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A REVISION OF THE FIRE ANTS,  
*SOLENOPSIS GEMINATA* GROUP  
(HYMENOPTERA: FORMICIDAE: MYRMICINAE)

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**A REVISION OF THE FIRE ANTS,  
SOLENOPSIS GEMINATA GROUP  
(HYMENOPTERA: FORMICIDAE: MYRMICINAE)**

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*Abstract.*—The subgenera and satellite genera of *Solenopsis* are reviewed. Synonymy under *Solenopsis* of all subgenera and of the genera *Bisolenopsis*, *Synsolenopsis*, *Paranamyrma*, and *Labauchena* is confirmed. Certain placement of the genus *Lilidris*, known from a single alate female, will require study of additional material, but *Lilidris* appears to be distinct from *Solenopsis*. The fire ants and their close relatives, *S. substituta* and *S. tridens*, are collectively designated as the *S. geminata* species group, which together with the parasitic *S. daguerrei* group (*Labauchena*) form a monophyletic lineage. *S. virulens*, a species phenetically similar to minors of *S. saevissima*, is also included in this revision, though it probably does not belong in the *S. geminata* group. Four native species, 2 introduced species, and 2 hybrid forms occur in North America. Seventeen species are known from South America. A key to major workers and illustrations of all species are included. Notes on the identification of queens are provided where these are sufficiently distinctive. The native North American species are *S. aurea* Wheeler, *S. amblychila* Wheeler **new status**, *S. geminata* (Fabricius), and *S. xyloni* (MacCook), and the introduced species are *S. invicta* Buren and *S. richteri* Forel from South America. *S. xyloni* × *S. geminata* and *S. invicta* × *S. richteri* are the hybrid forms. *S. invicta* × *S. richteri* is abundant and highly fertile in parts of Alabama, Mississippi and northwestern Georgia in North America, but this hybrid has not been observed in South America, even though the parent species have overlapping distributions in at least Santa Fé Province, Argentina. In South America, only *S. bruesi* Creighton **new status**, *S. gayi* (Spinola), *S. geminata* and *S. weyrauchi* **new species** occur in or to the west of the Andes. The latter is unusual in that it occurs at elevations up to 3,500 m or higher in the Peruvian Andes. To the east of the Andes are found *S. electra* Forel **new status**, *S. geminata*, *S. interrupta* Santschi, *S. invicta*, *S. macdonaghi* Santschi **new status**, *S. megergates* **new species**, *S. pusillignis* **new species**, *S. pythia* Santschi, *S. quinquecupis* Forel, *S. richteri*, *S. saevissima* F. Smith, *S. substituta* Santschi **new status**, and *S. tridens* Forel. With the exception of *S. geminata*, *S. saevissima*, and *S. invicta* (at least part of whose geographic range is in the rain forest region) most of the South American species are endemic to the monsoon tropics or warm temperate regions of the southern part of the continent. *S. virulens* (F. Smith) **new status**, probably not a member of the *S. geminata* group but superficially resembling them, inhabits the forests of Amazonia.

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“Fire ant” is the English name used by entomologists and many laymen for a group of formicid species traditionally placed in the subgenus *Solenopsis* (*Solenopsis*). In my experience, most English-speaking non-entomologists simply call them “red ants,” and the equivalent “*hormiga colorada*” is a prevalent name for them in some Spanish-speaking parts of Central and South America. Other names include “*hormiga brava*” (fierce ant) in Spanish, and “*formiga de fogo*” (fire ant), “*formiga lava-pé*”

(wash-foot ant, referring to what one might do to remove the stinging insects after stepping into a mound) and "*formiga tocinheira*" (lard ant) in Portuguese. Undoubtedly, *S. geminata* has acquired many vernacular names where it has become established in tropical Africa, Asia and Polynesia.

Certain fire ants, particularly *S. invicta*, are considered serious pests in the southeastern United States. In areas of human habitat modification, fire ants may form dense populations. They build conspicuous earthen mounds, which are aggressively defended by the painful stinging of often great numbers of workers. *S. invicta* and its relatives have similar habits in much of South America, but they are apparently viewed as no more than minor pests there. This is probably more indicative of a generally lower tolerance of the presence of insects among North Americans than of a real difference in impact of the ants.

