquecuspis Forel

(Figs. 33, 34, 43, 55, 66, 67, 81, 100, 101, 142, 143, 176, 178–181)

Solenopsis pylades var. *quinquecuspis* Forel 1913: 224. [Syntype workers. ARGENTINA. Buenos Aires Province. Bahia Blanca. 28-X-913 (=1913). Zelenko. NHMB.]

S. geminata saevissima var. *quinquecuspis*: Wheeler 1915: 397.

S. saevissima var. *quinquecuspis*: Santschi 1916: 381.

S. (*Solenopsis*) *saevissima quinquecuspis*: Creighton 1930: 86.

S. blumi Buren 1972: 20. [NMNH.]

Worker.—Head broad, cordate (Fig. 143). Head sculpture with small piligerous foveolae, approximately 0.01 mm in diameter. Median frontal streak present, sometimes indistinct. Median ocellus in largest major workers present (absent in Fig. 143). Mandibular costulae present throughout, sometimes obsolescent.

Mesonotum with 20–25 setae. Promesonotal suture in largest major workers angulate medially, sometimes projecting upward. Mesonotum in lateral view weakly convex (Fig. 142). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 142). Propodeum in largest major workers curves upward from metanotal groove higher than flattened posterior portion, appearing as anterior raised portion in lateral view. Postpetiole shape much broader than high. Postpetiole in posterior view with at least 0.75 transversely rugose to punctate-rugose, rugosity sometimes extending to dorsum. Color generally brown to dark brown on head, mesosoma, and median area of petiole. Gaster dark brown. Frons, clypeus, and T1 maculation brown orange.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 34). Eye sometimes with 3–12 setae protruding from between ommatidia, most setae ≤3X length of ommatidium, sometimes one or two ≤4X length of ommatidium. Median ocellus moderate, circular (Fig. 34). Lateral ocelli slightly ovate, small to moderate (Fig. 34). Clypeus projecting, carinal teeth stout and sharp, carinae indistinct between scrobes, slightly divergent ventrally (Fig. 34). Paracarinal teeth small, usually well defined (Fig. 34). Median clypeal tooth well developed (Fig. 34). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 34).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 33). Mesonotum without posteromedian furrow. Bidentate medial process present on metasternum. Wing venation as in Fig. 100.

Metasoma. Lateral faces of postpetiole weakly concave to weakly convex. Petiolar and postpetiolar spiracles slightly tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, pale brown to yellow and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length >0.30 mm) 2X longer than shortest pubescence (Fig. 33). Mandible with 10–12 fine costulae. Propodeum with fine striae throughout (Figs. 33, 55). Posterior face of petiolar nodes with 0.75 of lower surface finely striato-granulate. Often, median striae of postpetiole obsolescent laterally; normally 11–13 striae present (Fig. 43). Dorsum glabrous. Remaining integument smooth and polished. Color generally red brown. Venter of head, frons and coxae orange yellow. Gaster dark brown, sometimes orange anteriorly. T1 and S1 orange on basal 0.50 of disk, blending to red brown apically. Dark brown maculations present on mesonotum both anteromedially and on parapsidal lines (as in Fig. 52). Median longitudinal maculation sometimes reaches scutellum. Internal margins of ocelli not brown. Median frontal streak present (as in Fig. 50).

Morphometric Measurements. L ~7.1–7.7, HW 1.40–1.45, VW 0.81–0.95, HL 1.24–1.36, EL 0.40–0.44, OD 0.13–0.16, OOD 0.15–0.20, LOW 0.11–0.16, MOW 0.09–0.13, CD 0.17–0.20, MFC 0.15–0.23, EW 0.30–0.34, SL 0.94–1.01, PDL 0.17–0.19, LF1 0.08–0.11, LF2 0.07–0.10, LF3 0.06–0.09, WF1 0.06–0.07, FL 1.10–1.20, FW 0.26–0.31, MW 1.26–1.33, DLM 2.50–2.70, PRH 1.00–1.05, PL 0.65–0.72, PND 0.56–0.61, PH 0.66–0.75, PPL 0.25–0.34, DPW 0.50–0.71, PPW 0.60–0.74, PHB 0.36–0.44, N=7.

Male.—*Head.* Eye normally with 2–8 setae protruding from between ommatidia, setae length ≤3X length of ommatidium.

Ocelli large and prominent, elliptical (Fig. 67).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron broad, ~0.66 as wide as high (Fig. 66). Wing venation as in Fig. 101.

Metasoma. In cephalic view, dorsum of node with deep median impression, bilobate, sometimes lobes curve posteriorly. Petiolar spiracle distinctly tuberculate to not tuberculate. Postpetiolar spiracle distinctly tuberculate. Genitalia as in Fig. 81.

Coloration, Sculpturing, and Pilosity. Pubescence short, yellow, erect to suberect (0.25–0.30 mm in length) on mesonotum. Mesonotal pubescence dense (as in Fig. 73). Some shorter pubescence (0.15 mm in length) also on mesonotum. Pubescence longest on gena and vertex. Propodeum with base striato-granulate, medially coarsely granulate (Fig. 66). Integument coarsely granulate on area between eye and insertion of antenna, area between ocelli, margins of metapleuron, and base of petiolar node (Figs. 66, 67). Vertex and, sometimes, gena striato-granulate. Head usually glabrous and shiny anteroventral to lateral ocelli. Head otherwise granulate. Pronotum granulate posteriorly. Mesonotum sometimes with coarsely granulate to striate margins. Posterior surface of postpetiolar node coarsely granulate throughout, sometimes rugose. Lateral faces of scutellum striate (Fig. 66). Remaining integument smooth and polished. Color generally dark brown to black, legs brown. Antennal scape, pedicel and first flagellum brown, distal portion of flagellum blending to yellow apically. Mandibles yellow brown to brown.

Morphometric Measurements. L ~5.3–6.0, HW 1.02–1.10, VW 0.36–0.41, HL 0.77–0.82, EL 0.46–0.50, OD 0.09–0.12, OOD 0.14–0.23, LOW 0.10–0.14, MOW 0.11–0.14, CD 0.17–0.21, MFC 0.10–0.15, EW 0.32–0.37, SL 0.15–0.23, SW 0.07–0.12, PDL 0.05–0.08, PEW 0.11–0.16, LF1 0.15–0.22, LF2 0.10–0.17, LF3 0.15–0.19, WF1 0.09–0.12, FL 1.05–1.22, FW 0.16–0.21, MW 1.41–1.52, DLM 2.36–2.53, PRH 0.90–0.96, PL 0.64–0.67, PND 0.54–0.60, PH 0.25–0.28, PPL 0.24–0.35, DPW 0.50–0.62, PPW 0.61–0.70, PHB 0.20–0.28, N=8.

Fourth instar worker larva.—*Head.* Large, subpyriform in anterior view (height 0.49 mm, width 0.55 mm) (Figs. 176, 178). Cranium slightly broader than long (Figs. 176, 178). Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 176, 178). Occipital setal row with 6–8 simple setae, 0.09–0.13 mm long (Fig. 181); rarely some specimens with 1–2 denticulate setae (Figs. 178, 180). First setal row on vertex with 2 simple setae, 0.09–0.11 mm long (Figs. 176, 178). Second setal row on vertex with 4 simple setae, 0.12–0.13 mm long (Figs. 176, 178). Setae ventral to antenna level simple, 0.15–0.19 mm long (Figs. 176, 178). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.06–0.11 mm long (Figs. 176, 178). Labrum small, short (breadth 2X length), slightly narrowed medially (Figs. 176, 178). Labrum with 4 sensilla and 2 setae on anterior surface of each half. Ventral border with 4–6 sensilla on each half. Each half of posterior surface of labrum with 2–3 isolated sensilla. Straight medial portion of mandible with 1–4 teeth that decrease in size dorsally (Fig. 179). Maxilla with apex conical, palpus peg-like with 5 sensilla, each bearing one spinule. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with patch of

spinules dorsal to each palpus, in short rows of 2–3. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 2 types. Simple setae (0.04–0.10 mm long) arranged in transverse row of 6–8 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites, some with short denticulate tips. Bifid setae (0.07–0.11 mm long) occur elsewhere, base 0.5X length, branches more or less perpendicular to base, tips recurved. Setae on thoracic dorsum with short base (<0.2X length).

Length. Approximately 3.8 mm.

Material examined.—Various specimens (FSCA). Also, see Appendix A.

Distribution.—The current range of *S. quinquecuspis* extends south from Rio Grande do Sul, Brazil through Uruguay and into Argentina (Fig. 202). In Argentina, it occurs in Buenos Aires and La Pampa Provinces and the eastern edges of Santa Fé and Córdoba Provinces (Fig. 202).

Comments.—The gynes of *S. quinquecuspis* are similar to the darker colored gynes of *S. invicta.* However, the OI of *S. quinquecuspis* is normally larger than that of *S. invicta.*

The gynes of the darker varieties of *S. richteri* could be confused for *S. quinquecuspis*. In this case, the mesonotum of *S. richteri* is completely darkened and the mesonotal maculae are indiscernible. Also for *S. richteri*, the maculation on the first segment of the gaster covers the anterior 0.75 and it may end abruptly posteriorly. For *S. quinquecuspis* the maculation fades out gradually posteriorly. For *S. quinquecuspis*, this gaster maculation is only on the anterior 0.50 or less and is never distinctly margined posteriorly.

The male of *S. quinquecuspis* is dark in coloration and is similar to most of the other darker species. The pubescence is longer and denser than in *S. saevissima*. The *S. quinquecuspis* male normally is more coarsely sculptured than *S. macdonaghi.* The gena is not granulate nor is it as sculptured as in *S. invicta*.

The larvae of *S. quinquecuspis* are distinct from the *S. saevissima* type by having simple setae on the head capsule. The larvae of *S. quinquecuspis* are similar to *S. macdonaghi* and *S. megergates*. Although the body of *S. quinquecuspis* is larger and the setae on the body have a shorter base compared to *S. macdonaghi,* they are virtually indistinguishable. These larvae are much larger than the larvae of *S. richteri* (as expected given adult worker size), and lack multibranched setae and rugae on the head capsule.

Studies of nuclear and mtDNA genetic markers in *S. quinquecuspis* suggest that this species hybridizes with *S. invicta* and *S. richteri* in an area where the ranges of all three species overlap, in the vicinity of Rosario, Santa Fe Province, Argentina (Ross and Shoemaker 2005). In other areas of the range of *S. quinquecuspis*, there is no genetic evidence for such hybridization (Ross and Trager 1990).

Solenopsis richteri Forel

(Figs. 35, 36, 48, 68, 69, 82, 83, 102, 103, 144, 145, 185–189)

Solenopsis pylades var. *richteri* Forel 1909: 267. Syntype workers. [Syntype workers, gynes, males. ARGENTINA. Buenos Aires. Richter. MHNG.]

S. pylades var. *tricuspis* Forel 1912: 397. Syntype workers.

S. geminata saevissima var. *richteri*: Wheeler 1915: 397.

S. saevissima var. *richteri*: Santschi 1916: 281.

S. saevissima var. *tricuspis*: Santschi 1916: 281. [NHMB?]
S. (*Solenopsis*) *saevissima richteri*: Creighton 1930: 87.
S. saevissima var. *oblongiceps* Santschi 1936: 405. [NHMB]
S. saevissima richteri: Wilson 1952: 66.
S. richteri Buren 1972: 4. Worker, gyne, male.

Worker.—Head ovate to weakly cordate (Fig. 145). Head sculpture with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak absent. Median ocellus in largest major workers absent (Fig. 145). Mandibular costulae present, obsolescent medially. Humerus distinctly angulate, with distinct tuberculate boss. Mesonotum with 20–26 setae. Promesonotal suture curved medially, never projecting upward. Propodeum sculpture glabrous posteroventral to spiracle (Fig. 144). Postpetiole shape as high as or higher than broad. Postpetiole with lower 0.50 or less transversely rugose to punctate-rugose, dorsum and face dorsal to sculpture nitid, glabrous. Color generally black with mandibles, lateral areas of clypeus, antennal fossae, mesosomal sutures, and T1 maculations dark brown to yellow brown.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 36). Eye sometimes with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Median ocellus large (Fig. 36). Lateral ocelli small to moderate (Fig. 36). Median ocellus circular, lateral ocelli slightly ovate (Fig. 36). Clypeus projecting, carinal teeth stout and sharp, carinae sometimes indistinct, less so dorsally, slightly divergent ventrally (Fig. 36). Paracarinal teeth small, usually well defined (Fig. 36). Median clypeal tooth well developed (Fig. 36). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 36).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 35). Mesonotum with indistinct, median furrow on posterior 0.25 or less. Bidentate median process present on metasternum. Wing venation as in Fig. 102.

Metasoma. Lateral faces of postpetiole weakly to strongly concave. Petiolar and postpetiolar spiracles tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, pale brown to yellow and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Pubescence orange on T1 orange integumental maculation. Mesosoma with longest pubescence (length >0.30 mm) 2X longer than shortest pubescence (Fig. 35). Mandible with several coarse, distinct costulae, obsolescent medially. Propodeum with fine striae posteriorly, anterior 0.25 polished (Fig. 35). Posterior surface of petiolar node with 0.75 of lower surface with fine striae, dorsum polished. Posterior surface of postpetiolar node with 0.75 of lower surface finely striate, 12–14 striae present, median striae sometimes obsolescent laterally (Fig. 48), dorsum is polished to slightly granulate. Remaining integument smooth and polished. Two color forms exist. Dark form is dark brown except antennal scape black, flagellum brown to orange, both T1 and S1 with medial orange maculation, other sternites brown with dark brown apices, and petiole sometimes orange with dark brown dorsum. Maculations on T1 and S1 are well defined laterally and apically. Light form is orange except brown on vertex, around compound eyes, apically

on T1, and preapically on remaining tergites. Both forms have dark brown maculations anteriorly on pronotum, anteromedian area of mesonotum, area around parapsidal lines, sometimes on median area of axillae, anteromedian and triangular posteromedian area of scutellum, medially on anepisternum, and medially and laterally on propodeum (as in Fig. 52). Both forms have dark brown finger-like projections of pigment from preapical tergal bands to apical setae. Internal margins of ocelli dark brown. Median frontal streak usually absent, not discernable from surrounding integument.

Morphometric Measurements. L ~7.5–8.5, HW 1.4–1.5, VW 1.0–1.2, HL 1.2–1.3, EL 0.3–0.5, OD 0.1–0.2, OOD 0.15–0.20, LOW 0.08–0.10, MOW 0.10–0.15, CD 0.15–0.20, MFC 0.20–0.25, EW 0.30–0.40, SL 0.92–1.23, PDL 0.18–0.23, LF1 0.01–0.16, LF2 0.07–0.1, LF3 0.08–0.11, WF1 0.07–0.10, FL 1.10–1.23, FW 0.21–0.32, MW 1.40–1.55, DLM 2.46–2.73, PRH 1.00–1.12, PL 0.72–0.91, PND 0.51–0.60, PH 0.60–0.72, PPL 0.39–0.53, DPW 0.59–0.69, PPW 0.59–0.71, PHB 0.28–0.51, N=10.

Male.—*Head.* Eye normally with 2–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Ocelli large and prominent, elliptical (Fig. 69).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron broad, ~0.66 as wide as high (Fig. 68). Wing venation as in Fig. 103.

Metasoma. In cephalic view, dorsum of node transverse to having shallow median impression and weakly bilobate, sometimes lobes curve posteriorly. Petiolar spiracles distinctly tuberculate to not tuberculate. Postpetiolar spiracle distinctly tuberculate to greatly tuberculate, tubercles higher than width of base. Genitalia as in Figs. 82 and 83.

Coloration, Sculpturing, and Pilosity. Pubescence short, yellow, erect to suberect and of uniform length over body (0.15–0.20 mm), longest on gena and vertex. Mesonotal pubescence dense (as in Fig. 73). Propodeum with base striato-granulate, medially glabrous (Fig. 68). Integument coarsely granulate in area between eye and insertion of antenna, area between ocelli, pronotum, posterior portion of metapleuron, and base of petiolar node (Figs. 68, 69). Gena granulate, sometimes weakly striato-granulate. Head otherwise granulate. Posterior surface of postpetiolar node with lower 0.50 of surface striato-granulate, remainder polished. Metapleuron sometimes with striae both dorsally and ventrally. Lateral faces of scutellum striate (Fig. 68). Remaining integument smooth and polished. Color generally red brown to black. Antennae and legs yellow brown. Mandibles brown.

Morphometric Measurements. L ~6.1–6.5, HW 1.0–1.1, VW 0.4–0.5, HL 0.7–0.8, EL 0.4–0.5, OD 0.12–0.13, OOD 0.1–0.2, LOW 0.10–0.12, MOW 0.10–0.15, CD 0.17–0.23, MFC 0.10–0.15, EW 0.3–0.40, SL 0.15–0.20, SW 0.1–0.12, PDL 0.08–0.10, PEW 0.10–0.14, LF1 0.15–0.25, LF2 0.12–0.15, LF3 0.14–0.16, WF1 0.07–0.11, FL 1.1–1.2, FW 0.15–0.22, MW 1.39–1.52, DLM 2.40–2.62, PRH 0.89–1.12, PL 0.58–0.73, PND 0.51–0.60, PH 0.49–0.61, PPL 0.20–0.30, DPW 0.61–0.70, PPW 0.48–0.73, PHB 0.10–0.22, N=12.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.52 mm, width 0.55 mm) (Figs. 185, 189). Cranium slightly broader than long (Figs. 185, 189). Antenna with 2 or 3 sensilla, each bearing spinule (Figs. 185, 189). Integument of head with fine rugae. Occipital setal row with 6–8 simple setae, 0.08–0.14 mm, rarely

some specimens with single bifid to denticulate seta, base ~0.8–0.95X total length of seta (Fig. 185). First setal row on vertex with 2 simple setae, 0.09–0.11 mm long (Figs. 185, 189). Second setal row on vertex with 4 simple setae, inner 2 setae orientated farther from first setal row on vertex, appear out of alignment with row, 0.09–0.15 mm long (Figs. 185, 189). Setae ventral to antenna level simple, 0.11–0.18 mm long (Figs. 185, 189). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.06–0.10 mm long (Figs. 185, 189). Labrum small, short (breadth 2.8X length), slightly narrowed medially. Labrum with 4 minute sensilla and 2 setae on dorsal surface of each half and apex with 5–7 sensilla on each half. Each half of epipharynx with 2–3 isolated sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally (Fig. 188). Maxilla with apex conical, palpus peg-like with 5 sensilla, each bearing one spinule. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with isolated patches of spinules dorsal to each palpus. Labial palpus slightly elevated with 5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle larger than others. Body setae of 3 types. Simple setae, slightly curved (0.08–0.15 mm long), arranged in transverse row of 6–12 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites. Bifid setae (0.06–0.09 mm long) occur elsewhere, base ~0.5X length. Multibranched setae occur rarely in the area immediately posterior to head on thoracic dorsum (Figs. 186, 187).

Length. 2.7–3.1 mm.

Material examined.—Various specimens (FSCA). Also, see Appendix A.

Distribution.—In South America, the range of *S. richteri* extends from Paraná State, Brazil south and west from Misiones Province to Mendoza Province in Argentina (Fig. 203). This species also has been introduced into North America, where it is currently confined to the northwestern corner of Alabama, the northeastern corner of Mississippi, and south-central Tennessee. A broad *S. richteri* x *invicta* hybrid zone exists south and east of the *S. richteri* range, including much of Mississippi, northern Alabama, and the northwestern corner of Georgia (Shoemaker et al. 1996, Gardner et al. 2008, Oliver et al. 2009).

Comments.—The gynes of the lighter varieties of *S. richteri* and *S. interrupta* are very similar in coloration due to the first tergite of the gaster sometimes having an orange tergal maculation with a distinct posterior margin. In many cases, the gynes of these two species are difficult to differentiate. However, they differ in the sculpturing of the postpetiole. Also, *S. richteri* gynes are normally darker in coloration and the OOI is much smaller than in *S. interrupta*. The workers of *S. interrupta* are larger than *S. richteri* and easily separated. Gynes of *S. richteri* in the United States are of the light form and are similar to those found in the northern range of the species in southern Brazil. This is probably the point of origin for the United States population.

The gynes of *S. richteri* from the westernmost areas of the native range tend to be more darkly colored than the eastern representatives, resembling somewhat the darker *S. invicta* gynes. However, *S. richteri* gynes are much darker in coloration and usually have a distinct tergal maculation on the gaster. Also, the lateral margins of the postpetiole are more concave than in *S. invicta*. The gynes of *S. richteri* have weakly concave to straight lateral margins.

Males of *S. richteri* are similar in coloration to many of the species within the species-group. However, the OOI of *S. richteri* is much smaller than in

S. interrupta. Also, the males of *S. richteri* sometimes have a very distinct tuberculate postpetiolar spiracle. Usually in populations in the United States and in the southern part of the native range near Buenos Aires, the tuberculate postpetiolar spiracle is smaller and not as distinct. Males of *S. richteri* tend to have stronger sculpturing in the United States than they do in South America.

The larval stage described by Wheeler and Wheeler (1977) was collected in Walker County, Alabama. At the time of collection, this area was likely part of the *S. richteri* x *invicta* hybrid zone (Vander Meer et al. 1985, Vander Meer and Lofgren 1988). These specimens probably represent the larvae of *S. richteri* x *invicta*, rather than pure *S. richteri*. The description differs from that given above for *S. richteri* in several characters, the most conspicuous of which is the stated presence of bifid and denticulate setae on the head capsule. This is much more reminiscent of *S. invicta*. True *S. richteri* larvae lack bifid setae on the head capsule. The larvae differ from *S. quinquecuspis* by the presence of multi-branched setae and fine rugae on the head capsule, as well as being smaller in size.

Genetic studies of *S. richteri* in its native range have revealed pronounced nuclear and mtDNA differentiation between populations from southern Brazil and central Argentina (Ross and Shoemaker 2005), consistent with a long-term absence of gene flow between ants occupying these distant parts of its range.

Solenopsis saevissima (Smith)

(Figs. 37, 38, 49, 70, 71, 73, 84, 85, 90, 91, 104, 105, 146, 147, 177, 182–184)

Myrmica saevissima F. Smith 1855: 166. [Syntype ? worker. BRAZIL. Para State. Tapajós. Bates. BMNH.]

Solenopsis moelleri Forel 1904: 174. [MHNG.]

S. moelleri var. *gracilior* Forel 1904: 174. [MHNG?]

S. geminata var. *incrassata* Forel 1908: 362. [MHNG?]

S. geminata pylades Forel 1909: 262.

S. saevissima var. *morosa* Santschi 1916: 380. [NHMB.]

S. geminata saevissima var. *picea* Wasmann 1918: 70.

S. saevissima var. *perfida* Santschi 1923: 266. [NHMB.]

S. (*Solenopsis*) *saevissima saevissima*: Creighton 1930: 80–83.

S. saevissima var. *picea*: Kistner 1982: 73–74.

Worker.—Head subquadrate to weakly ovate (Fig. 147). Head sculpture with small piligerous foveolae, <0.01 mm in diameter. Median frontal streak absent. Median ocellus in largest major workers absent (Fig. 147). Mandibular costulae present throughout. Mesonotum with 20–25 setae. Promesonotal suture in largest major workers gently curved medially, never projecting upward (Fig. 146). Mesonotum weakly convex in lateral view (Fig. 146). Propodeum sculpture glabrous posteroventral to spiracle (Fig. 146). Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view with lower 0.33–0.50 transversely rugose, upper surface glabrous and shiny. Color generally red brown to dark brown.

Gyne.—*Head.* Slightly broader than long, quadrate, sides of head convex from eyes to occipital angles, straight to nearly straight ventral to eyes (Fig. 38). Eye sometimes with 3–4 setae protruding from between ommatidia, setal length ≤3X width of ommatidium. Median ocellus large, circular (Fig. 38). Lateral ocelli moderate to large, slightly ovate (Fig. 38). Clypeus projecting,

carinal teeth stout and sharp, carinae well defined, less so dorsally, slightly divergent ventrally (Fig. 38). Paracarinal teeth small, sometimes poorly defined (Fig. 38). Median clypeal tooth poorly developed, usually absent (Fig. 38). Approximately 0.50 of eye dorsal to midpoint of head (Fig. 38).

Mesosoma. Parapsidal lines present on posterior 0.50 of disk (Fig. 37). Mesonotum with indistinct, median furrow on posterior one-sixth or less. Median bidentate process present on metasternum. Wing venation as in Figs. 90, 104.

Metasoma. Lateral faces of postpetiole weakly to strongly concave. Petiolar and postpetiolar spiracles tuberculate in some cases.