The concern about fire ants has created recognition of the need for a thorough revision of the fire ants, which is the purpose of this paper. Since Creighton's (1930) revision of *Solenopsis*, there has been no attempt to revise the subgenus *Solenopsis*, nor even to define it. More recent revisionary works are those of Wilson (1952), Snelling (1963) and Buren (1972). In these papers, coverage was limited to only a few species, and the authors (and Creighton, for most taxa) did not examine type specimens of the *Solenopsis* taxa described by Forel and Santschi, who described most of the named forms in the group. For this study, I have had the opportunity to study at least part of the syntype series of most taxa, those of *S. pylades*, *S. interrupta* and of some of the synonyms of *S. geminata* being the exceptions. Types of the former two were examined by W. F. Buren in 1974, and I have made use of his notes in my assessment of these taxa. Also, I have on loan from USNM a series of *S. interrupta* with the same collection data as the type series, which I believe to be workers from the same colony. Barry Bolton (BMNH) has examined types of the taxa synonymized with *S. geminata* in this paper described by Frederick Smith, and I accept his judgement that they do not differ specifically from *S. geminata*.

#### METHODS AND TERMINOLOGY

##### Recognition of major workers

This revision is based primarily on the major workers of fire ants, for it is generally in this subcaste that species-specific characteristics are best expressed. It is thus appropriate here that I discuss the term "major worker." In an attempt to arrive at a definition of the term, I made plots of maximum head width vs. head length of workers of all sizes for several fire ant species, pooling conspecific specimens from various colonies and localities. The resulting plots are weakly diphasic, i.e., showing a slightly different slope in the upper portion (Wilson, 1971, p. 141). One might call any worker falling within the upper phase of such a plot a major. Those experienced with fire ants in the field (Tschinkel, 1988a; Wojcik, unpubl.) note that the major workers of less populous colonies are not as large as those of very large colonies, but are clearly recognizable as major workers, especially by their characteristic head shape. On the other hand, worker populations from polygyne colonies or very young colonies do not, on casual observation contain any readily recognizable major workers (but see Tschinkel, 1988a), yet the largest workers of such populations may work out in the key. Thus, while "major worker" cannot be defined in absolute size terms,

for purposes of this paper, major workers may be loosely defined as the upper  $\frac{1}{3}$  to  $\frac{1}{4}$  of the worker size distribution for most colonies.

### Characters and possible pitfalls

Characters used for describing and identifying fire ants are of the sort commonly used in ant taxonomy. Some traditional characters, such as pilosity and surface sculpture patterns, are of limited use in fire ants because of the great homogeneity in these features across species in the group. The most useful characters are major worker head shape and color pattern. These and some other characters are discussed below.

Head shape of minor workers, males, and queens is nearly uniform throughout the fire ants. However, the head shape of major workers is often diagnostic. The difference in shape between heads of closely related species may be subtle, so I have made every attempt to carefully illustrate the typical head shape, and to provide metric clues to recognizing it. The user of this revision should be aware that not every specimen examined will look "typical," so that some isolated specimens will not be identifiable by this suite of characters.

It is virtually traditional in ant taxonomy to warn readers of the dangers of over-reliance on color as a means for identifying ants, and color variation in some fire ant species can be vexing, especially since it may alter the superficial appearance of other characteristics. Morphological analysis by a color neutral method such as scanning electron microscopy might do much to avoid this problem. Much local and regional color variation, superimposed on broader clinal patterns, is characteristic in the species *S. saevissima*, *S. invicta*, *S. geminata* and *S. xyloni*, all abundant and widely distributed species. It may then seem contradictory that color patterns of the remaining, less widely distributed species provide generally reliable characters for species recognition, and they are of some utility even in the above-mentioned species. Thus, color is frequently used in the descriptions and key to species. The danger in this is not that the color characters are not useful, but that there is so much variation in interpretation of color terms. I have thus limited myself to using English color names. I have found the Munsell system of naming soil colors useful as a general model for naming ant colors, but have not followed it exactly. *All color descriptions are based on observations of specimens at 25× under bright incandescent illumination.* Keep in mind that smaller workers and occasional majors with aberrant color patterns will be difficult to identify by color.

It is expected that genetic and chemical characterization of fire ant species will help overcome the deficiencies of a taxonomy based upon strictly morphological features, though it is safe to predict that new and unforeseen difficulties will arise as these types of data accumulate. For example, we have at the moment no clear concept of the ecological or evolutionary significance of the variation in alkaloid components seen in fire ant worker venom by R. K. vander Meer and colleagues (USDA fire ant project, unpubl.). Their data leave considerable room for varying taxonomic interpretations. Genetic data on fire ant species being developed by K. G. Ross (Ross and Trager, 1991) seem to me inherently less susceptible to misinterpretation, but there is no doubt both sets of data will greatly enhance our general ability to further refine the taxonomy of these ants.