Coloration, Sculpturing, and Pilosity. Piligerous foveolae small, sparse, width <0.01 mm in diameter, larger on head than on thorax and abdomen. Pubescence simple, golden and erect, longer and denser on head than elsewhere, longest on anterior edge of clypeus. Mesosoma with longest pubescence (length >0.30 mm) 2X longer than shortest pubescence (Fig. 37). Mandible with 9–11 fine, distinct costulae present throughout. Propodeum with fine striae posteriorly, anterior 0.25 polished (Fig. 37). Posterior surface of petiolar node with lower 0.75 of surface with fine striae, dorsum polished. Posterior surface of postpetiolar node with lower 0.75 of surface with coarse striae, 4–7 striae present, median striae weak to obsolescent laterally, dorsum polished (Fig. 49). Remaining integument smooth and polished. Color varies from dark brown to pale yellow on front of head, lateral portions of mesonotum, mandibles, mesosternum, appendages and apical portions of gaster segments. Color brown on vertex, interior margins of ocelli, medial area of mesonotum, parapsidal lines, lateral margins of T1 and preapical transverse areas on metasomal segments. Internal margins of ocelli dark brown. Median streak absent.

Morphometric Measurements. L ~7.1–8.0, HW 1.3–1.8, VW 0.5–0.9, HL 1.2–1.3, EL 0.4–0.6, OD 0.1–0.2, OOD 0.15–0.25, LOW 0.08–0.15, MOW 0.13–0.16, CD 0.15–0.22, MFC 0.20–0.25, EW 0.25–0.40, SL 0.89–1.12, PDL 0.18–0.25, LF1 0.1–0.14, LF2 0.07–0.1, LF3 0.07–0.12, WF1 0.09–0.12, FL 1.00–1.2, FW 0.19–0.31, MW 1.32–1.43, DLM 2.53–2.81, PRH 0.98–1.10, PL 0.58–0.82, PND 0.51–0.61, PH 0.52–0.83, PPL 0.28–0.43, DPW 0.48–0.83, PPW 0.60–0.91, PHB 0.27–0.51, N=13.

Male.—*Head.* Eye normally without setae protruding from between ommatidia. Ocelli large and prominent, elliptical (Fig. 71).

Mesosoma. Propodeum rounded, declivous face perpendicular, flat except with distinct to indistinct median longitudinal depression, basal face strongly convex transversely and longitudinally. Metapleuron sometimes not broad, ~0.33 as wide as high, but usually broader (Fig. 70), sometimes with transverse posterior carina. Wing venation as in Figs. 91 and 105.

Metasoma. In cephalic view, dorsum of node varies from transverse to bilobate with deep median impression. Petiolar and postpetiolar spiracles distinctly tuberculate to not tuberculate. Genitalia as in Figs. 84 and 85.

Coloration, Sculpturing, and Pilosity. Pubescence short, thin, yellow, erect to suberect and of uniform length over body (0.15–0.20 mm), longest on gena and vertex. Mesonotal pubescence sparse (Fig. 72). Propodeum with base striato-granulate, medially finely granulate (Fig. 70). Area between eye and insertion of antenna, area between ocelli, posterior portion of metapleuron, and

base of petiolar nodes granulate to weakly granulate (Figs. 70, 71). Vertex posterior to ocellar triangle glabrous (Fig. 71). Gena weakly striate. Posterior surface of petiolar node with lower 0.25 of surface with fine striae, lower 0.50 of surface granulate, sometimes granulations obsolescent medially, dorsum polished. Lateral faces of the scutellum striate. Remaining integument smooth and polished. Color generally red yellow to yellow brown. Antennae and legs pale yellow. Mandibles yellow.

Morphometric Measurements. L ~6.0–7.5, HW 0.89–1.10, VW 0.28–0.51, HL 0.70–0.81, EL 0.40–0.62, OD 0.05–0.11, OOD 0.18–0.32, LOW 0.10–0.22, MOW 0.15–0.25, CD 0.15–0.25, MFC 0.15–0.21, EW 0.30–0.40, SL 0.15–0.20, SW 0.09–0.15, PDL 0.05–0.12, PEW 0.09–0.15, LF1 0.10–0.21, LF2 0.10–0.15, LF3 0.15–0.20, WF1 0.09–0.10, FL 1.00–1.12, FW 0.15–0.21, MW 1.18–1.64, DLM 2.10–2.82, PRH 0.77–1.12, PL 0.50–0.61, PND 0.38–0.60, PH 0.30–0.61, PPL 0.18–0.44, DPW 0.40–1.03, PPW 0.43–0.94, PHB 0.30–0.40, N=12.

Fourth instar worker larva.—*Head*. Large, subpyriform in anterior view (height 0.40 mm, width 0.43 mm) (Figs. 177, 182). Cranium slightly broader than long (Figs. 177, 182). Antenna with 3 sensilla, bearing spinule (Figs. 177, 182). Occipital setal row with 4–8 bifid setae, base 0.5–0.66X total length of seta, 0.03–0.07 mm long (Figs. 177, 182, 183). First setal row on vertex with 2 bifid setae, base ~0.66X total length of seta, setae 0.03–0.07 mm long (Figs. 177, 182, 183). Second setal row on vertex with 4 setae, inner 2 setae simple, outer 2 setae with denticulate to bifid apices, 0.09–0.10 mm long (Figs. 177, 182, 183). Setae ventral to antenna level simple, 0.12–0.14 mm long (Figs. 177, 182). Clypeus with transverse row of 4 setae, inner setae shorter than outer setae, 0.03–0.09 mm long (Figs. 177, 182). Labrum small, short (breadth 2.3X length) (Figs. 177, 182). Labrum with 4–6 sensilla on dorsal surface of each half and apex with coarse isolated spinules. Each half of epipharynx with 2–3 isolated and 2 contiguous sensilla. Straight medial portion of mandible with 2–5 teeth that decrease in size dorsally. Maxilla with apex conical, palpus peg-like with 5 sensilla, 2 with spinules. Galea conical with 2 apical sensilla, each bearing one spinule. Labium with patch of spinules dorsal to each palpus, spinules coarse and isolated or in short rows of 2–3. Labial palpus slightly elevated with 4–5 sensilla, each bearing one spinule.

Body. Spiracles small, first spiracle slightly larger than others. Body setae of 2 types. Simple to denticulate setae (0.05–0.13 mm long) arranged in transverse row of 6–8 on ventral surface of each thoracic somite and on each of 3 anterior abdominal somites. Bifid setae (0.05–0.08 mm long) occur elsewhere, base ~0.5X length (Figs. 183, 184).

Length. Approximately 2.3 mm.

Material examined.—Various specimens (FSCA). Also, see Appendices A and B.

Distribution.—A light color variant of *S. saevissima* occurs throughout the Amazon basin (Fig. 201). The dark color variant occurs south from Goais and Bahia to São Palo State in Brazil (Fig. 201). The dark color variant occurs sporadically throughout the Amazon basin.

Comments.—This species is highly variable in both coloration and size of the workers and gynes. They range from the small dark forms in southern Brazil to the large orange brown forms in northern Brazil. These color forms are

not morphologically distinct, however, as there is an almost continuous cline in size and coloration. Recently, Ross et al. (2010) were able to distinguish five evolutionary independent lineages in nominal *S. saevissima* using genetic data (see Fig. 201). Discovery of differentiating characters and formal description of these putative species is still outstanding.

The gynes of *S. saevissima* lack mesonotal maculae like *S. electra, S. pusillignis*, and *S. macdonaghi*. Contrary to this, some callow gynes have integumental maculations on the mesonotum. These maculations are not distinctly margined and must fade as the gyne matures.

There is a large size variation of the males as well. However, the distribution is opposite to that of the workers and gynes. The larger males are normally found within colonies of the smaller, dark-form workers.

Males of *S. saevissima* are most similar to *S. pusillignis* due to their lighter coloration and to the region of the head posterior to the ocellar triangle being glabrous. The males of *S. saevissima* lack the large ocelli and mesonotal maculations possessed by males of *S. pusillignis*. Males of *S. saevissima* tend to have the OOI (2.50–3.50) larger than any other species (<2.70).

The larvae of *S. saevissima* are similar to *S. invicta*. Although *S. saevissima* larvae normally have a smaller head capsule than *S. invicta,* the setal characters are similar between the two species. Some larval specimens of *S. saevissima* have denticulate setae present on the body, which differs from *S. invicta*.

As is the case with *S. invicta* and *S. richteri*, extreme genetic differentiation of geographic populations of *S. saevissima* has been detected using mtDNA sequence data as well as nuclear microsatellite data (Shoemaker et al. 2006, Ross et al. 2010). In particular, specimens from Amazonian, southeastern Atlantic, and south-central Atlantic portions of the Brazilian range are highly divergent from specimens collected in central Brazil. The various color forms in this species are not concordant with the major genetic lineages.

Solenopsis weyrauchi Trager

Solenopsis weyrauchi Trager 1991: 190. [Holotype worker. "Abra Gavilán b. Caramarca, 2, 800 m. PERU. #709. ex. col. Weyrauch. LACM.]

Worker.—Head ovate to subrectangular. Head sculpture with small piligerous foveolae, ~0.01 mm in diameter. Median frontal streak present, sometimes consisting of 2 elongate darkened spots. Median ocellus in largest major workers absent. Mandibular costulae usually well developed throughout entire length, sometimes obsolescent near base. Mesonotum with 30 or more setae. Promesonotal suture in largest major workers gently curved medially, never projecting upward. Mesonotum weakly convex in lateral view. Propodeum sculpture glabrous posteroventral to spiracle. Postpetiole shape as high as or higher than broad. Postpetiole sculpture in posterior view with lower 0.50–0.75 transversely rugose, upper surface shiny with some piligerous foveolae present. Color of head, mesonotum and T1 maculation red yellow. Remainder of gaster black brown. Propodeum and dorsum of petiolar nodes yellow brown. Sometimes rear portion of head, frons around median streak, and pronotum yellow brown. T1 maculations with 2 small anterolateral spots.

Gyne.—Unavailable for study.

Male.—Unknown.

Fourth instar worker larva.—Unknown.

Material examined.—Three specimens from Bolivia, 6 km northeast of Potosí, 19° 32' S, 65° 43' W, 3900 m, 25. XII.1993, P.S. Ward (UCDC). These specimens were identified by J. C. Trager.

Distribution.—*Solenopsis weyrauchi* was previously known only from several widely spaced locations at high elevations in the Peruvian Andes. The holotype (unavailable for study) is from Cajamarca, Peru (Fig. 201). As the new locality data suggest and as Trager (1991) predicted, the range of *S. weyrauchi* likely extends throughout the Andes, at least from Peru to Bolivia, but perhaps as far northward as Columbia and southward as Argentina and Chile.

Discussion

Delineation of Species Groups within Solenopsis

Trager (1991) placed the worker-polymorphic fire ants along with three monomorphic *Solenopsis* species (*S. substituta*, *S. tridens,* and *S. virulens*) in the *S. geminata* species-group, although he admitted the inclusion of *S. virulens* was somewhat arbitrary. Trager referred to smaller groupings within the *S. geminata* species-group as species complexes, and subsets of complexes as subcomplexes. The *S. geminata* species-group is informal and its monophyly has yet to be demonstrated. This situation, coupled with the unwieldy terminology of complexes and subcomplexes, has led us to propose a new classification of fire ants (Table 4).

Solenopsis virulens is placed in the *S. virulens* species-group, which is defined by the following: workers monomorphic, eye small with 20–60 facets, first flagellomere as broad as or broader than long, and postpetiole not dilated. This species-group is presumably closely related to the *S. nigella* species-group *sensu* Moreno-Gonzalez (2001), which is equivalent to *Euopthalma* of Creighton minus *S. globularia.*

Solenopsis tridens and *S. substituta* are placed in the *S. tridens* species-group, which is defined by monomorphic workers with a long scape, long first flagellomere (at least 1.5X longer than broad), propodeal carinae, and an elongate petiolar peduncle. This species-group is equivalent to the *S. tridens* complex of Trager.

The *S. geminata* species-group includes *S. geminata, S. xyloni, S. amblychila, S. aurea, S. gayi,* and *S. bruesi*. This species-group is defined by strongly polymorphic workers with a short scape, long first flagellomere (at least 1.5X longer than broad), reduced or absent median clypeal tooth, and a ventral petiolar process. This species-group is equivalent to the *S. geminata* complex of Trager. No apomorphies are apparent for the species-group, and it may be defined entirely by symplesiomorphies.

Finally, the *S. saevissima* species-group includes *S. metallica* n. sp., *S. daguerrei, S. electra*, *S. hostilis, S. interrupta, S. invicta, S. macdonaghi, S. megergates, S. pusillignis, S. pythia, S. quinquecuspis, S. richteri, S. saevissima,* and *S. weyrauchi*. This group is defined by strongly polymorphic workers with a long scape, long first flagellomere (at least 1.5X longer than broad), strongly developed median clypeal tooth, weak sculpturing, and a small or absent ventral petiolar process. This species-group is equivalent to the *S. saevissima* complex of Trager.

There is some molecular support for the monophyly of these groups (Krieger and Ross 2005, Shoemaker et al. 2006), although taxon sampling is incomplete and branch support is often weak. As

such, the proposed species complexes should be viewed as preliminary until the evolutionary relationships of the fire ants have been robustly estimated using diverse charcter sets.

Morphology of Sexuals

Creighton (1930, 1950) stated that both males and gynes of *Solenopsis* appear to offer better characters for specific determinations than do the workers. Because individuals of the sexual caste tend to be larger than the worker caste and have a less generalized and reduced anatomy, they could provide characters, such as those from male genitalia and wing venation, that are not obtainable from workers and are useful for identification purposes (Creighton 1930, 1950). This study found that the amount of intraspecific variation occurring in the adult males and gynes was equivalent to that of workers, making the taxonomic information gained from these castes no better than that obtained from workers. Furthermore, the morphometric measurements and indices (Tables 5, 6) of the adult males and gynes alone are inadequate for determining species. Given a choice, workers still offer the most reliable and numerous characters, and these characters alone usually are sufficient for making accurate species identifications. Even though the morphology and morphometrics of sexuals are of limited use alone, they greatly improve the accuracy of identifications of fire ants when used in concert with data for the workers.

Male Genitalia

For many Hymenoptera, the male genitalia are of great diagnostic utility. Sexual selection is hypothesized to often drive the rapid divergence of the morphology of male genitalia once speciation occurs (Eberhard 1985). Also, because the male genitalia are structurally complex, the likelihood that related species would become similar in this structure through parallelism is low (Mayr 1969). Thus, genitalic characters are potentially useful for distinguishing even closely related species. This is not the case for *Solenopsis*. Although there are slight differences between the *S. fugax* species-group and several of the other fire ant species-groups, this study found that the male genitalia of the species within the *S. saevissima* species-group were relatively homogeneous and uninformative (Figs. 74–86). After study of the genitalia of many *Solenopsis* exemplars, we also conclude that characters used by Baroni-Urbani (1968) to raise *Diplorhoptrum* to the generic level are not found in all of the species he placed in this taxon. Furthermore, *Diplorhoptrum* species such as *S. tennesseensis* and *S. abdita* have genitalia more closely resembling those of the fire ants than those of the European *Diplorhoptrum* species, *S. fugax*. This information provides additional support for the synonymy of *Diplorhoptrum* with *Solenopsis*, as proposed by Bolton (1987).

Wing Venation

Although wing venation in *Solenopsis* may provide valuable data for inferring the higher-level phylogeny of the tribe Solenopsidini in the future, as proposed by Brown and Nutting (1950), it appears to be too conservative within the *S. saevissima* species-group to be phylogenetically informative (Pitts et al. 2005). Moreover, wing venation tends to be too similar across species and too variable within species (Figs. 87–108) to provide diagnostic information.

Although some slight differences exist, the wing venation of the *S. saevissima* species-group is remarkably similar to that of other groups, such as the *S. geminata* species-group (Figs. 109-114, 116), the

S. tridens species-group (Figs. 115, 117, 118), the *S. globularia* species-group (Fig. 123), and some members of the *S. molesta* species-group (Figs. 124–125). Furthermore, distantly related species such as *S. nigella gensterblumi*, *S.* nr. *nigella,* and an unidentified *Solenopsis* species are similar in their venation as well (Figs. 119–122). Some species in the *S. molesta* species-group have diagnostic wing venation, such as the reduction of the r-rs cross vein (Fig. 129), but others do not (Figs. 127–129). In general, wing venation provides few taxonomically informative characters for the genus.

Intraspecific variation and individual aberrations in wing venation were commonly observed, including: 1) swelling in the Rs+M vein in the radial cell of a *S. pusillignis* gyne (Fig. 87) and *S. richteri* gyne (Fig. 102); 2) coarseness of the Rs vein and the veins delineating the radial cell in individuals of several species (Figs. 89, 93, 95); 3) swellings on the Cu vein of a *S. macdonaghi* male (Fig. 97); 4) swellings on the Rs+M vein in the median cell of a *S. megergates* gyne (Fig. 98). These abnormalities are found in other species-groups and are probably characteristic of the genus *Solenopsis* as a whole (Figs. 109, 119, 122, 125) (see also Ross and Robertson 1990). In some cases, certain veins are misplaced so that the venation looks unique (Fig. 109), but usually the other wing on the same individual is normal. Such asymmetry has been documented for *Oxyepoecus*, a close relative of *Solenopsis* (Kempf 1974). This variation exists as well for both spectral and nebulous veins.

The lack of the m-cu cross vein for the gynes of *S. metallica* (Fig. 89) and the reduction of wing venation in *S. daguerrei* (Figs. 106, 108) are constant for all specimens seen and are considered characters rather than abnormalities. The lack of the m-cu cross vein for *S. metallica* was observed in all four forewings of the two gynes from different nests examined. All specimens of *S. daguerrei* had reduced wing venation, albeit to various degrees.

Other observed morphological abnormalities are noted here. A single gyne of *S. megergates* had two median ocelli and had coarse striations throughout the ocellar triangle (Fig. 54). These complete striations were seen only in this single atypical specimen. One gyne of *S. quinquecuspis* had four propodeal spiracles (Fig. 55). These two specimens did not otherwise differ from the typical gynes of their species. Lastly, two gynandromorphs of *S. quinquecuspis* were discovered, as will be discussed elsewhere.

Larval Morphology

Wheeler and Wheeler (1976, 1986, 1991) found that larval morphology could be used to differentiate ant genera and provided a generic key using larval characters. In some cases, higher level taxonomy of Formicidae has been redefined using larval morphology (Wheeler and Wheeler 1970). Many species-level larval descriptions have been published for Formicidae, but in only three cases has larval morphology been used for phylogenetic purposes (Wheeler and Wheeler 1970, Schultz and Meier 1995, Pitts et al. 2005).

The larval stages of ten species within the *Solenopsis saevissima* species-group are described in this study, eight for the first time. The morphology of these species is very similar, yet some variation occurs. Wheeler and Wheeler (1977) reported that *S. invicta* differed from *S. richteri* x *invicta* (described as *S. richteri*) in the number of setae on the dorsal side of the labrum and the number of sensilla on the ventral margin of the

labrum. The present survey of many specimens and species revealed that minute features such as these are quite variable within species and thus are not very useful in species determinations. Mandibular dentition is of limited use due to varying degrees of wear resulting from feeding. *Solenopsis saevissima* species-group larvae are of little systematic significance because most larval features are broadly overlapping and continuous among species. However, two general groups of species can be defined on the basis of larval characters. One group includes those species with bifid setae dorsal to the antennal margin (*S. metallica*, n. sp., *S. interrupta*, *S. invicta*, *S. pusillignis*, *S. saevissima*), a condition termed the *S. saevissima* type. The other group contains those species with setae dorsal to the antennal margin that are usually simple or dentate (*S. macdonaghi*, *S. megergates*, *S. quinquecuspis*, and *S. richteri*), a condition termed the *S. megergates* type. This latter type appears on the basis of the inferred species phylogeny to be the apomorphic condition in the species-group (Pitts et al. 2005).

Acknowledgments

We thank T. L. Pitts-Singer (USDA-ARS Bee Biology and Systematics Laboratory, Logan, Utah), S. D. Porter (USDA-ARS), and Colin Brammer (Department of Biology, Utah State University, Logan) for critically reviewing drafts of this paper; S. Cover (MCZ), C. Flechtmann (ICIB), L. E. Gilbert (Department of Zoology, University of Texas, Austin), J. T. Huber (CNCI), I. Löbl (MHNG), S. D. Porter (USDA-ARS), L.A. Stange (FSCA), L. Calcaterra (USDA-ARS), and P. S. Ward (UCDC) for loans of specimens; J. M. Carpenter (AMNH), P. Folgarait (Unidad de Investigación en Interacciones Biológicas, Universidad Nacional de Quilmes, Buenos Aires, Argentina), J. Heraty (Department of Entomology, University of California at Riverside), C. Kugler (Biology Department, Radford University, Virginia), T. R. Schultz (NMNH), R. R. Snelling (LACM), J. C. Trager (Shaw Arboretum of Missouri Botanical Gardens, Missouri), D. B. Wahl (AEIC), and J. Wheeler for providing information and advice for this project. We are grateful for J. Wiley's effort in providing access to the large alcohol collection of *Solenopsis* from the FSCA. We are thankful for the assistance provided by M. A. Farmer and J. A. Shields of the Center of Ultrastructural Studies, University of Georgia for SEM support. The following institutions provided support to JPP for this study: the Canadian National Insect Collection for a CanaColl grant for travel to Ottawa, Canada in 1999, and the American Museum of Natural History for a Theodore Roosevelt Memorial Fund grant for travel to the Southwestern Research Station, Portal, Arizona during 2000. We thank W. Sherbrooke for his hospitality and help during JPP's stay at the Southwestern Research Station, M. C. Mescher for important logistic support in South America, and T. L. Pitts-Singer for collecting assistance while at the SWRS. JPP is also grateful for the financial support provided by the University of Georgia, Department of Entomology. GPC is grateful for the financial support provided by the Smithsonian Institution Peter Buck Fellowship. This research was funded by United States Department of Agriculture grant 99–35302–8629 provided to KGR, JVM, and D. D. Shoemaker and National Science Foundation grant DEB-1354479 to KGR and D. D. Shoemaker.

Literature Cited

Anonymous. 2001. *Solenopsis invicta* Buren, 1972 (Insecta, Hymenoptera): Specific name conserved. Bulletin of Zoological Nomenclature 58: 156–157.

Ascunce, M. S., C.-C. S. Yang, J. Oakey, L. Calcaterra, W.-J. Wu, C.-J. Shih, J. Goudet, K. G. Ross, and D. Shoemaker. 2011. Global invasion history of the fire ant *Solenopsis invicta*. Science 331: 1066–1068.

Baack, E. J. and L. H. Rieseberg. 2007. A genomic view of introgression and hybrid speciation. Current Opinion in Genetics and Development 17: 513–518.

Baroni-Urbani, G. 1968. Über die eigenartige Morphologie der männlichen Genitalien des Genus *Diplorhoptrum* Mayr (Hymenoptera: Formicidae) und die taxonomischen Sclussfolgerungen. Zeitschrift für Morphologie der Tiere 63: 63–74.

Bolton, B. 1987. A review of the *Solenopsis* genus-group and a revision of the Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). Bulletin of the British Museum (Natural History), Entomology 54: 263–452.

Bolton, B. 1995. A New General Catalogue of the Ants of the World. Harvard University Press, Cambridge, Massachusetts. (updated: May 2016; http://www.antwiki.org/wiki/New_General_Catalogue).

Borgmeier, T. 1949. Formigas novas ou pouco conhecidas de Costa Rica. Revista Brasileira de Biologia 9: 201–210.

Borgmeier, T. 1959. Myrmecologische Studien. 2. Anais de Academia Brasileira de Ciencias 31: 309–319.

Bourke, A. F. G. and N. R. Franks. 1991. Alternative adaptations, sympatric speciation, and the evolution of parasitic, inquiline ants. Biological Journal of the Linnean Society 43: 157–178.

Briano, J. A., L. A. Calcattera, D. P. Wojcik, D. F. Williams, W. A. Banks, and R. S. Patterson. 1997. Abundance of the parasitic ant *Solenopsis daguerrei* (Hymenoptera: Formicidae) in South America, a potential candidate for the biological control of the Red Imported Fire Ant in the United States. Environmental Entomologist 26: 1143–1148.

Brown, W. L. Jr. and W. L. Nutting. 1950. Wing venation and phylogeny of the Formicidae (Hymenoptera). Transactions of the American Entomological Society 75: 113–132.

Bruch, C. 1916. Contribución al Estudio de las Hormigas de la Provincia de San Luis. De La Revista del Museo de la Plata 23: 291–354.

Bruch, C. 1930. Notas preliminaries acerca de *Labauchena dagurrei* Santschi. Revista de la Sociedad Entomologia Argentina 13: 73–82.