Geographical distribution is another characteristic that may help distinguish fire ant species, but one must exercise some caution in its use, since fire ant species are readily transported to new localities where they may become established. The successful establishment of *S. invicta*, *S. richteri* and *S. geminata* in lands far from their native ranges is well known, but it appears that some disjunct populations of these and other species within South America may be the result of introductions.

#### Measurements

Measurements were made at 40× or 50× on a Nikon SMZ-10 or Wild M5 stereo dissecting microscope, respectively. For polymorphic species, approximate ranges (including absolute maxima) are reported only for workers with  $HL > 0.99$  mm. For monomorphic species, the full known size range is given. When a single individual of a species was notably larger than all others measured, or when specimens from a single locality averaged larger than the others measured, data for such specimens are reported in parentheses following the "normal" range. Measurements of holotypes of new species are listed separately. Abbreviations and definitions for these measurements and indices calculated from them (and other abbreviations used in the text) are given below. Other measurements and proportions, both for majors and for other castes are defined as necessary in the text. Measurements and indices:

HL—Head length; in full face view (defined below), the distance along the sagittal axis of the head between the anterior midpoint of the clypeus (exclusive of median clypeal tooth) and the posterior margin of the head or, if posterior margin concave, between the clypeal margin and a line tangent to the two most posterior points of the rear margin.

HW—Head width; in full face view, the maximum width of head behind the eyes.

SL—Scape length; length of shaft of antennal scape, exclusive of basal articulation.

EL—Eye length; maximum diameter of compound eye.

PW—Pronotum width; maximum width of pronotum in dorsal view.

AL—Thorax (alitrunk) length; distance from anterior base of pronotum (exclusive of anterior "cervical flange," which is often hidden from view) to posterior edge of metapleuron.

CI—Cephalic index;  $HW \times 100/HL$ .

SI—Scape index;  $SL \times 100/HW$ .

OI—Ocular index;  $EL \times 100/HL$ .

#### Abbreviations for viewing orientations:

ffv—Full face view of the head, whereby which one obtains the greatest straight-line distance between the midpoints of the clypeal border and the vertex (posterior border). Viewing axis is approximately perpendicular to the surface of the frons.

lv—Profile or strict lateral view.

pdv—Posterodorsal view, useful for examination of some features of the thorax, and of the petiole and postpetiole.

## Depositories of specimens:

AMNH—American Museum of Natural History, New York.

BMNH—British Museum (Natural History), London.

FSCA—Florida State Collection of Arthropods, Gainesville.

IML—Instituto Miguel Lillo, Tucumán, Argentina.

LACM—Los Angeles County Museum of Natural History.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA.

MZSP—Museu de Zoologia, Universidade de São Paulo, Brazil.

USNM—United States National Museum, Washington, DC.

## RESULTS

In this section, I first discuss classification within the genus *Solenopsis* and of some supposedly separate but closely related groups. I then characterize the fire ants in a general description of morphology of major workers, followed by brief summaries from the literature of other characteristics. A key to workers follows, and this is followed by accounts of the species complexes and subcomplexes and their contained species. Minor workers of most species are nearly or indeed indistinguishable. Males are poorly known and in most cases can reliably be sorted only to species complex, and are thus not keyed or described. The queens, while more readily distinguishable than males, are for many species poorly represented in collections, and in identifying them, one must usually rely on associated major workers. In a few cases where queens are the most morphologically distinctive caste, diagnostically useful queen characters are pointed out in the notes accompanying species descriptions.

Synonymic notes on the subgenera and satellite  
genera of *Solenopsis*

The subgenera of *Solenopsis*, and the related genera (sometimes considered subgenera) *Bisolenopsis*, *Synsolenopsis*, *Lilidris*, *Labauchena*, and *Paranamyрма* were synonymized into *Solenopsis* with little explanation by Ettershank (1966). Bolton (1987) presented arguments supporting these synonymies, especially that of the subgenus *Diplorhoptrum*. Ettershank recognized three “natural” groups in *Solenopsis*: the fire ants, the “small species,” and the socially parasitic forms. Aside from the fire ants, which are a natural (though paraphyletic) species group, I believe the groupings in *Solenopsis* will sort out very differently from Ettershank’s when the genus is subjected to phylogenetic analysis.