Buren, W. F. 1972. Revisionary studies on the taxonomy of the imported fire ants. Journal of the Georgia Entomological Society 7: 1–26.

Buschinger, A. 2009. Social parasitism among ants: a review (Hymenoptera: Formicidae). Myrmecological News 12: 219–235.

Calcaterra, L. A., J. A. Briano, and D. F. Williams. 2000. New Host for the Parasitic Ant *Solenopsis daguerrei* (Hymenoptera: Formicidae) in Argentina. Florida Entomologist 83: 363–365.

Callcott, A. M. A. and H. L. Collins. 1996. Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918-1995. Florida Entomologist 79: 240–251.

Chialvo, P., D. Gotzek, D. Shoemaker, and K. G. Ross. 2018. Genetic analysis reveal cryptic diversity in the native North American fire ants (Hymenoptera: Formicidae: *Solenopsis*). Systematic Entomology 43: 109–122.

Comstock, J. H. 1918. The wings of insects. Comstock, Ithaca, New York.

Creighton, W. S. 1930. The new world species of the genus *Solenopsis* (Hymenoptera: Formicidae). Proceedings of the American Academy of Arts and Sciences 66: 39–151.

Creighton, W. S. 1950. The ants of North America. Bulletin of the Museum of Comparative Zoology at Harvard College 104: 1–585.

Crozier, R. H. 1979. Genetics of sociality. In H. R. Hermann, ed. Social Insects, Vol. I. Academic Press, New York, N.Y.

Davis, L. R. and M. Deyrup. 2006. *Solenopsis phoretica*, a new species of apparently parasitic ant from Florida (Hymenoptera: Formicidae). Florida Entomologist 89: 141–143.

Deyrup, M. and Z. A. Prusak. 2008. *Solenopsis enigmatica*, a new species of inquiline ant from the island of Dominica, West Indies (Hymenoptera: Formicidae). Florida Entomologist 91: 70–74.

Eberhard, W. G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Massachusetts.

Ettershank, G. 1966. A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton*. Australian Journal of Zoology 14: 73–171.

Fabricius, J. C. 1804. Systema Piezatorum. Brunsvigae.

Fischman, B. J., S. H. Woodard, and G. E. Robinson. 2011. Molecular evolutionary analyses of insect societies. Proceedings of the National Academy

of Sciences of the United States of America 108: 10847–10854.

Forel, A. 1908. Ameisen aus Sao Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Herm. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 58: 340–418.

Forel, A. 1909. Ameisen aus Guatemala usw., Paraguay und Argentinien. Deutsche Entomologische Zeitschrift 1909: 239–269.

Forel, A. 1911. Ameisen des Herrn. Prof. v. Ihering aus Brasilien (Sao Paulo usw.) nebst einigen anderen aus Südamerika und Afrika. Deutsche Entomologische Zeitschrift 1911: 285–312.

Forel, A. 1912. Formicides néotropiques. Part IV. 3me sous-famille Myrmicinae Lep. (suite). Mémoires de la Société Entomologique de Belgique 20:1–32. .

Forel, A. 1913. Fourmis d'Argentine, d'Brésil, d'Guatémala et de Cuba. Reçues de MM. Bruch, Prof. v. Ihering, Mlle Baez, M. Peper et M. Rovereto. Bulletin de la Société Vaudoise des Sciences Naturelles, 49: 203–250.

Forel, A. 1914. Formicides d'Afrique et d'Amerique nouveaux ou peu connus. Bulletin de la Société Vaudoise des Sciences Naturelles 50: 211–288.

Fujita, M. K., A. D. Leaché, F. T. Burbrink, J. A. McGuire, and C. Moritz. 2012. Coalescent-based species delimitation in an integrative taxonomy. Trends in Ecology and Evolution 27: 480–488.

Galkowski, C., J. Casevitz-Weulersse, and H. Cagniant. 2010. Redescription de *Solenopsis fugax* (Latreille, 1798) et notes sur les *Solenopsis* de France [Hymenoptera, Formicidae]. Revue française d'entomologie 32: 151–163.

Gardner, W. A., S. Diffie, R. K. Vander Meer, and M. A. Brinkman. 2008. Distribution of the fire ant (Hymenoptera: Formicidae) hybrid in Georgia. Journal of Entomological Science 43: 133–137.

Gotzek, D., H. J. Axen, A. V. Suarez, S. Helms Cahan, and D. Shoemaker. 2015. Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. Molecular Ecology 24: 374–388.

Gotzek, D., and K. G. Ross. 2007. Genetic regulation of colony social organization in fire ants: An integrative overview. Quarterly Review of Biology 82: 201–226.

Gotzek, D., D. D. Shoemaker, and K. G. Ross. 2007. Molecular variation at a candidate gene implicated in the regulation of fire ant social behavior. PLoS ONE 2: e1088.

Guillebeau, L. P., P. Roberts, and N. C. Hinkle. 2002. Summary of Losses from Insect Damage and Costs of Control in Georgia, 2000. Georgia Agricultural Experiment Stations Special Publication 41-03. available at http://extension.uga.edu/publications/detail.html?number=SB41-03.

Helms Cahan, S. and S. B Vinson. 2003. Reproductive division of labor between hybrid and non-hybrid offspring in a fire ant hybrid zone. Evolution 57: 1562–1570.

Henshaw, M. T., N. Kunzmann, C. Vanderwoude, M. Sanetra, and R. H. Crozier. 2005. Population genetics and history of the introduced fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), in Australia. Australian Journal of Entomology 44: 37–44.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Huang, Y.-C., and J. Wang. 2014. Did the fire ant supergene evolve selfishly or socially? BioEssays 36: 200–208.

International Commission of Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, UK.

International Commission of Zoological Nomenclature. 2001. *Solenopsis invicta* Buren, 1972 (Insecta, Hymenoptera): Specific name conserved. Bulletin of Zoological Nomenclature 58: 156–157.

Jouvenaz, D. P. 1990. Approaches to biological control of fire ants in the United States. *In* Vander Meer, R. K., K. Jaffe, and A. Cedeño, eds. Applied Myrmecology: A World Perspective. Westview, Boulder, Colorado.

Kempf, W. W. 1974. A review of the Neotropical ant genus *Oxyepoecus* Santschi. Studia Entomologica 17: 471–512.

Krieger, M. J. B. and K. G. Ross. 2002. Identification of a major gene regulating complex social behavior. Science 295: 328–332.

Krieger, M. J. B. and K. G. Ross. 2005. Molecular evolutionary analyses of the odorant-binding protein gene *Gp-9* in fire ants and other *Solenopsis* species. Molecular Biology and Evolution 22: 2090–2103.

Kusnezov, L. 1953. *Bisolenopsis sea*. Un Nuevo género y especie de hormigas y sus relaciones con los géneros vecions. Memorias del museo de Entre Rios 31: 1–44.

Kusnezov, L. 1954. Un genero nuevo de hormigas (*Paranamyrma solenopsidis* nov. gen., nov. sp.)

y los problemas relacionados (Hymenoptera: Formicidae). Memorias del Museo de Entre Rios 30: 7–21.

Kusnezov, L. 1957. Die Solenopsidinen-Gattugen von Südamerika (Hymenoptera: Formicidae). Zoologischer Anzeiger 158: 266–280.

Kusnezov, L. 1958. *Lilidris metatarsalis* gen. et spec. nov. Acta Zoologica Lilloana 15: 189–193.

Lard, C. F., J. Schmidt, B. Morris, L. Estes, C. Ryan, and D. Bergquist. 2006. An Economic Impact of Imported Red Fire Ants in the United States of America. https://articles.extension.org/sites/default/files/Copy%20of%20the%20National%20Study.pdf [accessed 20 December 2017].

Lofgren, C. S. 1986. History of imported fire ants in the United States. *In* Lofgren, C. S. and R. K. Vander Meer, eds. Fire Ants and Leaf Cutting Ants: Biology and Management. Westview, Boulder, Colorado.

Lofgren, C. S., W. A. Banks, and B. M. Glancey. 1975. Biology and control of imported fire ants. Annual Review of Entomology 20: 1–30.

McCook, H. C. 1879. Family Formicidae. *In* Comstock, J. H., ed. Report upon Cotton Insects. Washington, D.C.

Mason, W. R. M. 1986. Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. Proceedings of the Entomological Society of Washington 88: 1–7.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill, New York, N.Y.

Moreno-Gonzalez, I. 2001. Systematics of the thief ants of North America (Hymenoptera: Formicidae: *Solenopsis*). Master of Science thesis. The University of Texas at El Paso, El Paso, Texas.

Nation, J. L. 1983. A new method using Hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. Stain Technology 58: 347–351.

Nolte, A.W. and Tautz D. 2010. Understanding the onset of hybrid speciation. Trends in Genetics 26: 54–58.

Oliver, J. B., R. K. Vander Meer, S. A. Ochieng, N. N. Youssef, E. Pantaleoni, F. A. Mrema, K. M. Vail, J. P. Parkman, S. M. Valles, W. G. Haun, and S. Powell. 2009. Statewide survey of imported fire ant (Hymenoptera: Formicidae) populations in Tennessee. Journal of Entomological Science 44: 149–157.

Pacheco, J. A. and W. Mackay. 2013. The New World Thief Ants of the Genus *Solenopsis* (Hymenoptera: Formicidae). Edwin Mellen Press, Lewiston.

Petralia, R. S. and S. B. Vinson. 1979. Developmental morphology of larvae and eggs of the Imported Fire Ant, *Solenopsis invicta*. Annals of the Entomological Society of America 72: 472–484.

Pitts, J. P. 2002. A cladistic analysis of the *Solenopsis saevissima* species- group (Hymenoptera: Formicidae). Ph.D. dissertation, University of Georgia, Athens, Georgia.

Pitts, J. P., J. V. McHugh, and K. G. Ross. 2005. Cladistic analysis of the fire ants of the *Solenopsis saevissima* species-group (Hymenoptera: Formicidae). Zoologica Scripta 34: 493–505.

Porter, S. D., D. F. Williams, R. Patterson, and H. Fowler. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies? Environmental Entomology 26: 373–384.

Robinson, G. E., R. D. Fernald, and D. F. Clayton. 2008. Genes and social behavior. Science 322: 896–900.

Ross, H. H. 1936. The ancestry and wing venation of the Hymenoptera. Annals of the Entomological Society of America 29: 99–111.

Ross, K. G., D. Gotzek, M. S. Ascunce, and D. D. Shoemaker. 2010. Species delimitation: a case study in a problematic ant taxon. Systematic Biology 59: 162–184.

Ross, K. G. and L. Keller. 1995. Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. Annual Review of Ecology and Systematics 26: 631–656.

Ross, K. G., M. J. B. Krieger, L. Keller, and D. D. Shoemaker. 2007. Genetic variation and structure in native populations of the fire ant *Solenopsis invicta*: evolutionary and demographic implications. Biological Journal of the Linnean Society 92:541–560.

Ross, K. G. and J. L. Robertson. 1990. Developmental stability, heterozygosity, and fitness in two introduced fire ants (*Solenopsis invicta* and *S. richteri*) and their hybrids. Heredity 64: 93–103.

Ross, K. G. and D. D. Shoemaker. 2005. Species delimitation in native South American fire ants. Molecular Ecology 14: 3419–3438.

Ross, K. G. and J. C. Trager. 1990. Systematics and population genetics of fire ants (*Solenopsis saevissima* complex) from Argentina. Evolution 44: 2113–2134.

Ross, K. G., R. K. Vander Meer, D. J. C. Fletcher, and E. L. Vargo. 1987a. Biochemical

phenotypic and genetic studies of two introduced fire ants and their hybrid (Hymenoptera: Formicidae). Evolution 41: 280–293.

Ross, K. G., E. L. Vargo, and D. J. C. Fletcher. 1987b. Comparative biochemical genetics of three fire ant species in North America, with special reference to the two social forms of *Solenopsis invicta* (Hymenoptera: Formicidae). Evolution 41: 979–990.

Ross, K. G., E. L. Vargo, and D. J. C. Fletcher. 1988. Colony genetic structure and gyne mating frequency in fire ants of the subgenus *Solenopsis* (Hymenoptera: Formicidae). Biological Journal of the Linnean Society 34: 105–117.

Santschi, F. 1916. Formicides Sudaméricains nouveaux ou peu connus. Physis Revista de la Sociedad Argentina de Ciencias Naturales 2: 365–399.

Santschi, F. 1925. Nouveaux formicides brésiliens et autres. Annales de la Société Entomologique de Belgique 64: 5–20.

Santschi, F. 1930. Un nouveau genre de fourmi parasite sans ouvières de l'Argentine. Revista de la Sociedad Entomologia Argentina 13: 81–83.

Santschi, F. 1934. Fourmis de Misiones et du chaco argentin. Revista de la Sociedad Entomológique Argentina 6: 23–34.

Schultz, T. R. and R. Meier. 1995. A phylogenetic analysis of the fungus-growing ants (Hymenoptera: Formicidae: Attini) based on morphological characters of the larvae. Systematic Entomology 20: 337–370.

Shattuck, S. O., S. D. Porter, and D. P. Wojcik. 1999. *Solenopsis invicta* Buren, 1972 (Insecta, Hymenoptera): proposed conservation of the specific name. Bulletin of Zoological Nomenclature 56: 27–30.

Shoemaker, D. D., K. G. Ross, and M. L. Arnold. 1996. Genetic structure and evolution of a fire ant hybrid zone. Evolution 50: 1958–1976.

Shoemaker, D. D., M. E. Ahrens, and K. G. Ross. 2006. Molecular phylogeny of fire ants of the *Solenopsis saevissima* species-group based on mtDNA sequences. Molecular Phylogenetics and Evolution 38: 200–215.

Silveira-Guido, A., P. San Martín, C. Ctisci-Pisano, and J. Carbonell-Bruhn. 1965. Investigations on the biology and biological control of the fire ant *Solenopsis saevissima richteri* Forel, in Uruguay. Final report. Departmento de Sanidad Vegetal, Facultad de Agronomía, Universidada de la República, Montevideo, Uruguay.

Smith, F. 1855. Descriptions of some species of Brazilian ants belonging to the genera *Pseudomyrma, Eciton*, and *Myrmica* (with observations on their economy by Mr. H.W. Bates). Transactions of the Entomological Society of London 3: 156–169.

Smith, F. 1858. Catalogue of Hymenopterous Insects in the Collection of the British Museum, 6 Formicidae. London.

Smith, C. R., A. L. Toth, A. V. Suarez, G. E. Robinson. 2008. Genetic and genomic analyses of the division of labour in insect societies. Nature Reviews Genetics 9: 735–748.

Spinola, M. 1851. Insectos. Orden 7. Hymenopteros. *In* Gay C., Historia Fisica y Politica de Chile. Zoologia, 6. Paris.

Thompson, C. R. 1980. Monograph of the *Solenopsis (Diplorhoptrum)* of Florida. Ph.D. dissertation. University of Florida, Gainesville, Florida.

Thompson, C. R. 1989. The thief ants, *Solenopsis molesta* group, of Florida (Hymenoptera: Formicidae). Florida Entomologist 72: 268–283.

Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). Journal of the New York Entomological Society 99: 141–198.

Tschinkel, W. R. 2006. The Fire Ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

USDA/ARS. 2005. Areawide Suppression of Fire Ants Webpage; http://fireant.ifas.ufl.edu/Imported.htm

Vander Meer, R. K. and C. S. Lofgren. 1988. Use of chemical characters in defining populations of fire ants, *Solenopsis saevissima* complex (Hymenoptera: Formicidae). Florida Entomologist 71: 323–332.

Vander Meer, R. K., C. S. Lofgren, and F. M. Alvarez. 1985. Biochemical evidence for hybridization in fire ants. Florida Entomologist 68: 501–506.

Vargo, E. L. and D. Fletcher. 1987. Effect of Queen Number on the Production of Sexuals in Natural-Populations of the Fire Ant, *Solenopsis invicta*. Physiological Entomology 12: 109–116.

Wang, J., Y. Wurm, M. Nipitwattanaphon, O. Riba-Grognuz, Y.-C. Huang, D. Shoemaker, and L. Keller. 2013. A Y-like social chromosome causes alternative colony organization in fire ants. Nature 493: 664–668.

Ward, P. S., S. G. Brady, B. L. Fisher, and T. R. Schultz. 2015. The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Systematic Entomology 40: 61–81.

Wetterer, J. K. 2011. Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). Myrmecological News 14: 21–35.

Wetterer, J. K. 2013. Exotic spread of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) beyond North America. Sociobiology 60: 50–55.

Wheeler, G. C. 1960. Techniques for the study of ant larvae. Psyche 77: 87–94.

Wheeler, G. C. and J. Wheeler. 1955. The ant larvae of the Myrmicinae tribe Solenopsidini. American Midland Naturalist 54: 119–141.

Wheeler, G. C. and J. Wheeler. 1970. Ant larvae of the subfamily Formicinae: Second supplement. Annals of the Entomological Society of America 63: 648–656.

Wheeler, G. C. and J. Wheeler. 1976. Ant Larvae: Review and Synthesis. Entomological Society of Washington, Memoirs 7: 1–108.

Wheeler, G. C. and J. Wheeler. 1977. Supplementary studies on ant larvae: Myrmicinae. Transactions of the American Entomological Society 103: 581–602.

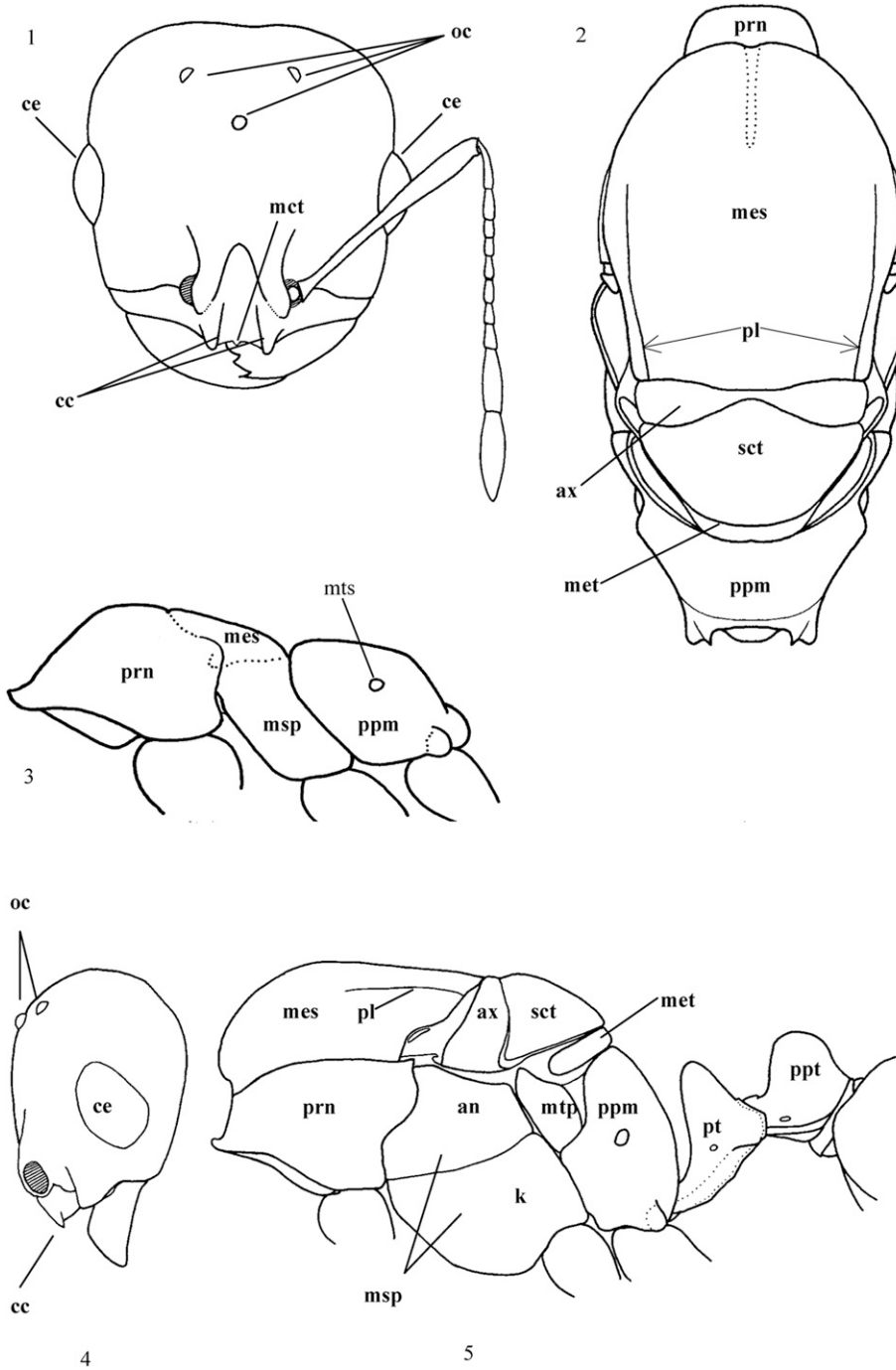
Wheeler, G. C. and J. Wheeler. 1986. Ten-year supplement to "Ant Larvae: Review and Synthesis." Proceedings of the Entomological Society of Washington 88: 684–702.

Wheeler, G. C. and J. Wheeler. 1991. Notes on ant larvae 1989–1991. Insecta Mundi 5: 167–173.

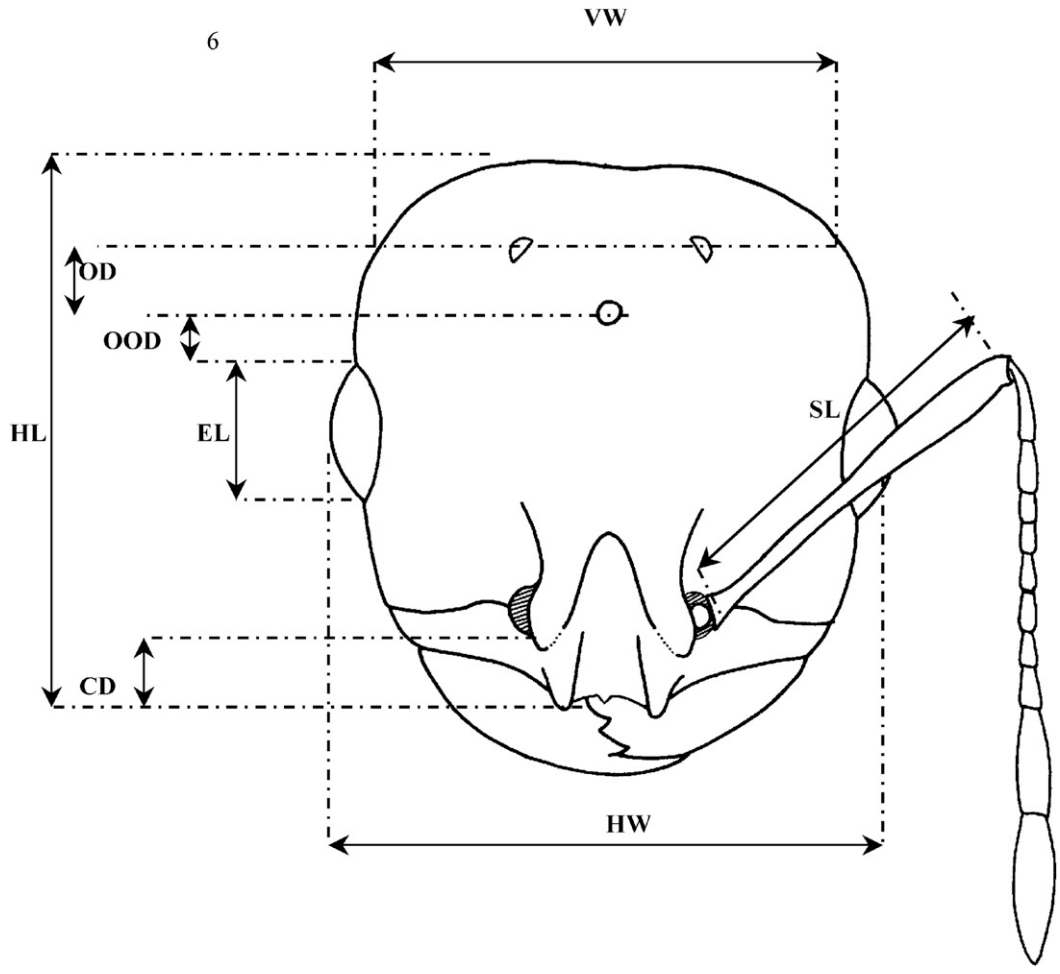
Wheeler, W. M. 1915. Some additions to the North American ant fauna. Bulletin of the American Museum of Natural History 34: 389–421.