For example, there seem to be several lineages of “small species.” Creighton (1930) grouped the subgenus *Diplorhoptrum* (here called the *S. fugax* group) into 5 species groups which may better account for the diversity within the “small species.” The phylogeny of Creighton’s (1930) 5 groups is unresolved, and the 5 species groups did not, furthermore, include all of the diversity represented by Ettershank’s “small species.” Additional groups of small *Solenopsis* not contained in the *S. fugax* group include the subgenera *Euophthalma*, *Granisolenopsis*, *Diagyne*, and *Oedaleocerus*, and the so-called genera *Bisolenopsis* and *Synsolenopsis*.

The distinctions between these taxa are anything but clearly defined, as the fol-

lowing examples will illustrate. (1) The single known species of *Granisolenopsis* seems to be a member of a South American complex of small *Solenopsis* species characterized by weakly polymorphic or dimorphic workers. Its major worker has head morphology convergently developed to resemble a minuscule *S. geminata*, and its queen has a narrow, permanently wingless thorax. Conditions approximating these are seen in some other small *Solenopsis* (all classified as *Diplorhoptrum*) from South America. (2) *S. globularia* (the type species of *Euophthalma*) and its varieties and subspecies are a group of small *Solenopsis* species which share several, apparently synapomorphic features with the *S. tenuis* complex of the *S. fugax* group and should be considered related to it. (3) *S. virulens* is treated along with the fire ants in this revision, but this is somewhat arbitrary, as the species has features suggesting relationship to *S. globularia* (see discussion of *S. virulens* for details). (4) On the other hand, a species described as a *Euophthalma*, *S. huachucana* is unmistakably a fire ant, namely the young queen and nanitic workers of *S. aurea*. (5) *Diagyne* has queens with distinctive mandibular dentition, but the workers are not distinguishable at the species-group level from the globularia-like *Euophthalma*. (6) The *Euophthalma* species outside of the *globularia*-*tenuis* group are apparently not differentiable from Kusnezov's (1957) genera *Bisolenopsis* and *Synsolenopsis*. The few specimens I have studied within these latter "genera" conform in some respects to my view of what ancestral *Solenopsis* may have looked like. They are markedly sculptured and sutured, have propodeal projections, relatively well-developed eyes, and flagellar segments of intermediate length between those of the fire ants and of the *S. fugax* group.

I also differ from Ettershank's classification by recognizing 2 distinct origins of workerless inquilinism in *Solenopsis*, namely "*Labauchena*" and "*Paranamyрма*." Both show strong signs of phylogenetic ties to the species groups containing their hosts, suggesting a recent common ancestry.

It is clear that the genus-level taxa (including subgenera) in and around *Solenopsis* are largely meaningless and inseparable. I thus reaffirm Ettershank's synonymy of the free-living taxa *Bisolenopsis* and *Synsolenopsis*, and of the parasitic genera *Labauchena* and *Paranamyрма* under *Solenopsis*. And though there are a number of recognizable species groups in the genus, I agree with Ettershank (1966) and Bolton (1987) in not formally recognizing any of the above genera and subgenera, since none appear to be clear-cut monophyletic groups.

*Lilidris*, represented by a single queen described by Kusnezov (1958) may not, however, belong in *Solenopsis*. Its antenna, though 10-segmented, bears an apparently 3-segmented club. The wing venation of *Lilidris* is a little different from any known *Solenopsis*, but venation is variable in *Solenopsis*, and very likely will encompass that of *Lilidris* when studied in more species. The anterior metatarsal "brush" of *Lilidris* is also distinctive.

Based on the above, I refer henceforth to the fire ants and their close relatives, *S. substituta* and *S. tridens*, as the *S. geminata* group. Note that this group is informal and paraphyletic (or even polyphyletic, if *S. virulens* is included). A strictly monophyletic formal taxon containing the fire ants should also properly include the species in "*Labauchena*." The latter are derived, with modifications typical of inquiline ants, from ancestors that would be placed within the *saevissima* complex. Revision of these rarely collected inquilines is not attempted in this paper.

Within the *S. geminata* group, I refer to smaller groupings of related species as

species complexes, and at a still lower level, subcomplexes. These are briefly characterized at the beginning of the descriptions of their included species.