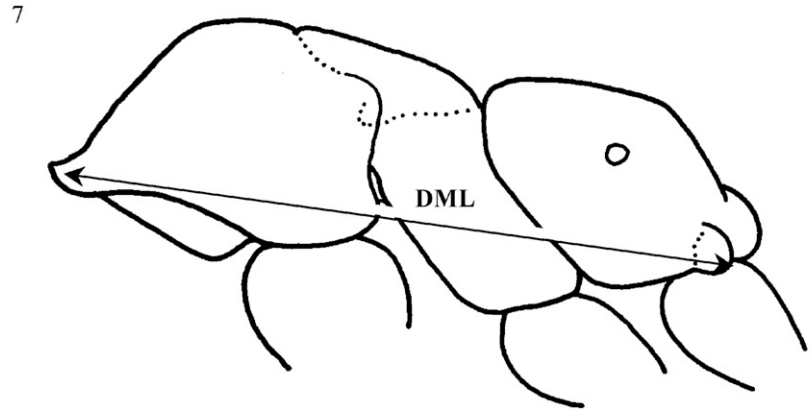
Wilson, E. O. 1952. O complexo *Solenopsis saevissima* na America do Sul (Hymenoptera: Formicidae). Memórias do Instituto Oswaldo Cruz 50: 49–68.

Wojcik, D. P. 1990. Behavioral interactions of fire ants and their parasites, predators, and inquilines. *In* Vander Meer, R. K., K. Jaffe, and A. Cedeño, eds. Applied Myrmecology: a world perspective. Westview, Boulder, Co.

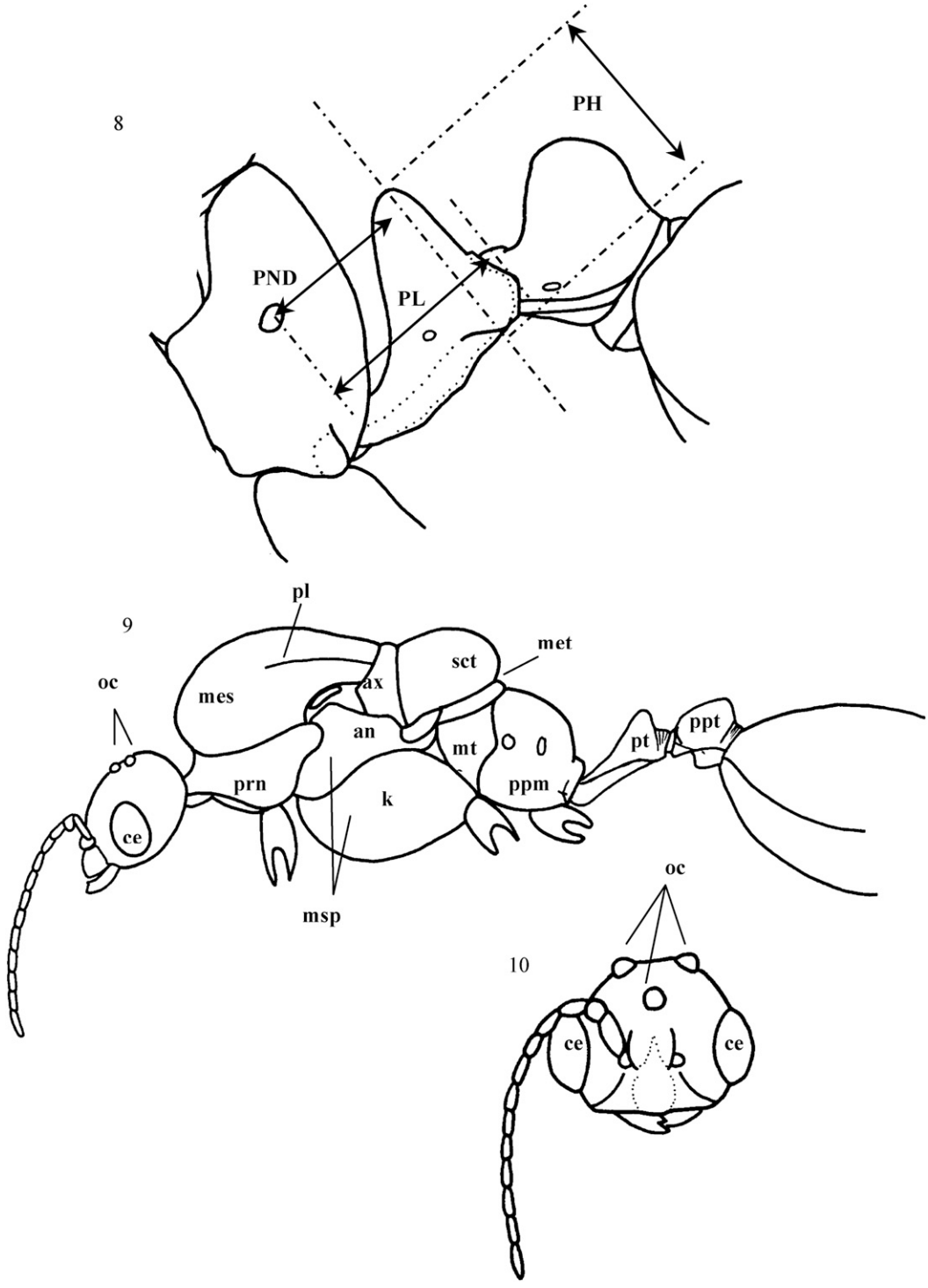


Figs. 1–5. 1, Head of *Solenopsis* gyne, dorsal view. 2, Mesosoma of *Solenopsis* gyne, dorsal view. 3, Mesosoma of *Solenopsis* worker, lateral view. 4, Head of *Solenopsis* gyne, lateral view. 5, Mesosoma of *Solenopsis* gyne, lateral view. (anepisternum (an), axillae (ax), compound eyes (ce), ocelli (oc), clypeal teeth (cc), katepisternum (k), median tooth (mct), mesonotum (mes), metanotum (met), metapleural spiracle (mts), metapleuron (mtp), mesopleuron (msp), parapsidal lines (pl), propodeum (ppm), postpetiole (ppt), pronotum (prn), petiole (pt), and scutellum (sct)).

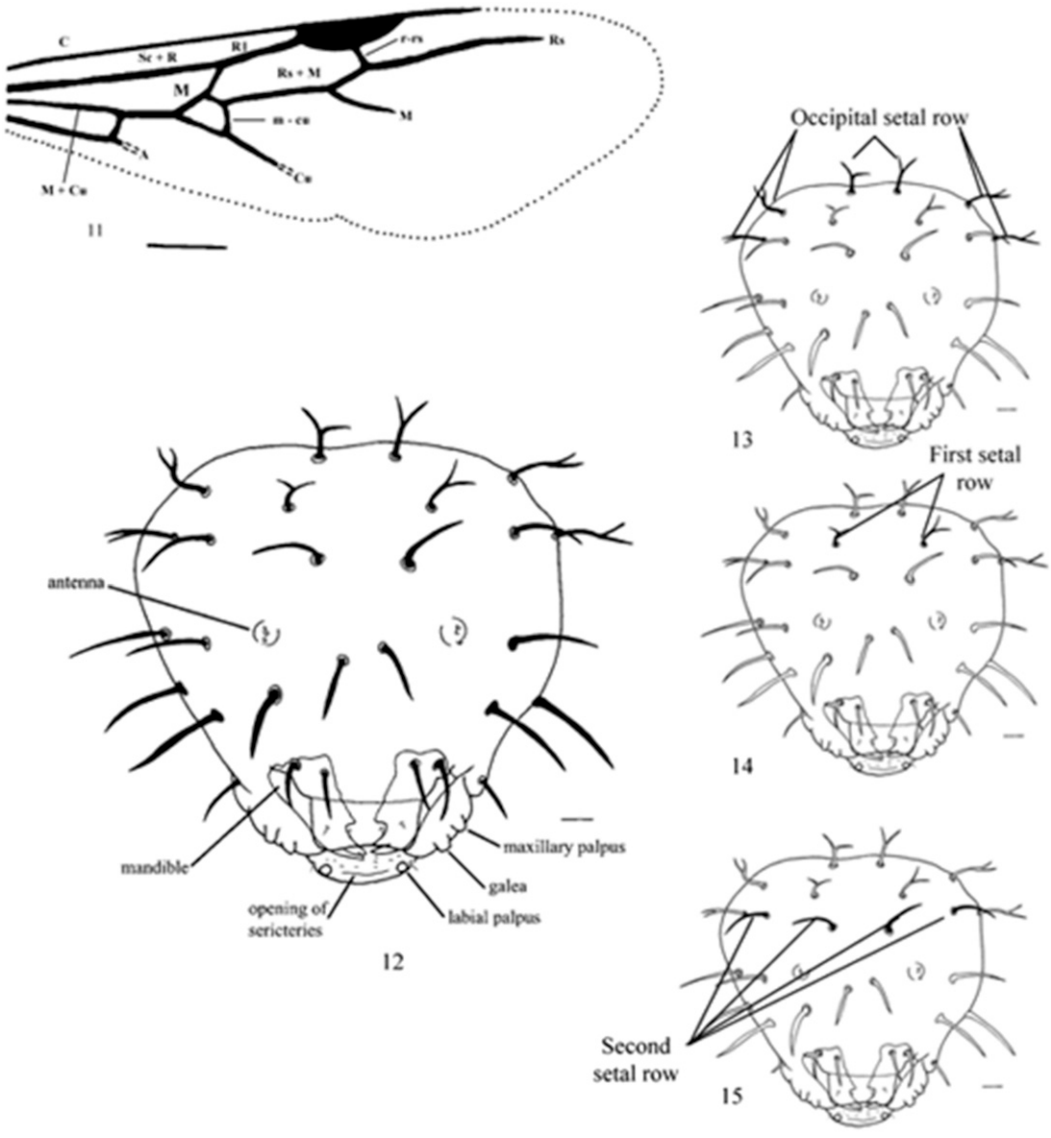




Figs. 6–7. 6, Head of *Solenopsis* gyne with measurements noted, dorsal view. 7, Mesosoma of *Solenopsis* worker, lateral view.



Figs. 8–10. 8, Petiole of *Solenopsis* gyne with measurements noted, lateral view. 9, Head and mesosoma of *Solenopsis* male, lateral view. 10, Head of *Solenopsis* male, dorsal view. (anepisternum (an), axillae (ax), compound eyes (ce), katepisternum (k), mesonotum (mes), metanotum (met), mesopleuron (msp), metapleuron (mt), ocelli (oc), parapsidal lines (pl), propodeum (ppm), postpetiole (ppt), pronotum (prn), petiole (pt), and scutellum (sct)).

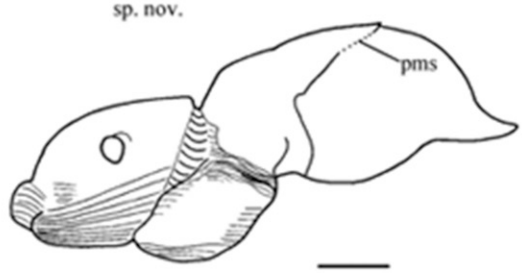


Figs. 11–15. 11, Forewing of *Solenopsis* gyne showing wing venation. 12, Larval head capsule of typical *Solenopsis*. 13, *Solenopsis* larval head capsule, occipital setal row darkened. 14, *Solenopsis* larval head capsule, first setal row on vertex darkened. 15, *Solenopsis* larval head capsule, second setal row on vertex darkened.

16. *S. metallica*, sp. nov.

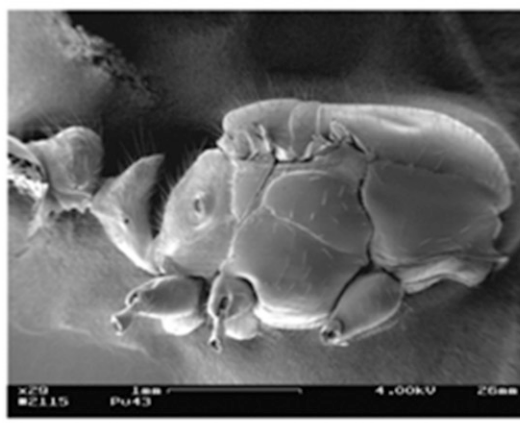
17. *S. metallica*, sp. nov.

20. *S. metallica*, sp. nov.

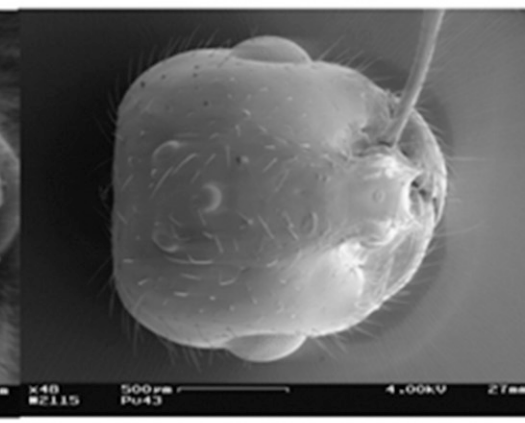


18. *S. metallica*, sp. nov.

19. *S. metallica*, sp. nov.

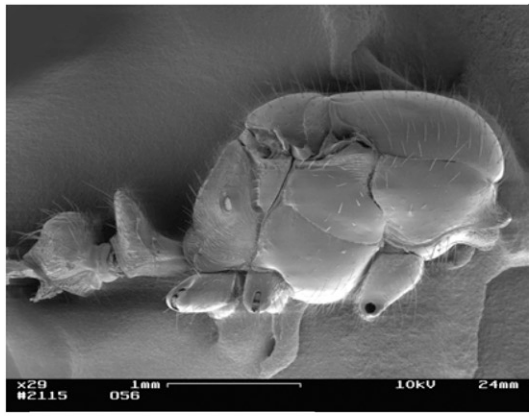


21. *S. interrupta*

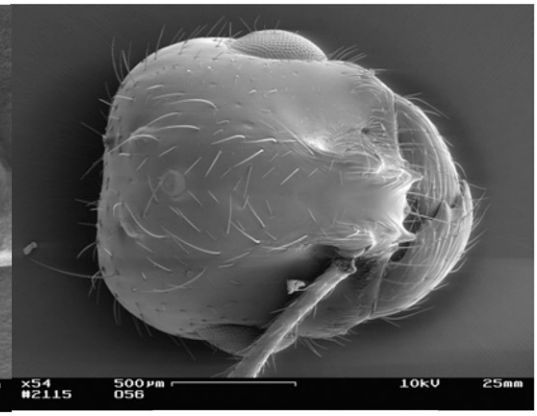


22. *S. interrupta*

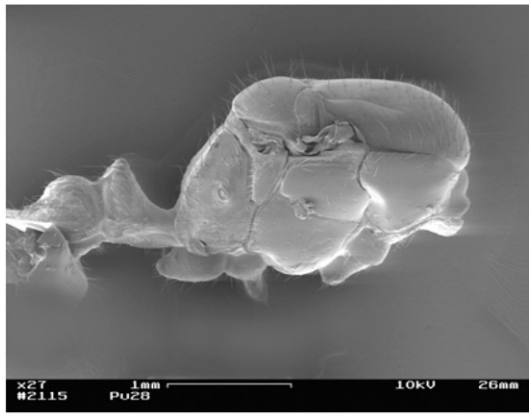
Figs. 16–22. 16, Head of major worker of *Solenopsis metallica* sp. nov., dorsal view, scale = 0.22 mm. 17, Head of minor worker of *S. metallica* sp. nov., dorsal view, scale = 0.22 mm. 18, Mesosoma of major worker of *S. metallica* sp. nov., lateral view, scale = 0.22 mm (pms = promesonotal suture). 19, Postpetiole of major worker of *S. metallica* sp. nov., rear view, scale = 0.22 mm. 20, Head of gyne of *S. metallica* sp. nov., dorsal view, scale = 0.22 mm. 21, Mesosoma of gyne of *S. interrupta*, lateral view. 22, Head of gyne of *S. interrupta*, dorsal view.



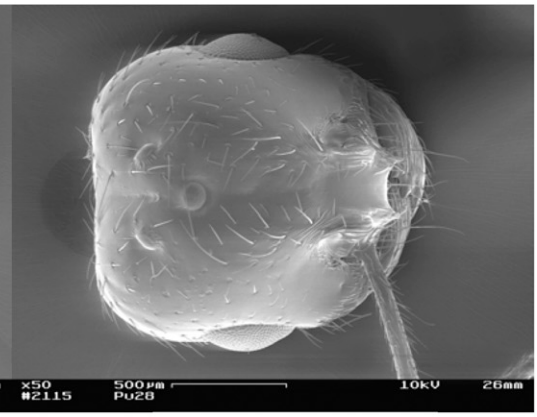
23. *S. invicta*



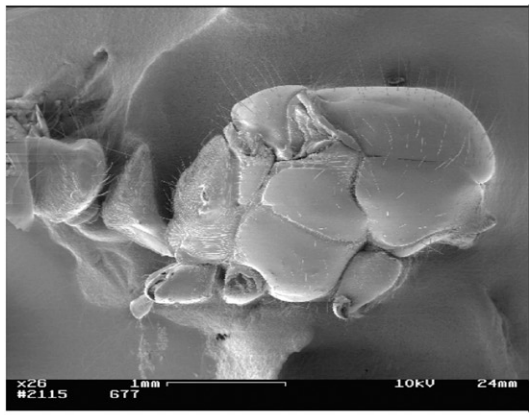
24. *S. invicta*



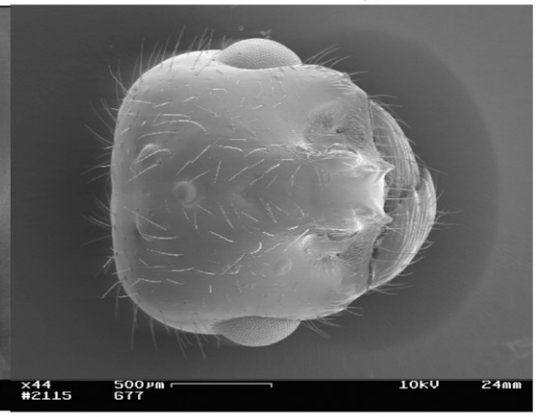
25. *S. macdonaghi*



26. *S. macdonaghi*

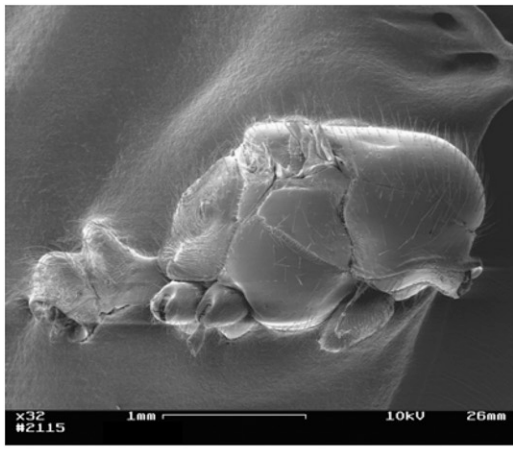


27. *S. megergates*

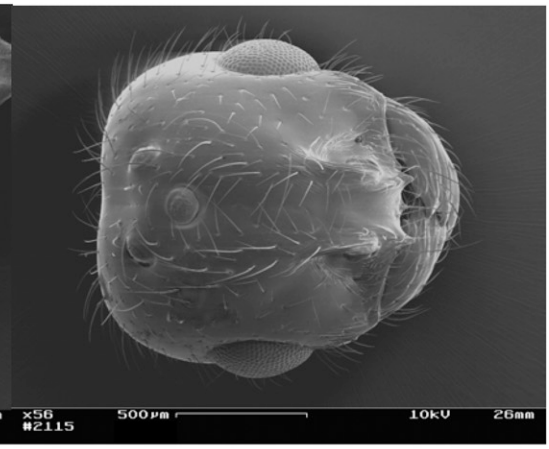


28. *S. megergates*

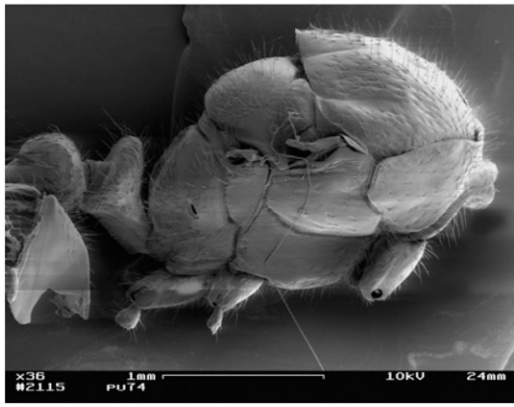
Figs. 23–28. *Solenopsis* gynes. 23, Mesosoma, *S. invicta*, lateral. 24, Head, *S. invicta*, dorsal. 25, Mesosoma, *S. macdonaghi*, latera. 26, Head, *S. macdonaghi*, dorsal. 27, Mesosoma, *S. megergates*, lateral. 28, Head, *S. megergates*, dorsal.



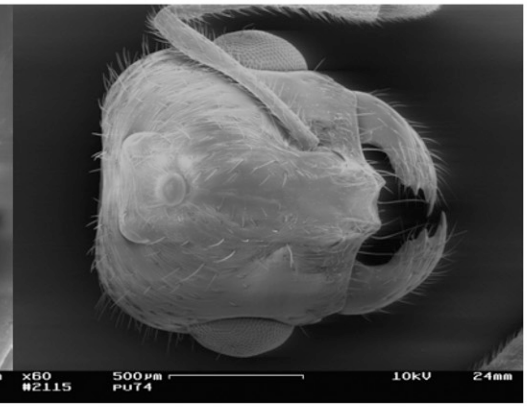
29. *S. pusillignis*



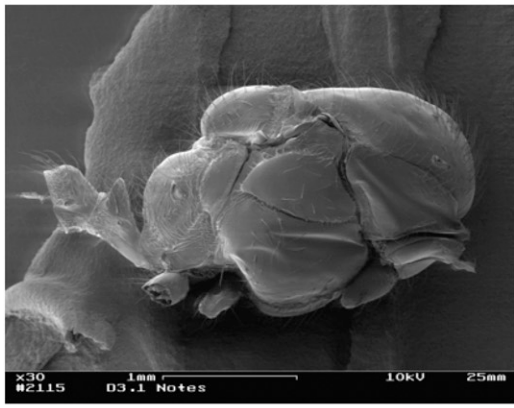
30. *S. pusillignis*



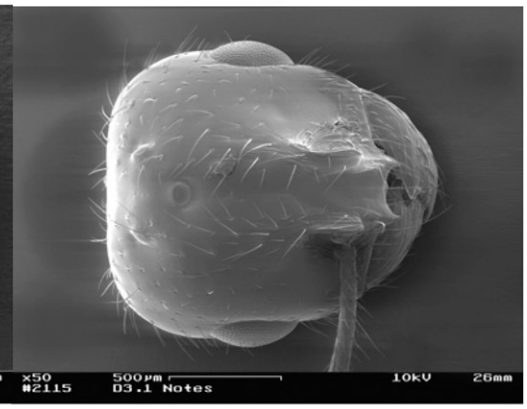
31. *S. pythia*



32. *S. pythia*

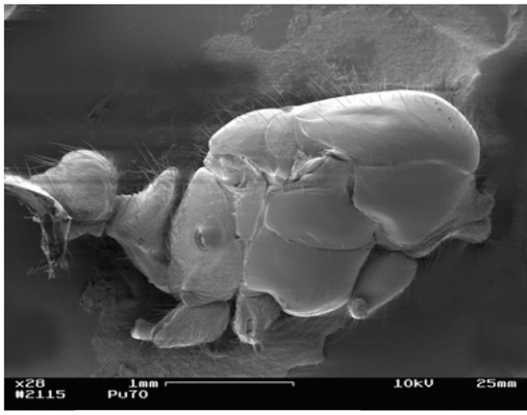


33. *S. quinquecuspsis*

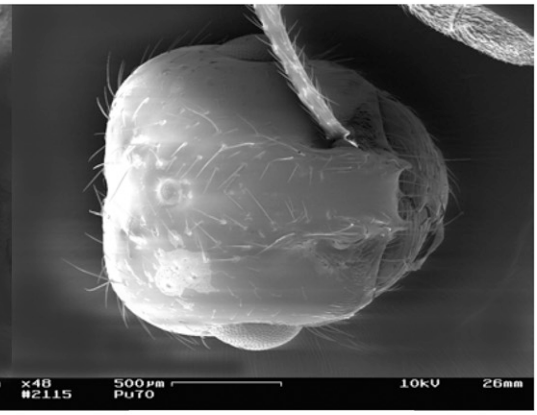


34. *S. quinquecuspsis*

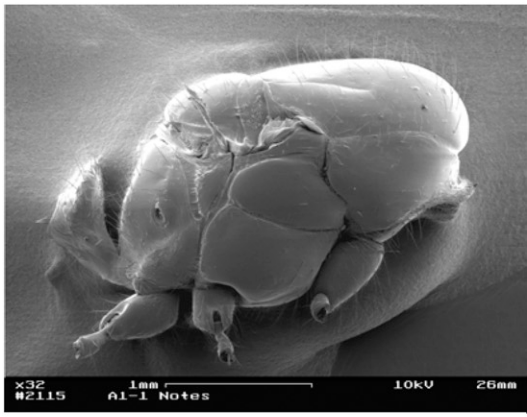
Figs. 29–34. *Solenopsis* gynes. 29, Mesosoma, *S. pusillignis*, lateral. 30, Head, *S. pusillignis*, dorsal. 31, Mesosoma, *S. pythia*, lateral. 32, Head, *S. pythia*, dorsal. 33, Mesosoma *S. quinquecuspis*, lateral. 34, Head, *S. quinquecuspis*, dorsal.



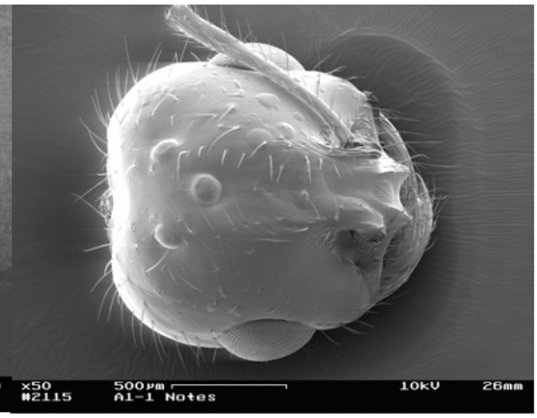
35. *S. richteri*



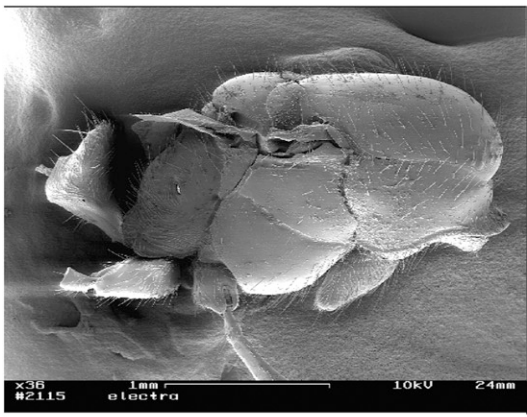
36. *S. richteri*



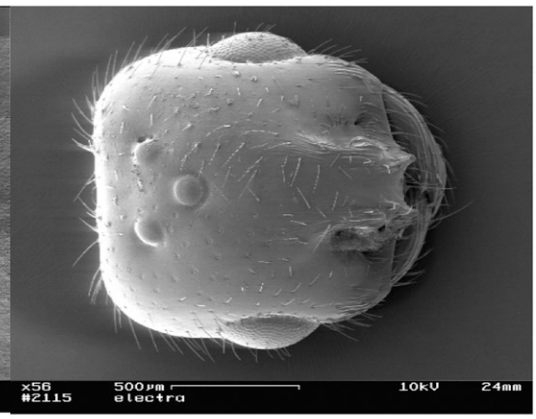
37. *S. saevissima*



38. *S. saevissima*

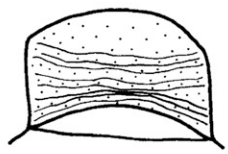


39. *S. electra*

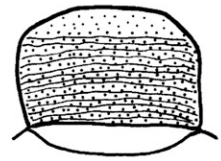


40. *S. electra*

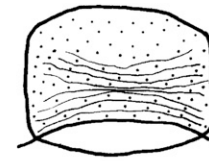
Figs. 35–40. *Solenopsis* gynes. 35, Mesosoma, *S. richteri*, lateral. 36, Head, *S. richteri*, dorsal. 37, Mesosoma, *S. saevissima*, lateral. 38, Head, *S. saevissima*, dorsal. 39, Mesosoma, *S. electra*, lateral. 40, Head, *S. electra*, dorsal.



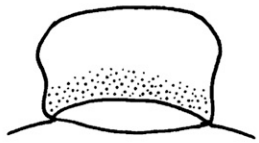
41. *S. macdonaghi*



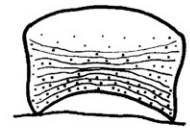
42. *S. invicta*



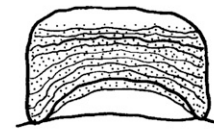
43. *S. quinquecuspis*



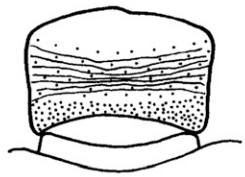
44. *S. metallica*, sp. nov.



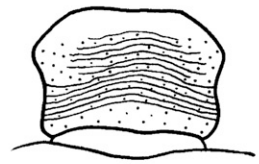
45. *S. pusillignis*



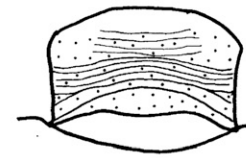
46. *S. pythia*



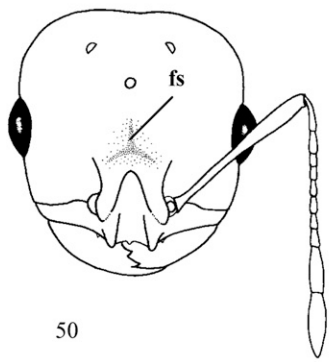
47. *S. interrupta*



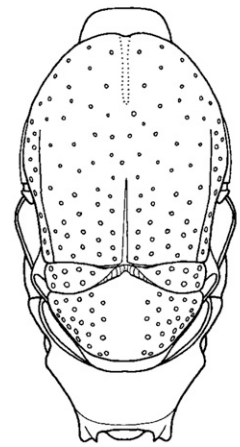
48. *S. richteri*



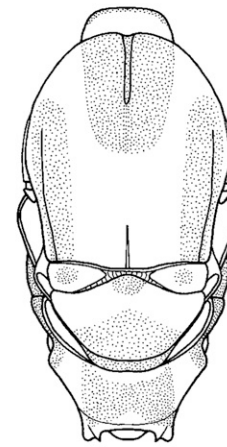
49. *S. saevissima*



50

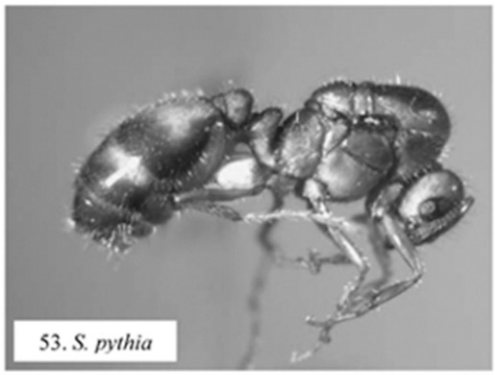


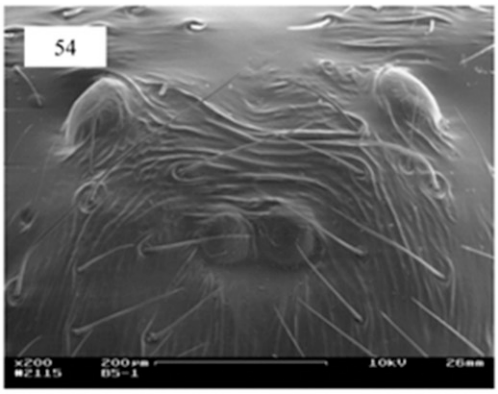
51. *S. pythia*

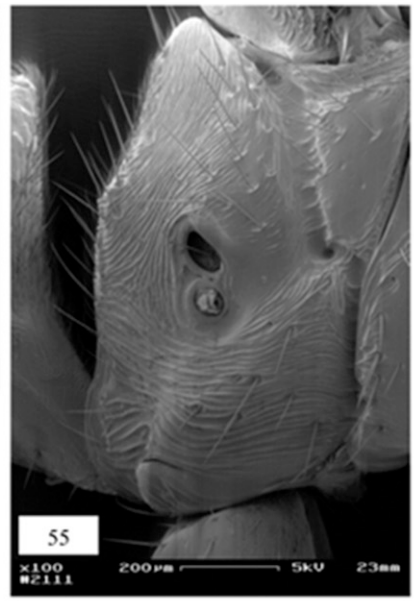


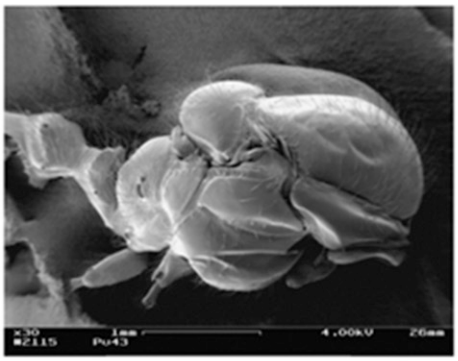
52. *S. interrupta*

Figs. 41–52. Postpetiole of *Solenopsis* gynes, posterior view. 41, *S. macdonaghi*. 42, *S. invicta*. 43, *S. quinquecuspis*. 44, *S. metallica* sp. nov. 45, *S. pusillignis*. 46, *S. pythia*. 47, *S. interrupta*. 48, *S. richteri*. 49, *S. saevissima*. *Solenopsis* gynes. 50, Head of *Solenopsis* sp. with median frontal steak (fs), dorsal view. 51, Mesosoma of *S. pythia* showing large foveolae, dorsal view. 52, Mesosoma of *Solenopsis* sp. showing maculae, dorsal view.

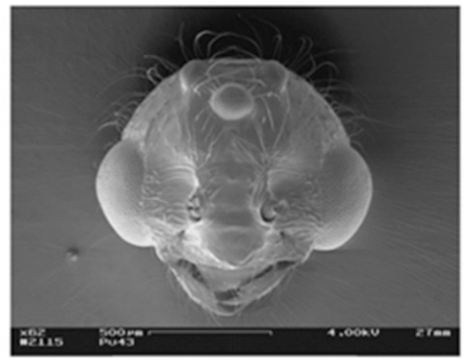






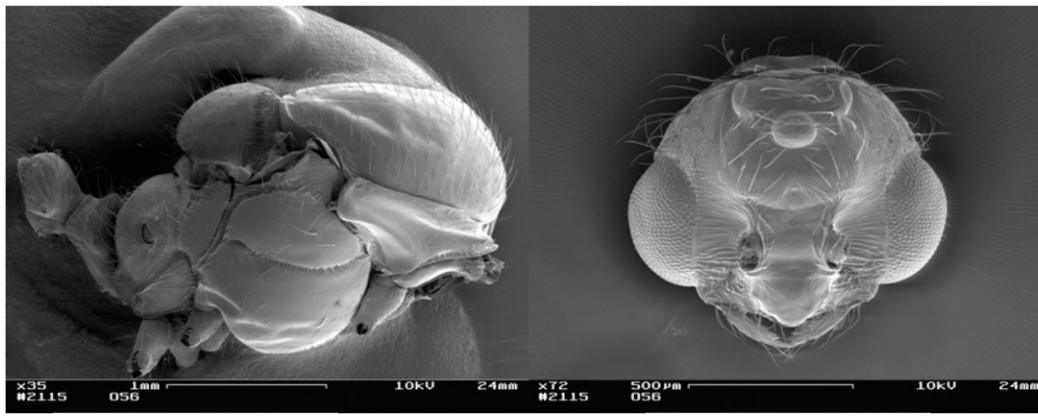


56. *S. interrupta*

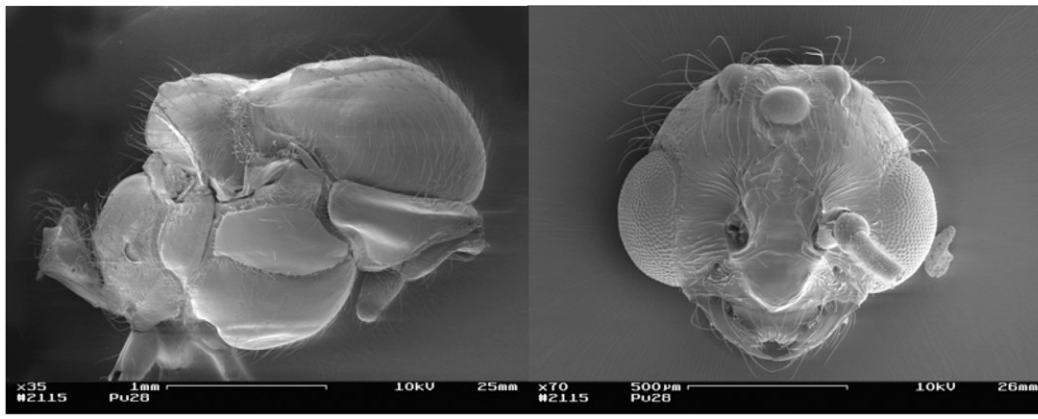


57. *S. interrupta*

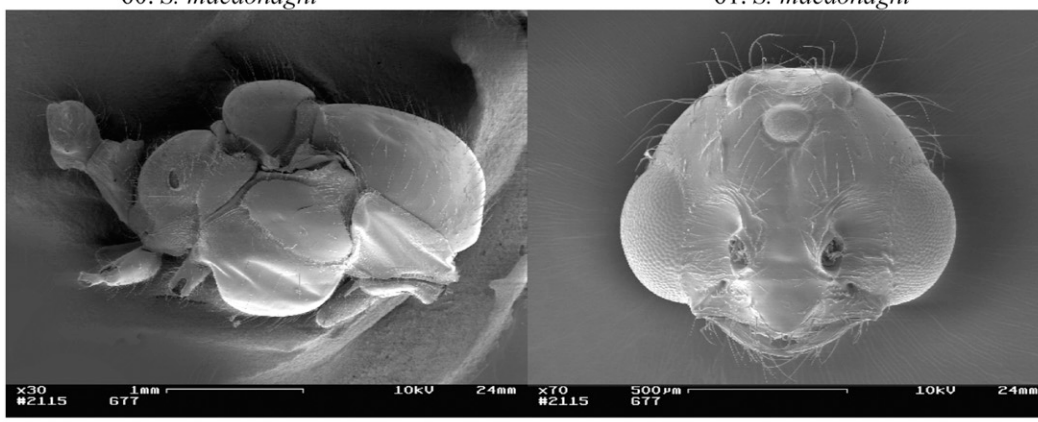
Figs. 53–57. *Solenopsis* spp. gynes, mesonoma, and head. 53, *S. pythia*, lateral view. 54, Ocellar triangle of *Solenopsis quinquecuspis* gyne with two median ocelli, dorsal view. 55, Propodeum of *S. quinquecuspis* gyne with four propodeal spiracles, lateral view. 56, Mesosoma of male of *S. interrupta*, lateral view. 57, Head of male of *S. interrupta*, dorsal view.



58. *S. invicta* 59. *S. invicta*

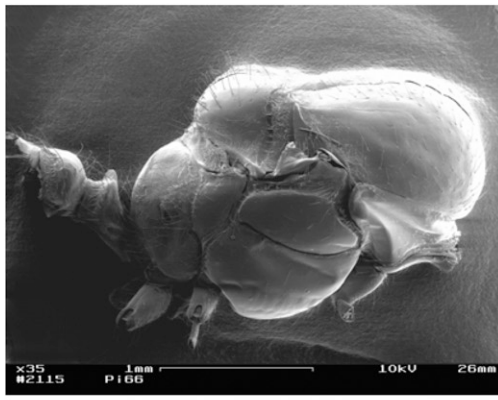


60. *S. macdonaghi* 61. *S. macdonaghi*



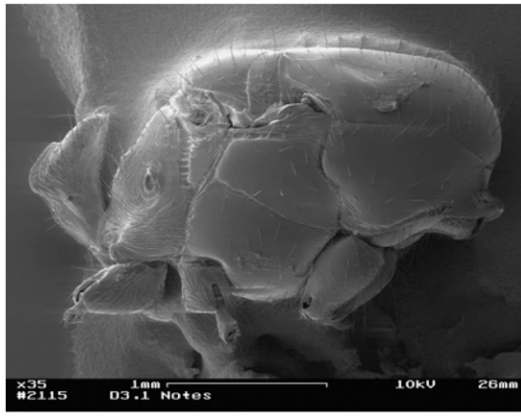
62. *S. megergates* 63. *S. megergates*

Figs. 58–63. *Solenopsis* males. 58, Mesosoma of *S. invicta*, lateral view. 59, Head of *S. invicta*, dorsal view. 60, Mesosoma of *S. macdonaghi*, lateral view. 61, Head of *S. macdonaghi*, dorsal view. 62, Mesosoma of *S. megergates*, lateral view. 63, Head of *S. megergates*, dorsal view.

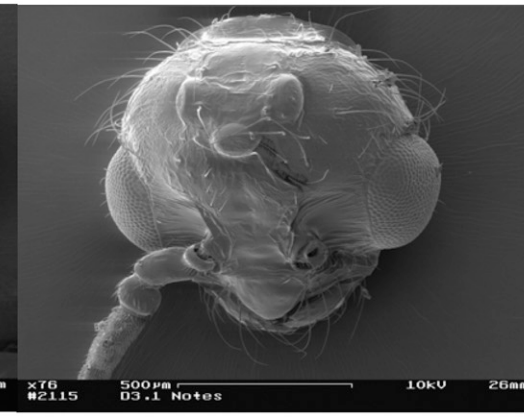


64. *S. pusillignis*

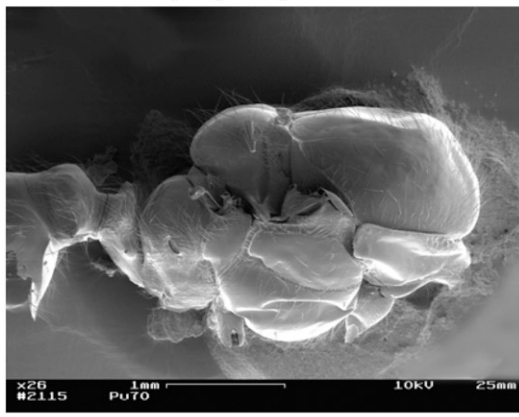
65. *S. pusillignis*



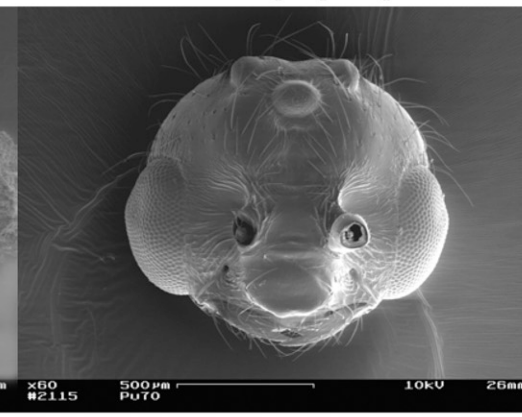
66. *S. quinquecuspis*



67. *S. quinquecuspis*

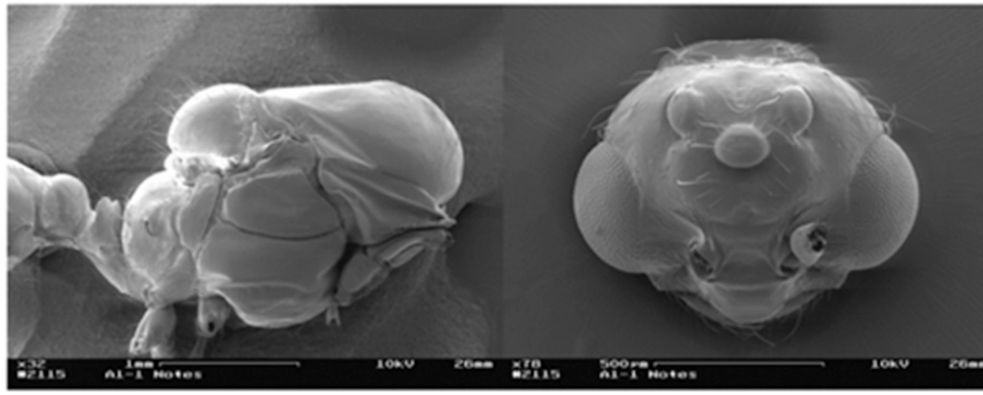


68. *S. richteri*



69. *S. richteri*

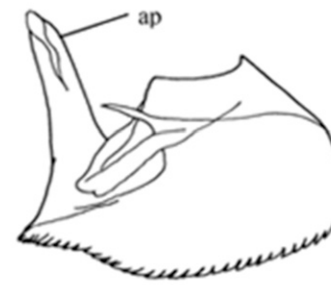
Figs. 64–69. *Solenopsis* males. 64, Mesosoma of *S. pusillignis*, lateral view. 65, Head of *S. pusillignis*, dorsal view. 66, Mesosoma of *S. quinquecuspis*, lateral view. 67, Head of *S. quinquecuspis*, dorsal view. 68, Mesosoma of *S. richteri*, lateral view. 69, Head of *S. richteri*, dorsal view.



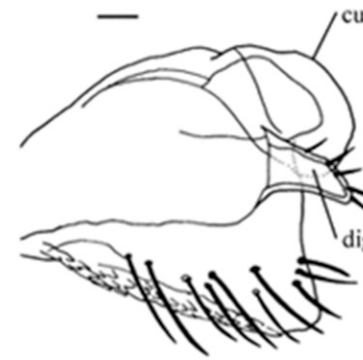
70. *S. saevissima*

71. *S. saevissima*

72. *S. saevissima*

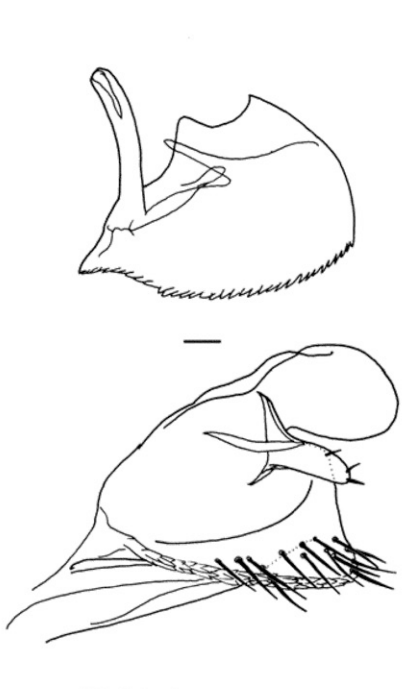


73. *S. interrupta*

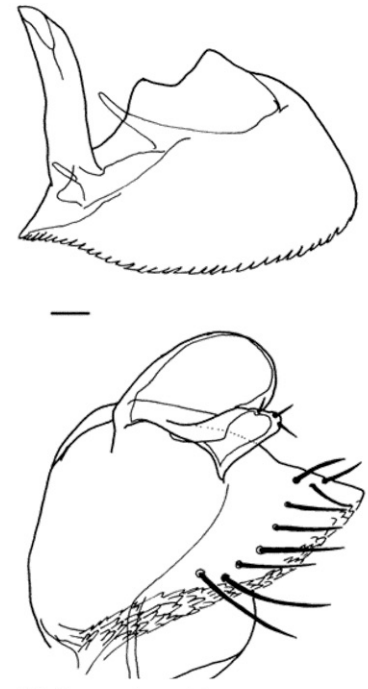


74. *S. interrupta*

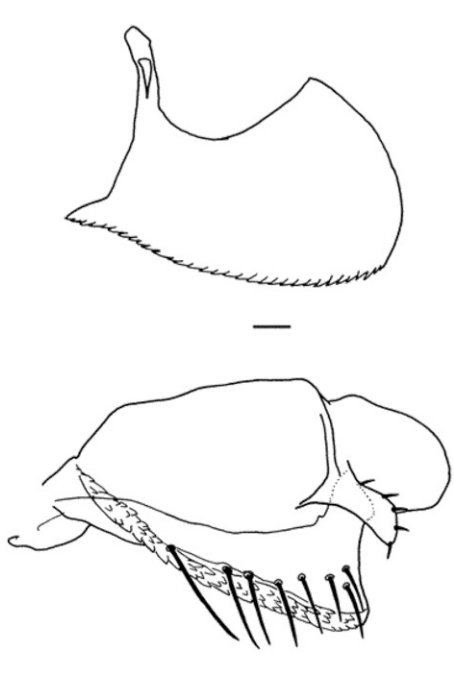
Figs. 70–74. *Solenopsis* males. 70, Mesosoma of *S. saevissima*, lateral view. 71, Head of *S. saevissima*, dorsal view. 72, Mesosomal dorsum of *S. saevissima*, dark form, lateral view. 73, Mesosomal dorsum of *S. interrupta*, dark form, lateral view. 74, Genitalia of *S. interrupta*, aedeagus, upper, scale = 62 µm (dorsal apodeme (ap)); volsella, lower, scale = 25 µm (cuspis (cus) and digitus (dig)).