### General description

A general morphological description of workers of the *S. geminata* group follows, provided to eliminate repetition of characteristics common to all species in the treatments of individual species, to provide a common basis for comparison, and for better understanding of the key and descriptions. A brief review from the literature of other characteristics of fire ants follows the morphological description.

### Morphology

The description proceeds anterior to posterior. The orientation necessary for proper viewing is indicated in parentheses. Features of the minors are presented parenthetically, for comparison with the monomorphic workers of *S. virulens* and of the *S. tridens* complex.

Head (ffv) usually longer than broad, usually widest behind eyes; sides straight to weakly convex in species with quadrate or trapezoidal head shape, more convex in those with elliptical, ovate or cordate head shape (minor head shape elliptical, ovate or subrectangular, widest at or in front of eyes); posterior border weakly to notably concave, or less often with angular emargination (faintly concave to convex in minors); the concavity 1–2× as wide as the distance between apices of frontal lobes; lower edge of distal border of clypeus bearing a large median seta, this usually borne on a projecting triangular tooth, the latter reduced or lost in some species; clypeal carinae divergent distad, usually projecting as isosceles-triangular teeth, these somewhat to notably larger than median tooth and always much larger than paracarinal teeth, which may be lacking (especially in smaller workers), carinal and paracarinal teeth more dorsad on clypeal border than median tooth; mandibles 4- or less often 3-toothed (teeth may be worn off in older specimens, but are always present at eclosion); mandible curved, distal portion of outer border usually at a weakly obtuse angle to basal portion (about 100°, angle larger in minors); mandibular costulae 6–10, complete throughout length of mandible or obsolete medially, sometimes bifurcate distally; eye (lv) ovate, elliptical or reniform, with from 45–100 facets (20–60 in minors); scapes (ffv) curved basally, thickest subapically; scape length significantly less to a little less than length between basal articulation of scape and most distant portion of posterior border, i.e., scape apex not surpassing posterior border of head (often as long or notably longer than this distance in minors and monomorphic species); anterodorsal pronotal border (pdv), weakly to notably convex; anterolateral pronotal corners variously developed, broadly rounded to distinctly angular and bearing obliquely or transversely oriented, “humeral bosses”; promesonotal suture chevron-shaped with a small dorsal projection at apex, or parabolic, or strongly convex, rarely obsolete, and this only in smaller majors (commonly so in minors); pronotum (lv) usually with steep anterior declivity set off from dorsum, pronotal dorsum forming an even convexity with mesonotal dorsum, or with a slight break in outline at point of anterior mesonotal projection; metanotal impression conspicuous, set off by steep, variously sculptured, posterior mesonotal and anterior propodeal declivities, the former declivity often higher than the latter (metanotal im-



pression shallower and less sculptured in minors); metanotal spiracles small, positioned dorsolaterally; propodeum (pdv) with dorsal face concave, descending through an even curve into declivous face; in profile (lv) propodeum usually appears angular because of longitudinal, posterolateral bosses or short rounded carinae (bosses lacking or weakly developed in minors so propodeal profile less or not at all angular); petiolar peduncle shorter than to slightly longer than base of node; profile of petiolar node cuneate or thick-squamose to globular, with anterior face straight to weakly convex and posterior face convex, the faces meeting through strongly convex dorsal portion; from behind outline of petiolar node (pdv) globular, subovate, or with more or less convex dorsal face meeting straight or weakly concave sides through rounded angles, sides convergent ventrad; profile (lv) of postpetiolar node in profile typically lower than that of petiole, appearing globular or nearly so, with a short posterior peduncle; from behind outline of postpetiolar node (pdv) globular to subtrapezoidal or subrectangular with dorsum convex (always more or less globular in minors); postpetiole varying from slightly to notably wider than petiole.

Integument mostly smooth; except for piligerous foveolae, and sculpture of mesometapleuron, propodeum, petiolar peduncle and rear face of postpetiole (sculpture always less developed in minors); diameter and sometimes shape of piligerous foveolae varying in diagnostically useful ways (small, round and inconspicuous in minors); sculpture of mesometapleuron consisting of longitudinal striae or rugae with varying levels of interstitial punctation; sculpture of propodeum and of postpetiole variable and often diagnostically useful at species level; declivous face of propodeum with weak transverse rugae or, more often, unsculptured on upper portion, on lower portion with concentric semicircular rugae continuous with those of metapleuron, but more widely spaced and usually lacking interstitial sculpture; petiolar peduncle usually faintly areolate or punctate, this sculpture continued posterad to base of node in some species; venter of petiole with longitudinal median carina and anteroventral process consisting of one to a few small teeth or a transparent flange, occasionally absent; dorsum of petiolar and postpetiolar nodes often weakly scalloped or longitudinally grooved; petiolar dorsum otherwise unsculptured; postpetiolar dorsum unsculptured or with sculpture resembling but weaker than that of postpetiolar posterior face; posterior face of postpetiole with varying, diagnostically useful combinations and distributions of transverse striae and punctation, especially on lower portion; sides of postpetiole usually striate-punctate; venter of postpetiole usually coarsely punctate with a few coarse longitudinal rugae.