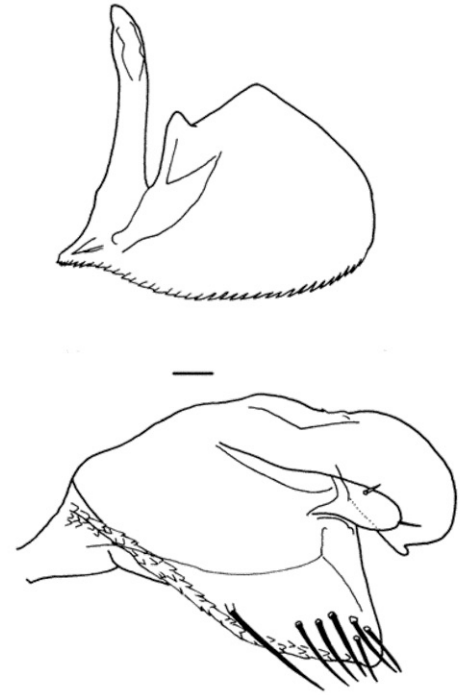
75. *S. invicta*



76. *S. macdonaghi*

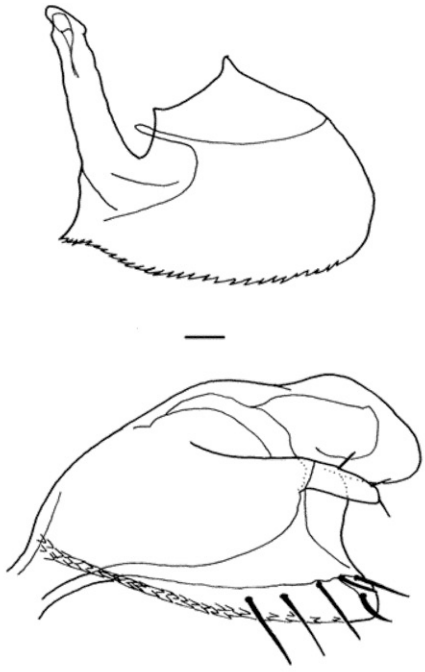


77. *S. macdonaghi*

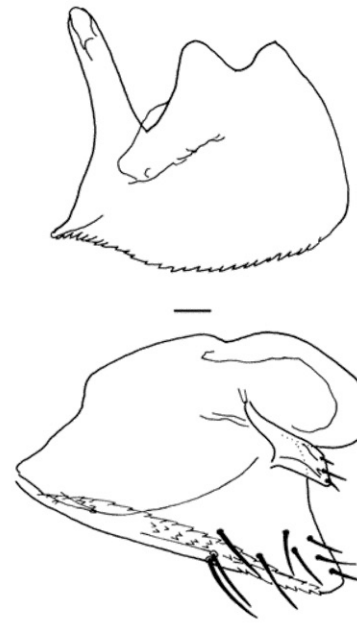


78. *S. megergates*

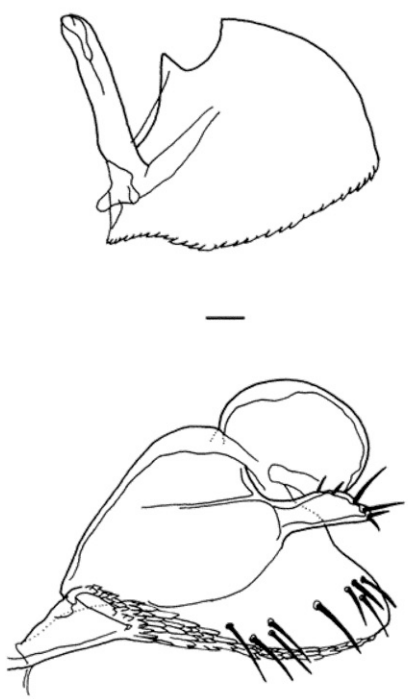
Figs. 75–78. Genitalia of male. 75, *Solenopsis invicta*. 76, *S. macdonaghi*. 77, *S. macdonaghi*. 78, *S. megergates*, aedeagus; upper, scale = 62 μm, volsella; lower, scale = 25 μm.



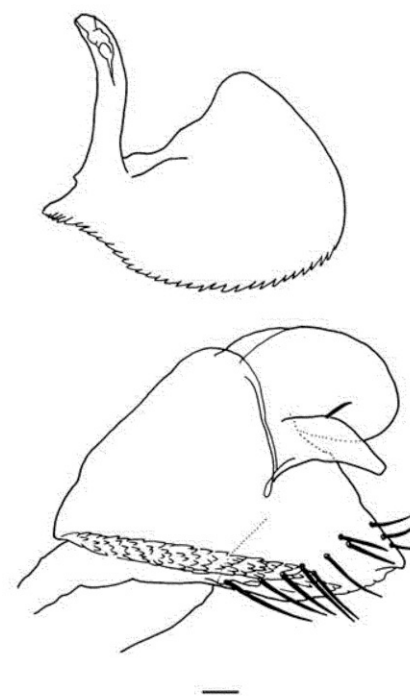
79. *S. megergates*



80. *S. pusillignis*

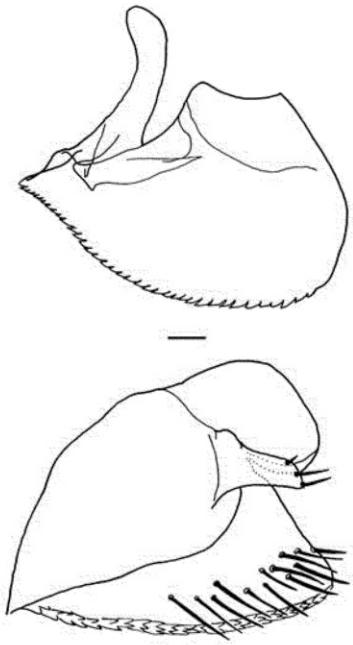


81. *S. quinquecuspis*



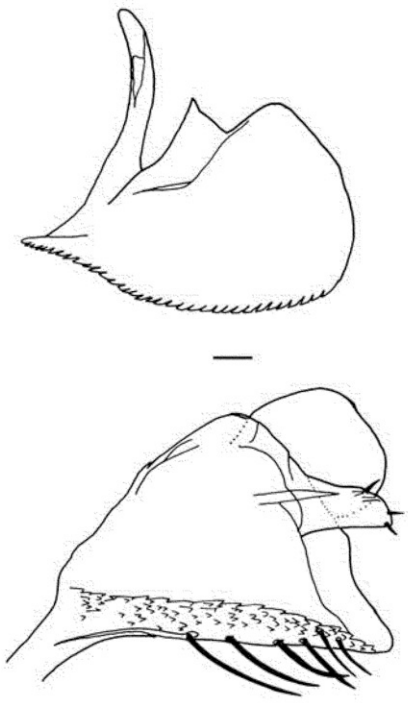
82. *S. richteri*

Figs. 79–82. Genitalia of male. 79, *Solenopsis megergates.* 80, *S. pusillignis.* 81, *S. quinquecuspis.* 82, *S. richteri;* aedeagus, upper, scale = 62 μm; volsella, lower, scale = 25 μm.

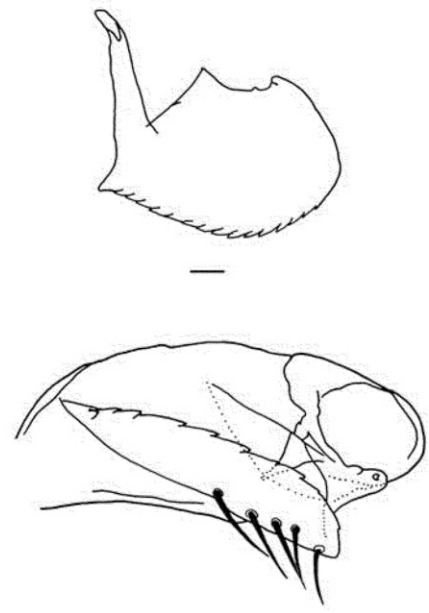


83. *S. richteri*

84. *S. saevissima*, light form

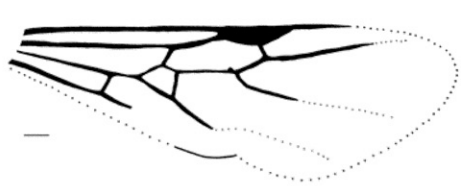


85. *S. saevissima*

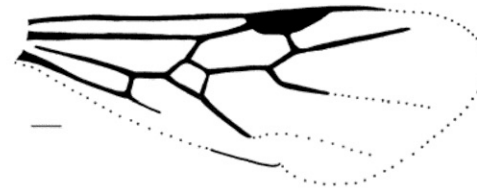


86. *S. daguerrei*

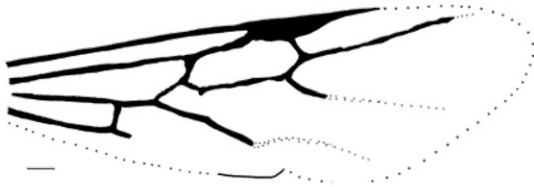
Figs. 83–86. 83, Genitalia of male: *Solenopsis richteri.* 84, *S. saevissima.* 85, *S. saevissima.* 86, *S. daguerrei;* aedeagus, upper, scale = 62 μm; volsella, lower, scale = 25 μm.



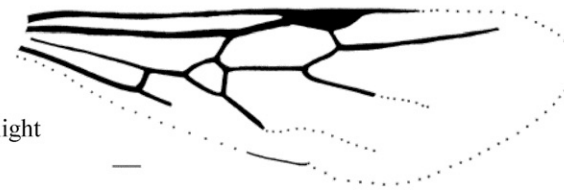
87. *S. pusillignis*, queen



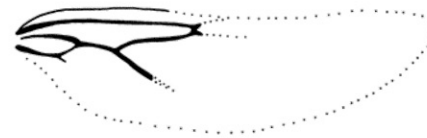
88. *S. pusillignis*, male

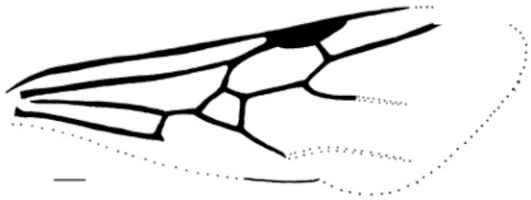


89. *S. metallica,* sp. nov., queen

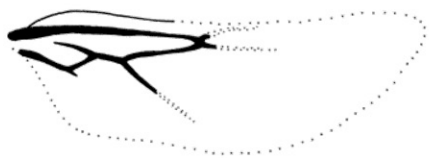


90. *S. saevissima*, light form, queen

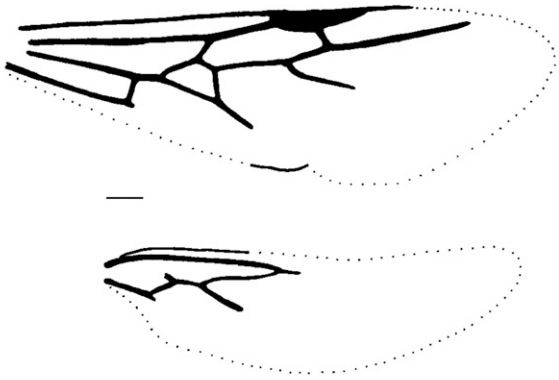




91. *S. saevissima*, light form, male

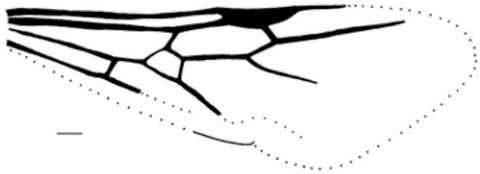


Figs. 87–91. *Solenopsis* wings. 87, Forewing of *S. pusillignis* gyne. 88, Forewing of *S. pusillignis* male. 89, *S. metallica* sp. nov. gyne. 90, *S. saevissima* gyne, light form. 91, *S. saevissima* male, light form; scale = 350 μm.



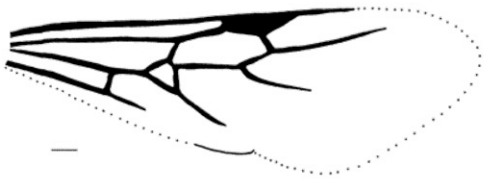
92. *S. interrupta*,
queen

93. *Solenopsis interrupta*,
male



94. *Solenopsis invicta*,
queen

95. *Solenopsis invicta*,
male

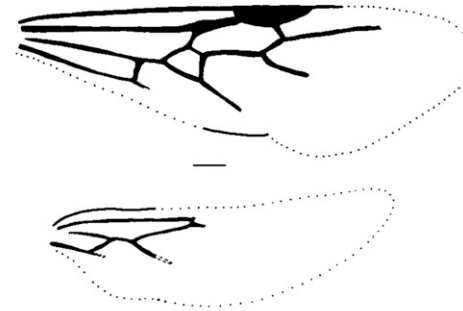


96. *Solenopsis macdonaghi*,
queen

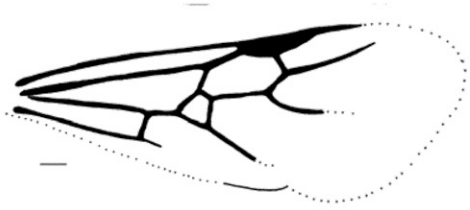
97. *S. macdonaghi*,
male

Figs. 92–97. *Solenopsis* wings. 92, *S. interrupta* gyne. 93, Forewing of *S. interrupta* male. 94, Forewing of *S. invicta* gyne. 95, Forewing of *S. invicta* male. 96, Forewing of *S. macdonaghi* gyne. 97, Forewing of *S. macdonaghi* male, scale = 350 μm.

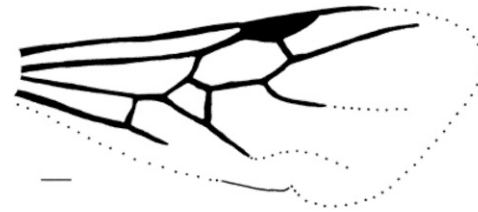
98. *S. megergates*, queen



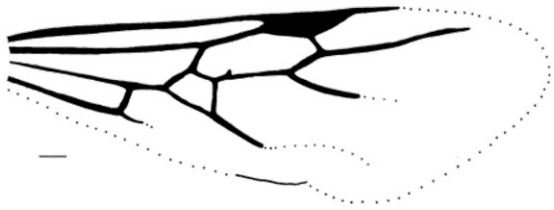
100. *S. quinquecuspis*, queen



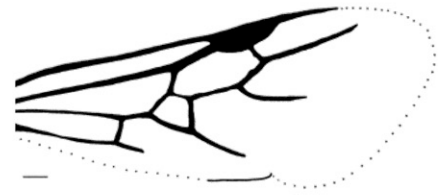
99. *S. megergates*, male



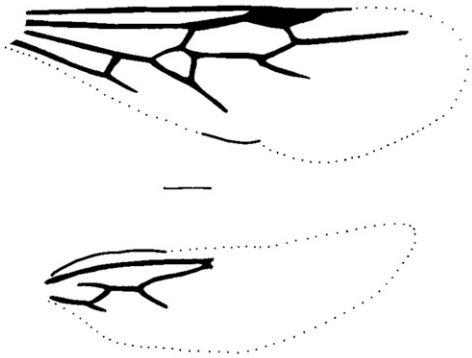
101. *S. quinquecuspis*, male



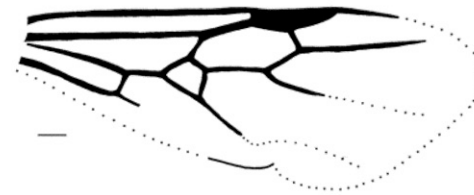
102. *S. richteri*, queen



103. *S. richteri*, male

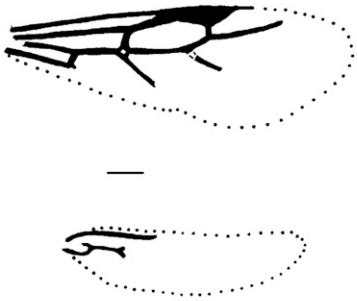


104. *S. saevissima*, queen

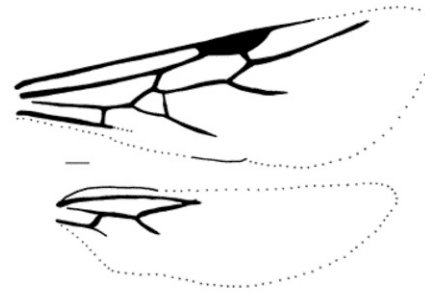


105. *S. saevissima*, male

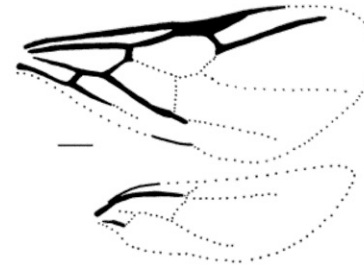
Figs. 98–105. *Solenopsis* wings. 98, *S. megergates* gyne. 99, *S. megergates* male. 100, Forewing of *S. quinquecuspis* gyne. 101, *S. quinquecuspis* male. 102, Forewing of *S. richteri* gyne. 103, Forewing of *S. richteri* male. 104, *S. saevissima* gyne. 105, Forewing of *S. saevissima* male, scale = 350 μm.



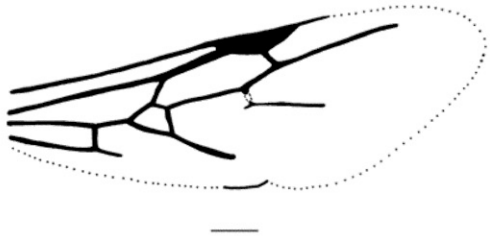
106. *S. daguerrei*,
queen



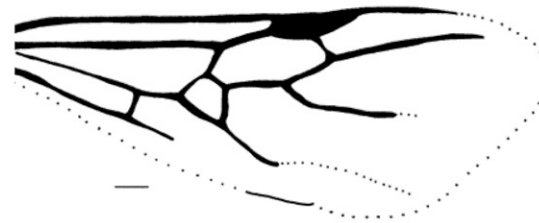
107. *S. electra*
queen



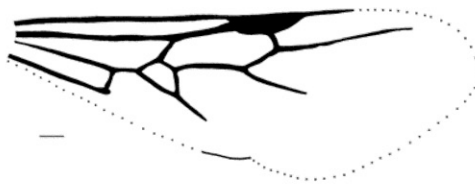
108. *S. daguerrei*,
male



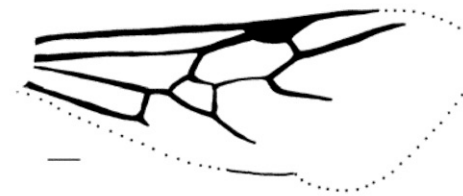
109. *S. geminata*,
queen



110. *S. geminata*,
male

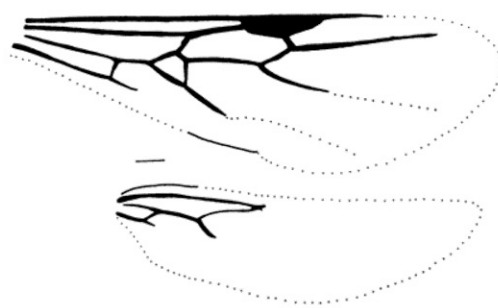


111. *S. xyloni*,
queen

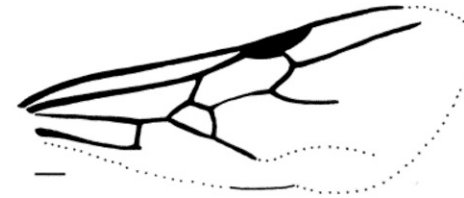


112. *S. xyloni*,
male

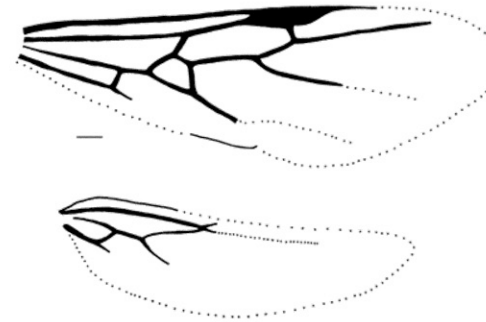
Figs. 106–112. *Solenopsis* wings. 106, *S. daguerrei* gyne. 107, *S. electra* gyne. 108, *S. daguerrei* male. 109, *S. geminata* gyne. 110, Forewing of *S. geminata* male. 111, Forewing of *S. xyloni* gyne. 112, Forewing of *S. xyloni* male, scale = 350 μm.



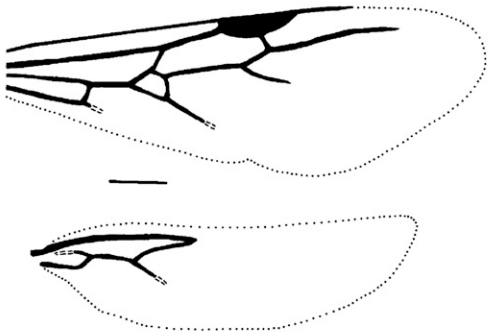
113. *S. amblychila*, queen



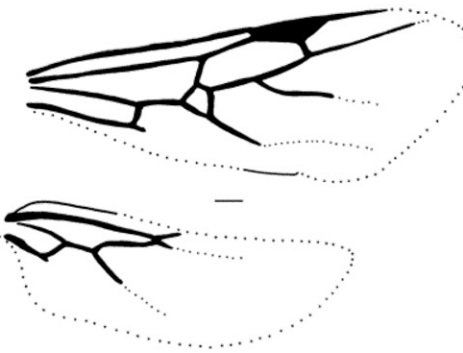
114. *S. amblychila*, male



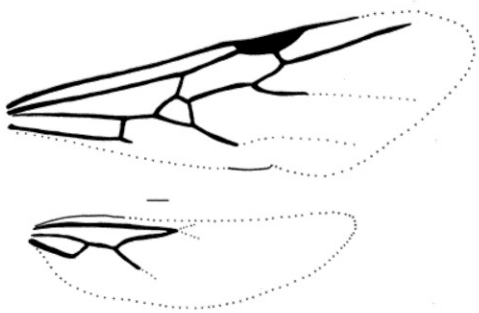
115. *S. tridens*, queen



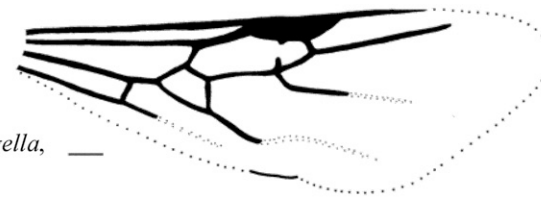
116. *S. aurea*, queen



118. *S. substituta*, male

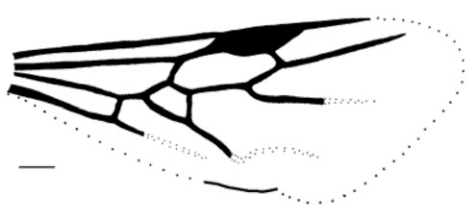


117. *S. substituta*, queen



119. *S.* nr *nigella*, queen

Figs. 113–119. *Solenopsis* wings. 113, *S. amblychila* gyne. 114, Forewing of *S. amblychila* male. 115, *S. tridens* gyne. 116, *S. aurea* gyne. 117, *S. substituta* gyne. 118, *S. amblychila* male. 119, Forewing of *S.* nr. *nigella* gyne, scale = 350 μm.

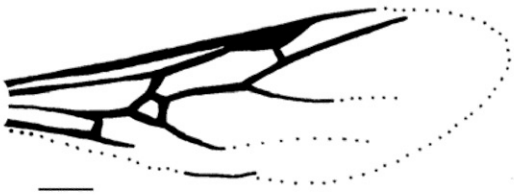


120. *S.* nr *nigella*,
male

121. *S.* sp.,
"thief ant" queen

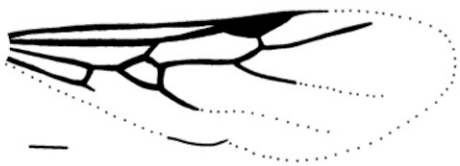
122. *S. n. gensterblumi,*
queen

123. *S. globularia littoralis*,
queen

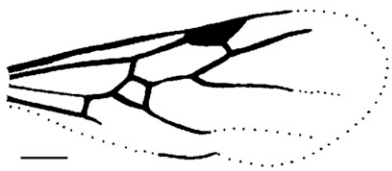


124. *S. picta*,
queen

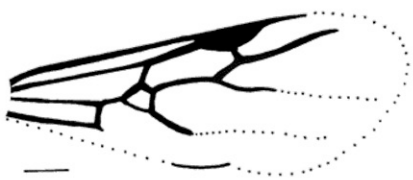
125. *S. picta*,
male



126. *S. abdita*,
queen



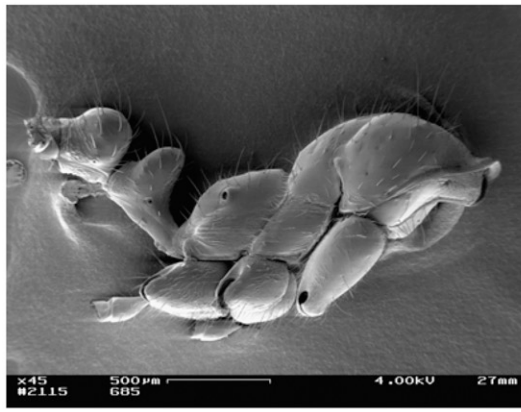
127. *S. tennesseensis,*
male



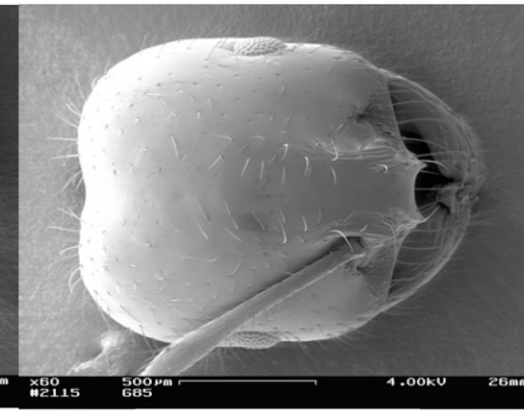
128. *S. abdita*,
male

129. *S. carolinensis*,
queen

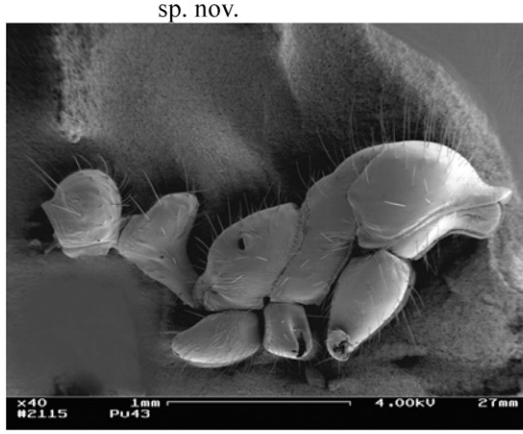
Figs. 120–129. *Solenopsis* forewings. 120, *Solenopsis* nr. *nigella* male. 121, *Solenopsis* sp. "thief ant" gyne. 122, *S. gensterblumi* gyne. 123, *S. globularia littoralis* gyne. 124, *S. picta* gyne. 125, *S. picta* male. 126, *S. abdita* gyne. 127, *S. tennesseensis* male. 128, *S. abdita* male. 129, *S. carolinensis* gyne, scale = 350 μm.



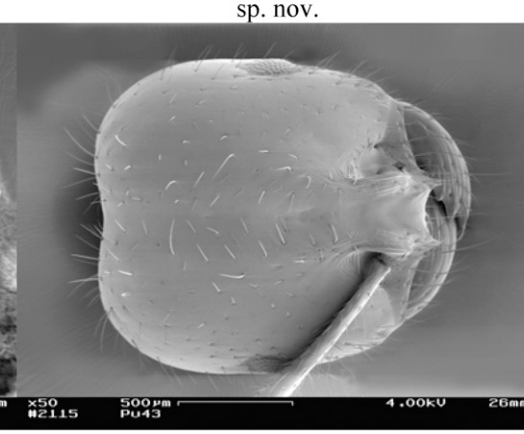
130. *S. metallica,* sp. nov.



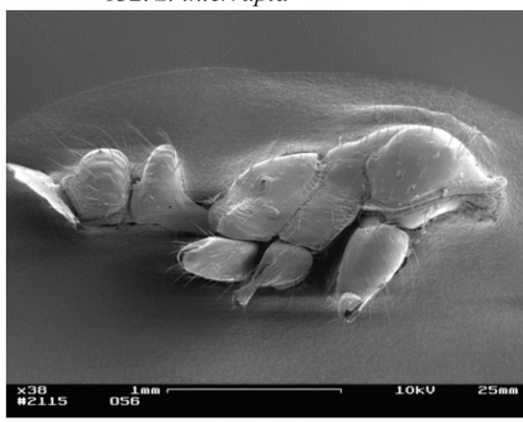
131. *S. metallica,* sp. nov.



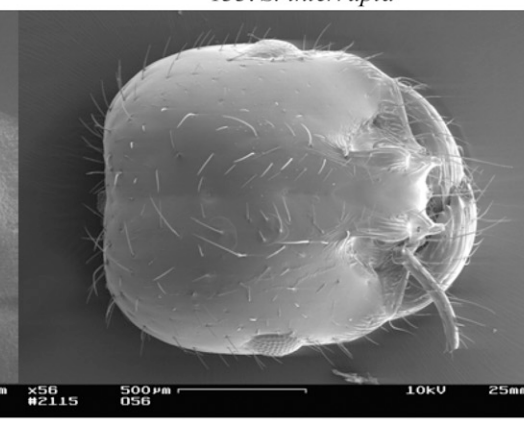
132. *S. interrupta*



133. *S. interrupta*

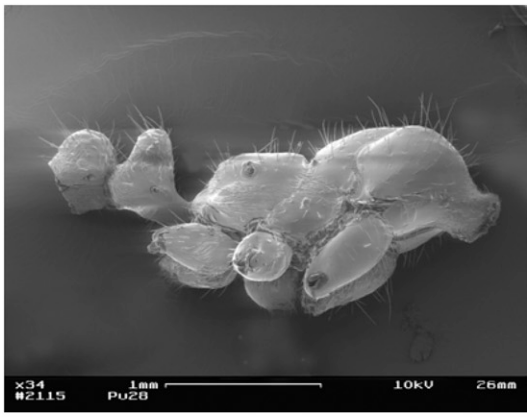


134. *S. invicta*

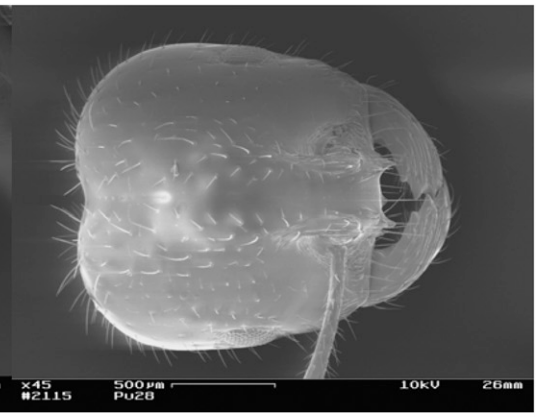


135. *S. invicta*

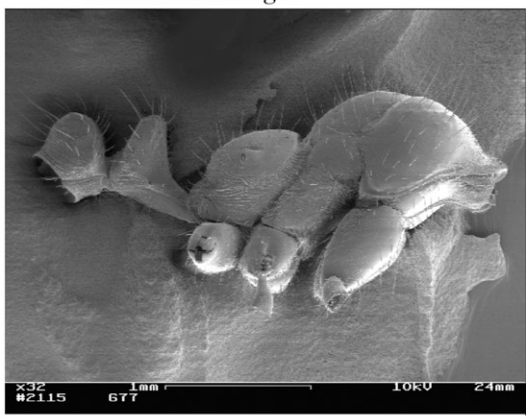
Figs. 130–135. *Solenopsis* major workers. 130, Mesosoma of *S. metallica* sp. nov., lateral view. 131, Head of *S. metallica* sp. nov., dorsal view. 132, Mesosoma of *S. interrupta*, lateral view. 133, Head of *S. interrupta*, dorsal view. 134, Mesosoma of *S. invicta*, lateral view. 135, Head of *S. invicta*, dorsal view.



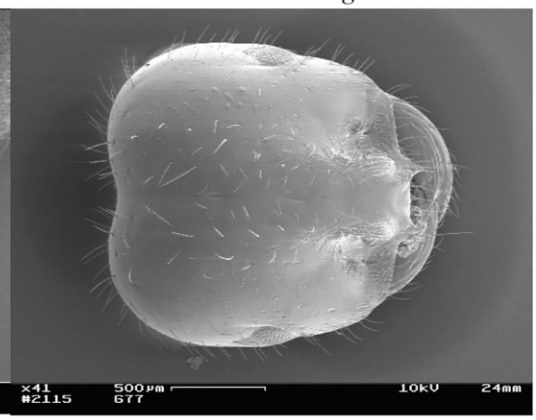
136. *S. macdonaghi*



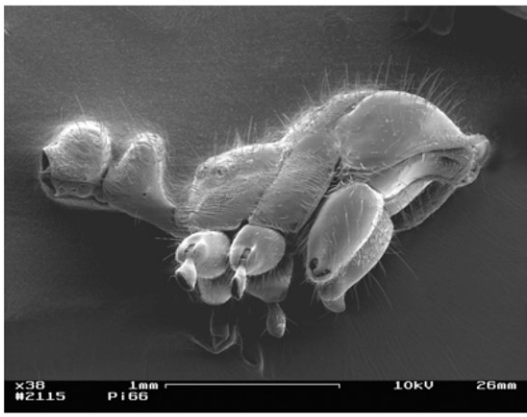
137. *S. macdonaghi*



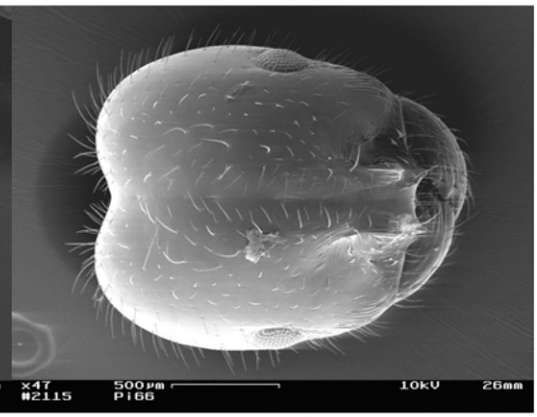
138. *S. megergates*



139. *S. megergates*

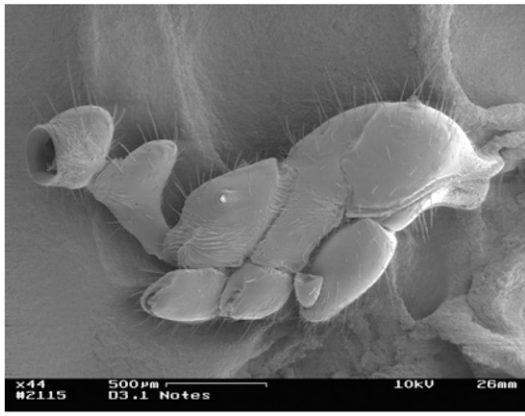


140. *S. pusillignis*

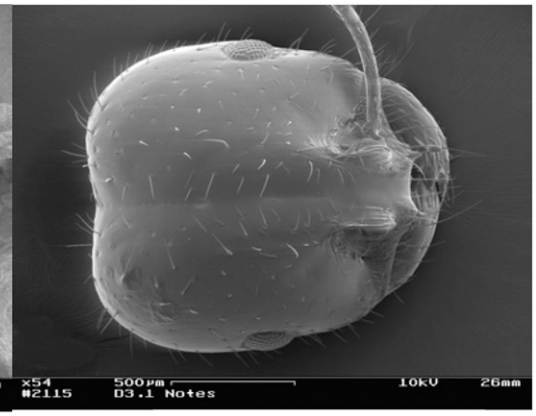


141. *S. pusillignis*

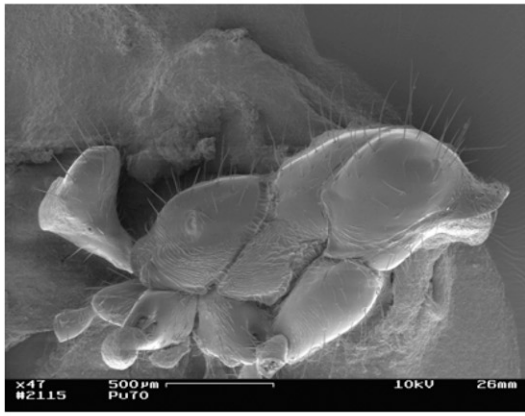
Figs. 136–141. *Solenopsis* major workers. 136, Mesosoma of *S. macdonaghi*, lateral view. 137, Head of *S. macdonaghi*, dorsal view. 138, Mesosoma of *S. megergates*, lateral view. 139, Head of *S. megergates*, dorsal view. 140, Mesosoma of *S. pusillignis*, lateral view. 141, Head of *S. pusillignis*, dorsal view.



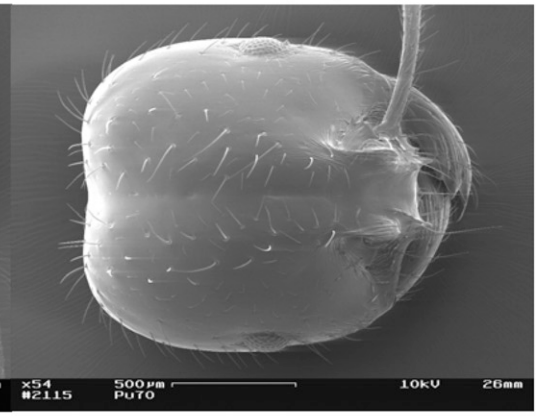
142. *S. quinquecuspis*



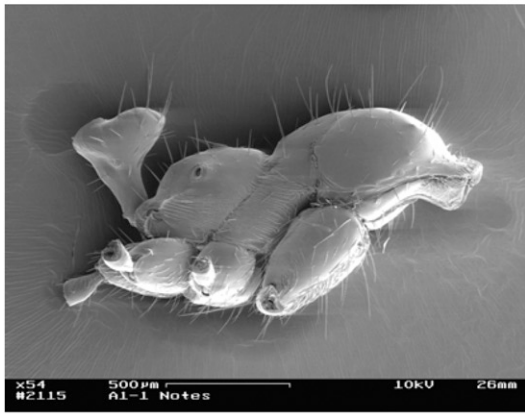
143. *S. quinquecuspis*



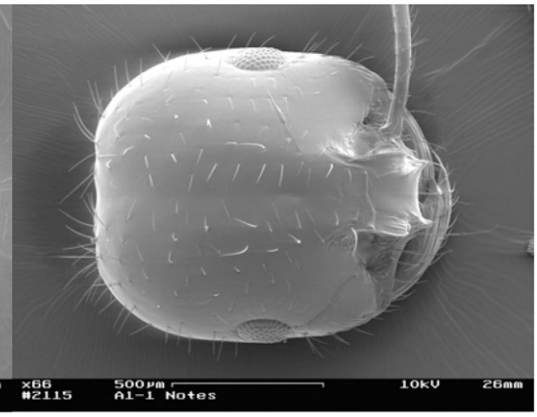
144. *S. richteri*



145. *S. richteri*

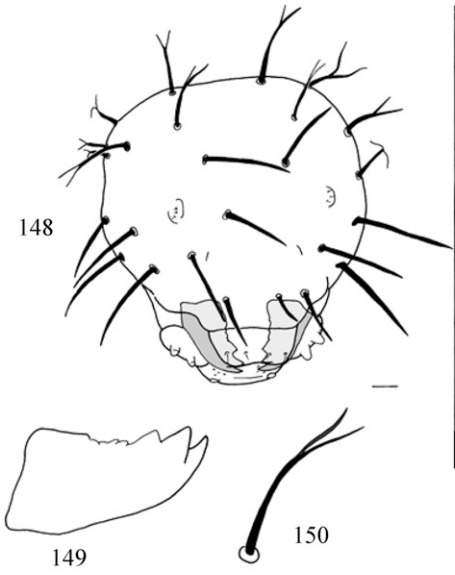


146. *S. saevissima*

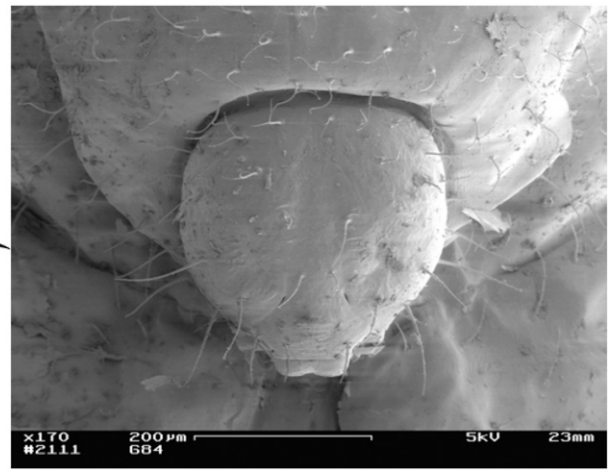


147. *S. saevissima*

Figs. 142–147. *Solenopsis* major workers. 142, Mesosoma of *S. quinquecuspis*, lateral view. 143, Head of *S. quinquecuspis*, dorsal view. 144, Mesosoma of *S. richteri*, lateral view. 145, Head of *S. richteri*, dorsal view. 146, Mesosoma of *S. saevissima*, lateral view. 147, Head of *S. saevissima*, dorsal view.

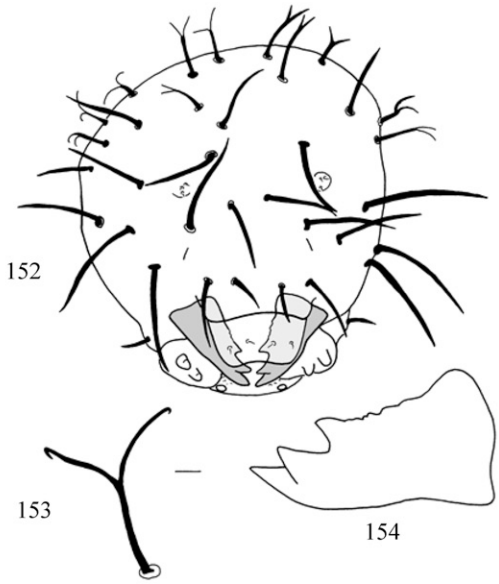


S. metallica,
sp. nov.

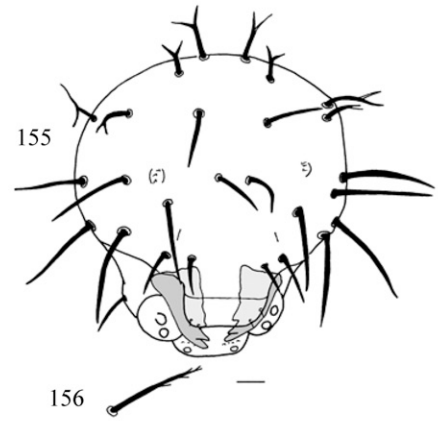


151. *S. metallica,* sp. nov.

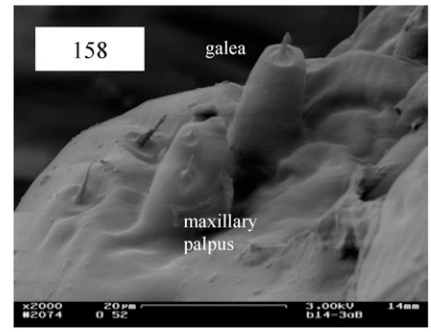
Figs. 148–151. *Solenopsis* larval structures. 148, Head capsule, *S. metallica* sp. nov., dorsal, scale = 46 µm. 149, Mandible, *S. metallica* sp. nov., scale = 18 µm. 150, Bifid setae on head capsule, *S. metallica* sp. nov., dorsal, scale = 18 µm. 151, Head capsule, *S. metallica* sp. nov., dorsal, scale = 18 µm.

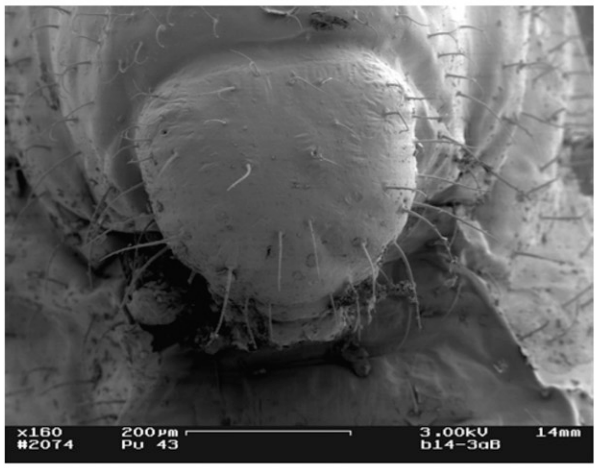


S. interrupta

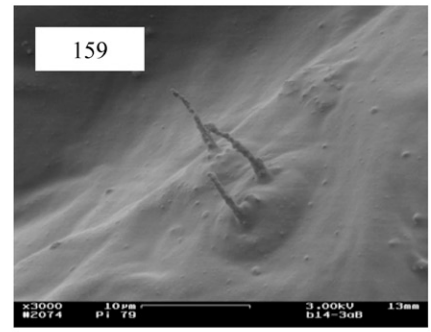


S. saevissima,
light form

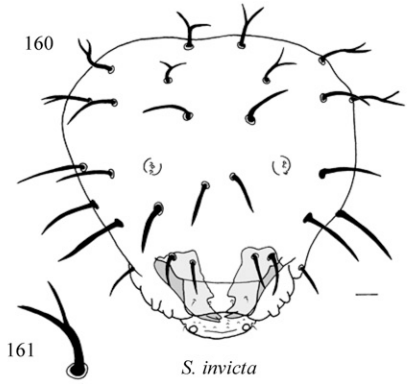




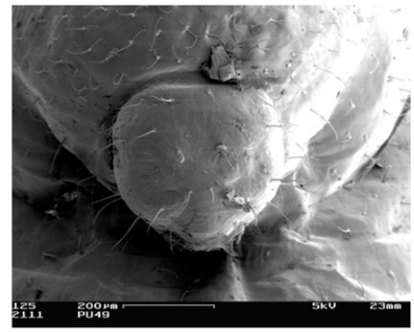
157. *S. interrupta*



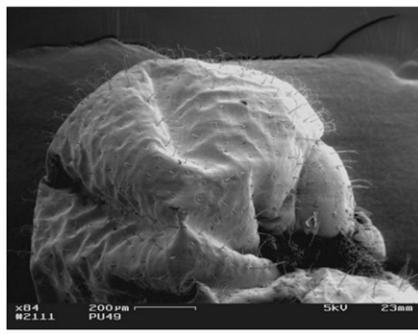
Figs. 152–159. *Solenopsis* larval structures. 152, Head capsule, *S. interrupta*, dorsal, scale = 46 µm. 153, Bifid setae on body, *S. interrupta*, dorsal, scale = 18 µm. 154, Mandible, *S. interrupta*, dorsal, scale = 18 µm. 155, Head capsule, *S. saevissima*, dorsal, scale = 46 µm. 156, Denticulate setae on body, *S. saevissima*, dorsal, scale = 46 µm. 157, Head capsule, *S. interrupta*, dorsal. 158, Maxillary palpus and galea, *S. invicta*, lateral. 159, Antennal setae, *S. pusillignis*, dorsal.



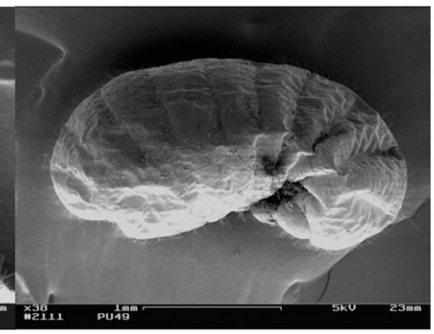
S. invicta



162. *S. invicta*

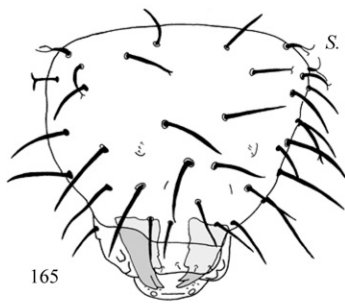


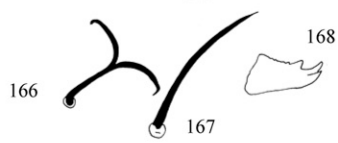
163. *S. invicta*

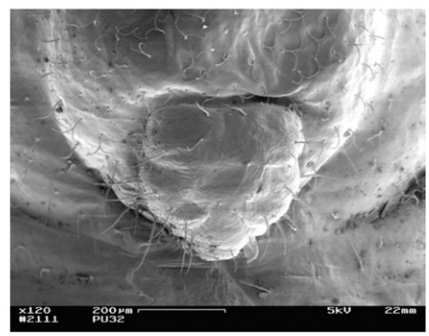


164. *S. invicta*

S. macdonaghi

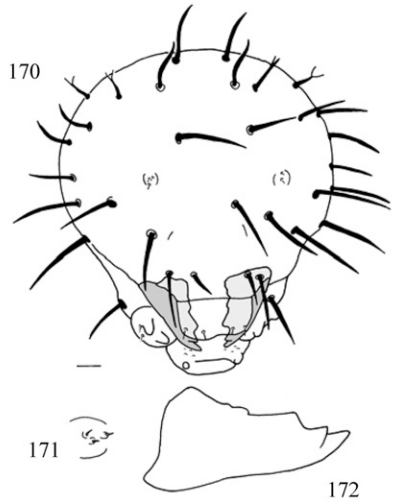




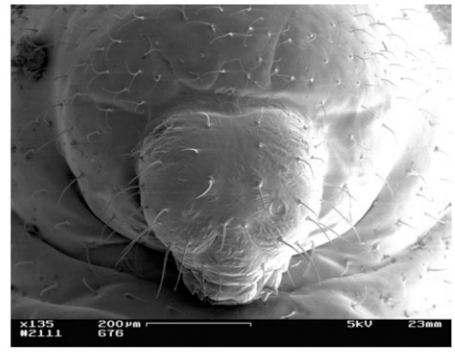


169. *S. macdonaghi*

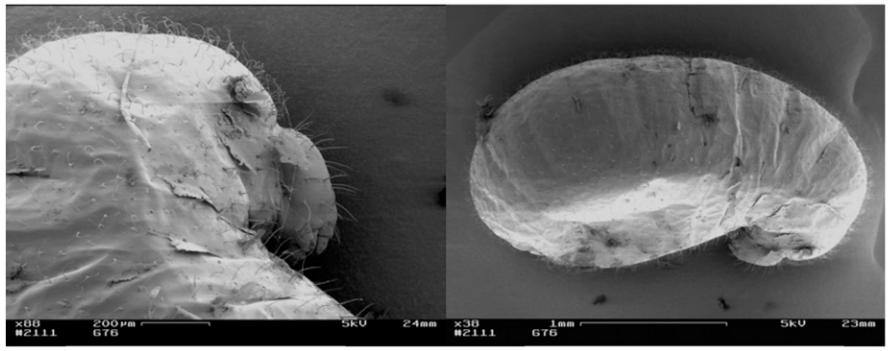
Figs. 160–169. *Solenopsis* larval structures. 160, Head capsule of *S. invicta*, dorsal view, scale = 46 µm. 161, Bifid setae on head capsule of *S. invicta*, scale = 18 µm. 162, Head capsule of *S. invicta*, dorsal view. 163, Head capsule of *S. invicta*, lateral view. 164, *S. invicta*, lateral view. 165, Head capsule of *S. macdonaghi*, dorsal view, scale = 46 µm. 166, Bifid setae on body of *S. macdonaghi*, dorsal view, scale = 18 µm. 167, Setae on head capsule of *S. macdonaghi*, dorsal view, scale = 18 µm. 168, Mandible of *S. macdonaghi*, dorsal view, scale = 46 µm. 169, Head capsule of *S. macdonaghi*, dorsal view.



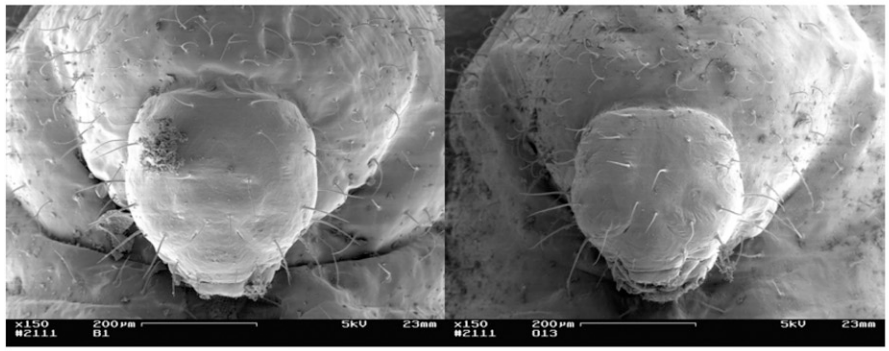
S. megergates



173. *S. megergates*

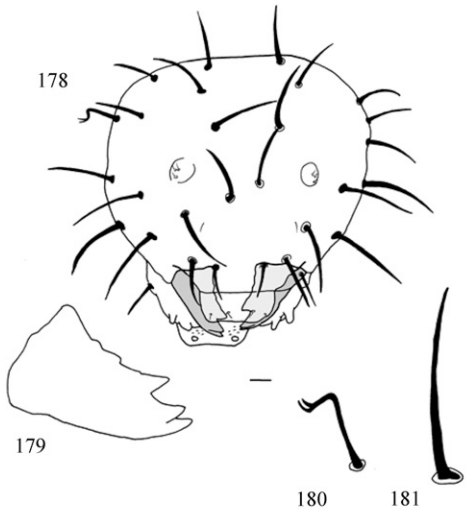


174. *S. megergates* 175. *S. megergates*

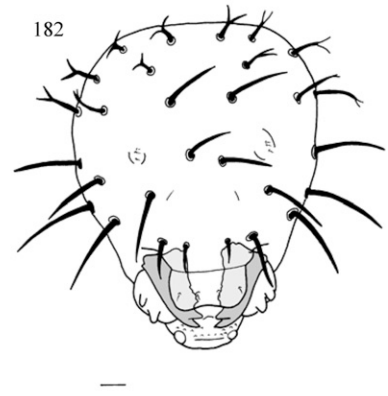


176. *S. quinquecuspis* 177. *S. saevissima*

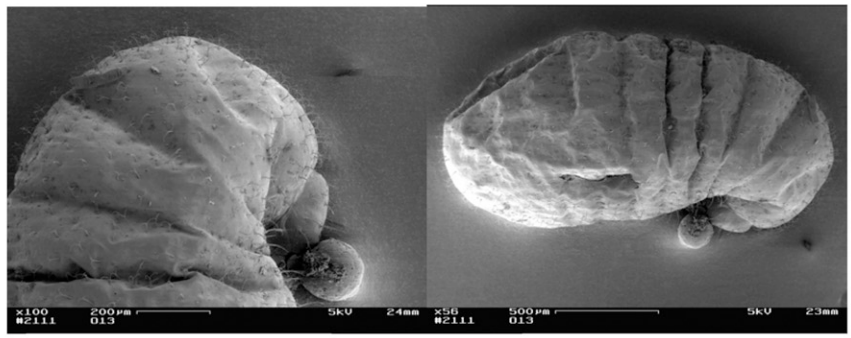
Figs. 170–177. *Solenopsis* larval structures. 170, Head capsule of *S. megergates*, dorsal view, scale = 46 µm. 171, Antenna of *S. megergates*, dorsal view, scale = 18 µm. 172, Mandible of *S. megergates*, dorsal view, scale = 18 µm. 173, Head capsule of *S. megergates*, dorsal view. 174, Head capsule of *S. megergates*, lateral view. 175, *S. megergates*, lateral view. 176, Head capsule of *S. quinquecuspis*, dorsal view. 177, Head capsule of *S. saevissima*, dorsal view.



S. quinquecuspis

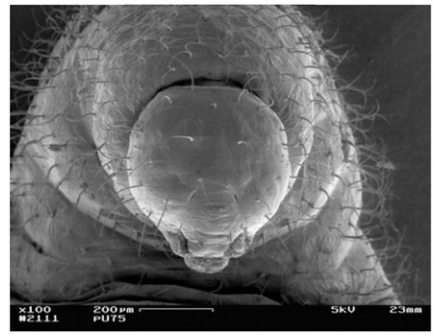


S. saevissima



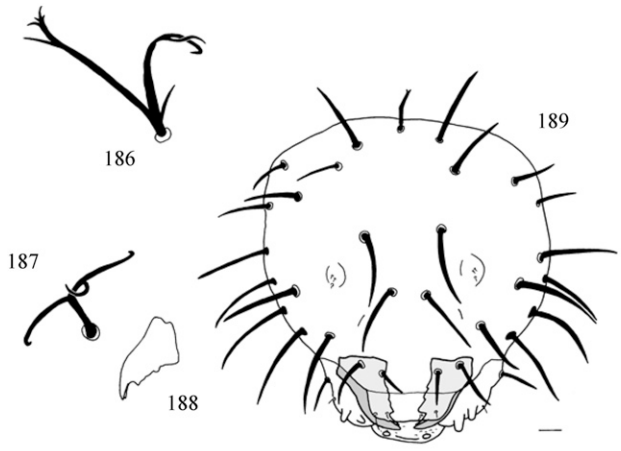
183. *S. saevissima*

184. *S. saevissima*

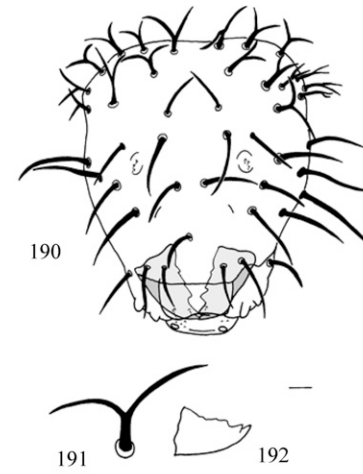


185. *S. richteri*

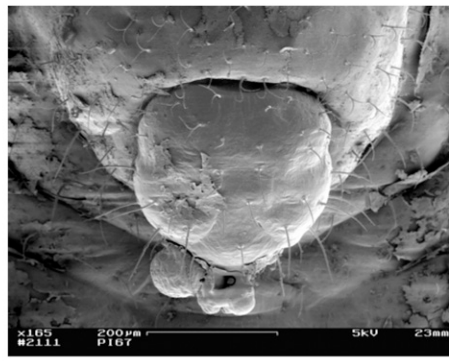
Figs. 178–185. *Solenopsis* larval structures. 178, Head capsule of *S. quinquecuspis*, dorsal view, scale = 46 µm. 179, Mandible of *S. quinquecuspis*, dorsal view, scale = 18 µm. 180, Bifid setae on head capsule of *S. quinquecuspis*, lateral view, scale = 18 µm. 181, Simple setae on head capsule of *S. quinquecuspis*, lateral view, scale = 18 µm. 182, Head capsule of *S. saevissima*, dorsal view, scale = 46 µm. 183, Head capsule of *S. saevissima*, lateral view. 184, *S. saevissima*, lateral view. 185, Head capsule of *S. richteri*, dorsal view.



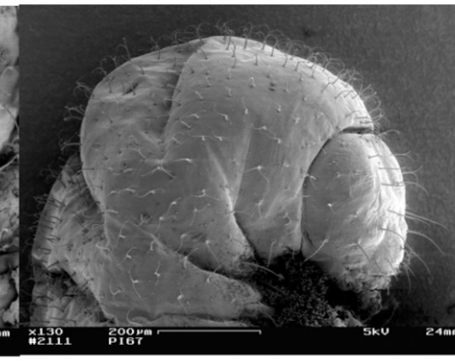
S. richteri



S. pusillignis

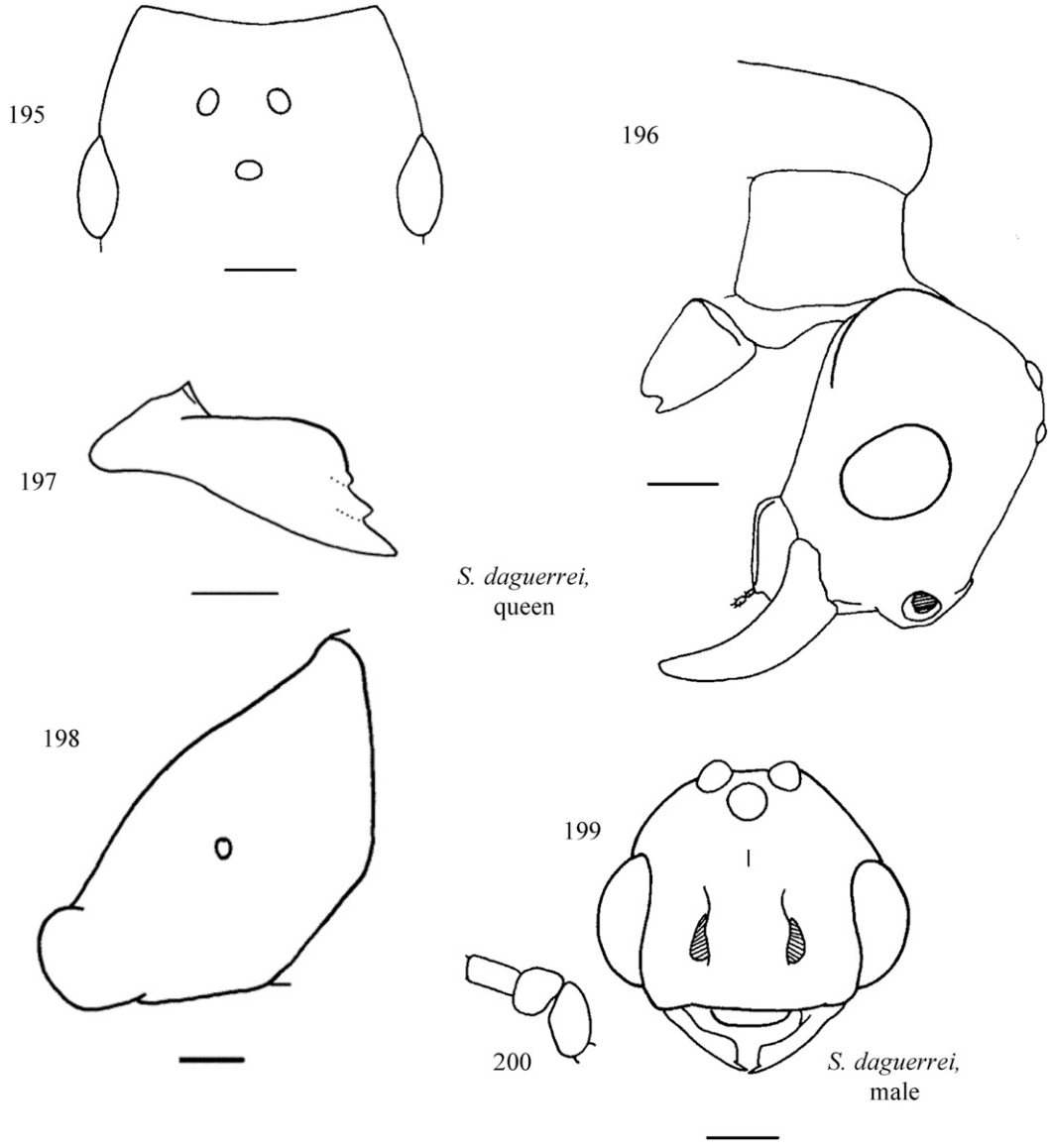


193. *S. pusillignis*



194. *S. pusillignis*

Figs. 186–194. *Solenopsis* larval structures. 186, Multi-branched setae on body of *Solenopsis richteri*, lateral view, scale = 18 µm. 187, Multi-branched setae on body of *S. richteri*, lateral view, scale = 18 µm. 188, Mandible of *S. richteri*, lateral view, scale = 46 µm. 189, Head capsule of *S. richteri*, dorsal view, scale = 46 µm. 190, Head capsule of *S. pusillignis*, dorsal view, scale = 46 µm. 191, Bifid setae on head capsule of *S. pusillignis*, lateral view, scale = 18 µm. 192, Mandible of *S. pusillignis*, lateral view, scale = 46 µm. 193, Head capsule of *S. pusillignis*, dorsal view. 194, Head capsule of *S. pusillignis*, lateral view.



Figs. 195–200. *Solenopsis daguerrei*. 195, Head of gyne, dorsal view. 196, Head and pronotum of gyne. 197, Mandible of gyne, dorsal view. 198, Propodeum of gyne, lateral view. 199, Head of male, dorsal view. 200, Scape, pedicel and flagellomeres 1–2 of male, lateral view, scale = 0.14 mm.

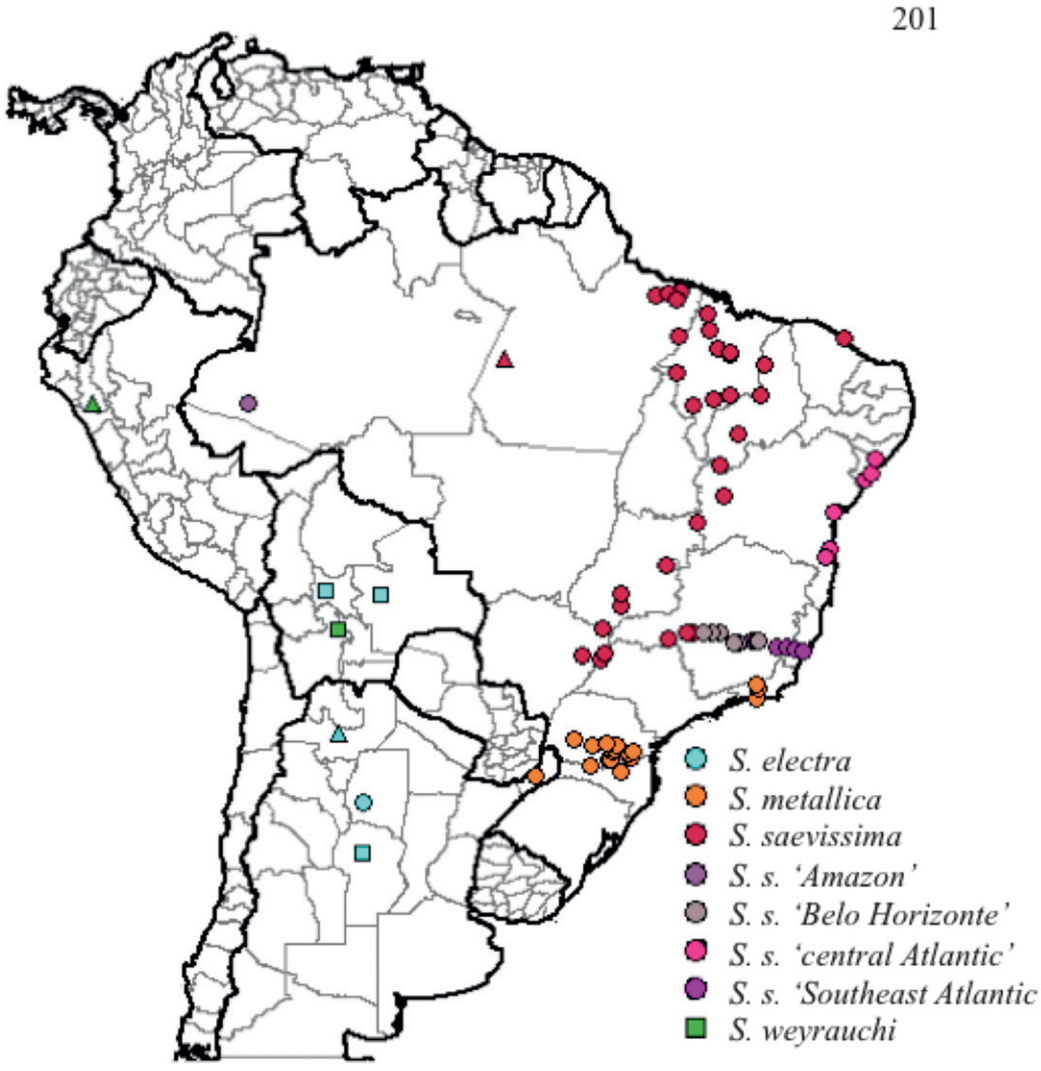


Fig. 201. Distribution of *Solenopsis electra*, *S. metallica* sp. nov., *S. saevissima*, and *S. weyrauchi*. Evolutionarily independent lineages (sensu Ross et al. 2010) of *S. saevissima* are also indicated. Collection localities from the collecting trips presented here are indicated by circles (○). Type localities are indicated by triangles (Δ), other reliable collection localities (Trager 1991) are indicated by squares (□).

Fig. 202. Distribution of *Solenopsis interrupta*, *S. macdonaghi*, *S. megergates, S. pythia,* and *S. quinquecuspis*. Collection localities from the collecting trips presented here are indicated by circles (○). Type localities are indicated by triangles (Δ), other reliable collection localities (Trager 1991) are indicated by squares (□).

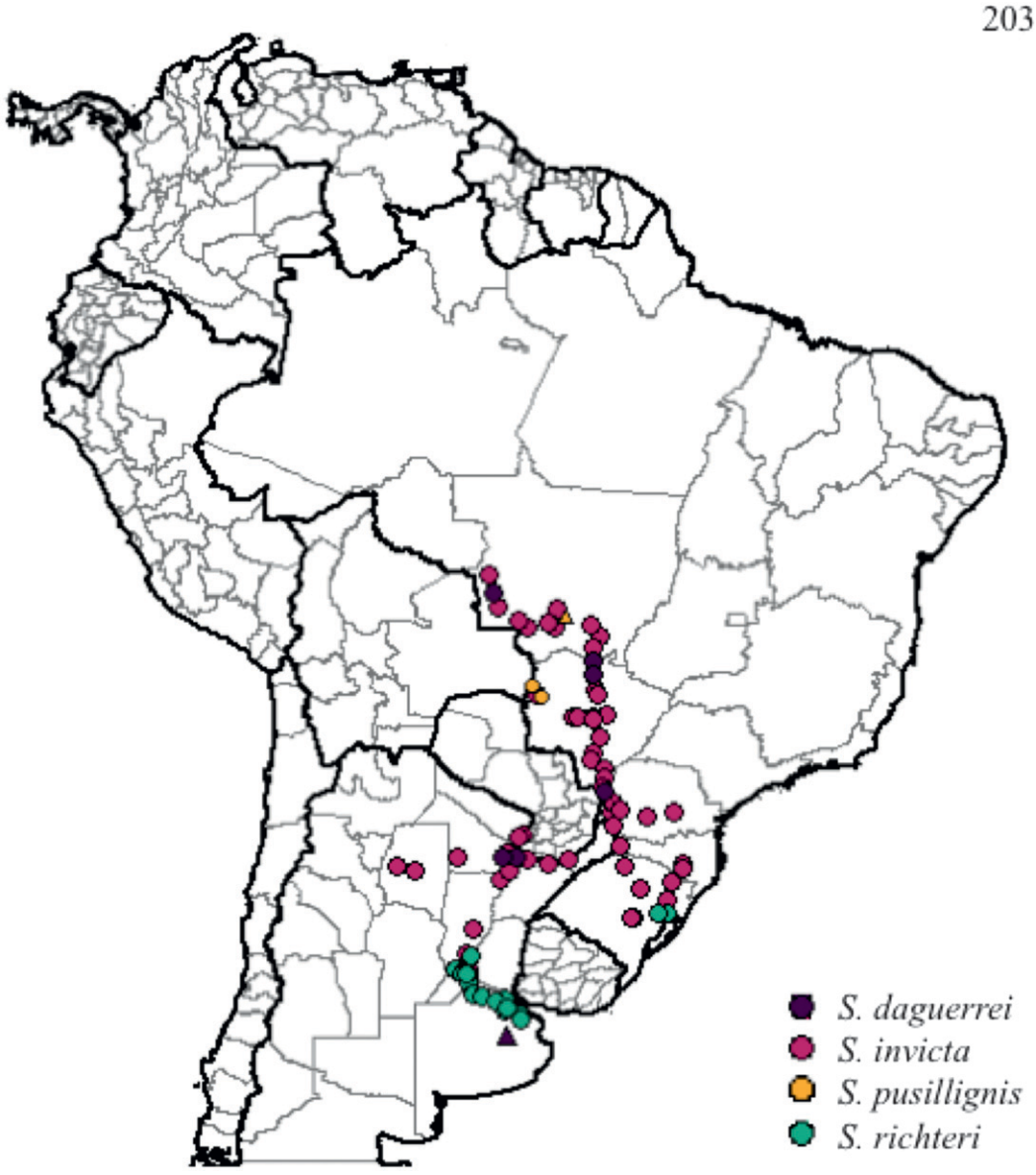


Fig. 203. Distribution of *Solenopsis daguerrei, S. invicta, S. pusillignis*, and *S. richteri*. Collection localities from the collecting trips presented here are indicated by circles (○). Type localities are indicated by triangles (Δ).