Pilosity composed of yellowish or reddish brown setae, these normally more or less cylindrical and tapering distally, or more precisely, narrowly conical; longer setae curved; mesonotum usually with at least 20 erect setae (less in minors); mesopleuron with few aside from those on ventral edge; in most species pilosity varies greatly in length on a single specimen, longest hairs on thoracic dorsum usually at least  $2.5 \times$  length of shortest; suberect pubescence present in a conspicuous patch on cervical flange of prothorax; less often, dilute, appressed pubescence often present on anterior face of petiolar node, and rarely some on propodeal dorsum.

Color ranging from nearly uniform honey-yellow to brownish black, in lighter shaded forms with at least posterior band of tergites usually notably darker; some species with more or less uniform color pattern in all samples; others spanning nearly the entire range for the species group, though typically not within a single colony;

(minor workers often darker and more uniformly colored than majors from the same colony).

### *Sting morphology*

Kugler (1978) published an extensive review of the myrmicine sting apparatus, to which the reader should refer for details. Kugler's analysis resulted in *Solenopsis* genus group containing *Megalomyrmex*, *Monomorium* (including *Chelaner*), and *Oxyepoecus*, known relatives of *Solenopsis* (Ettershank, 1966; Bolton, 1987). Also included in this group by Kugler was a pair of *Rogeria* species. Their relationship to *Solenopsis* is contradicted by other lines of evidence.

### *Malpighian tubules*

Brown (1988) surveyed Malpighian tubule numbers of ants. Among the above mentioned relatives of *Solenopsis*, 2 *Megalomyrmex* spp. (perhaps the most "primitive" genus in the group) had 5 Malpighian tubules, while all the remaining species (including 1 or 2 spp. from each of the other 3 genera had 4 tubules (a synapomorphy?). The tubules are not cryptonephric.

### *Larval morphology*

Wheeler and Wheeler (1960a) divided what were then considered to be members of the tribe Solenopsidini into six genus groups. The genera *Solenopsis*, *Monomorium*, *Oxyepoecus*, and *Megalomyrmex*, (and *Anergates*, now thought to be a member of the Tetramoriini) are grouped in the solenopsidiform genera; those with short, stout, superficially straight body form (but with anterior ventral portion of thorax curved), ends rounded, neck very short or lacking, and anus ventral. Later the Wheelers (1960b) described the larvae of *S. picta*, *S. pergandei*, and *S. globularia littoralis* (which I consider to belong to 3 distinct species groups) as "similar to *S. geminata*," differing in details of size and pilosity (confirming the close relationship of all *Solenopsis*).

### *Karyotypes*

Taber and Cokendolpher (1988) reported the karyotypes of *S. xyloni* specimens from Texas and Arizona, synthesized their results with those from previous work, and listed all pertinent references. Karyotypes of the 2 *S. xyloni* populations were identical, and their chromosome morphology closely resembled that of *S. aurea*, *S. invicta* and *S. saevissima*, but differed from that of *S. geminata* and *S. richteri*. The diploid complement is 32 in all species, but as indicated by their results, chromosome morphology varies in ways that appear to be unrelated to taxonomic groupings within the *S. geminata* group.

### *Venom and cuticular hydrocarbon chemistry*

Blum et al. (1985 and included references) have studied a variety of *Solenopsis* spp. and some in related genera. It appears that *Solenopsis* species exhibit a chemical synapomorphy of the presence of 2-alkyl-6-methylpiperidine alkaloids in the venom.

Furthermore, most species of *Solenopsis* and *Monomorium* contain another group of alkaloids, the 2,5-dialkyl-1-pyrrolines, alkaloids thus far unknown in any other ants. Alkyl side chain length and the proportions of components bearing different side chains vary within species, but in general, variation between species is much greater. The interspecific variation is already sufficiently characterized for some populations to be of taxonomic utility. Vander Meer and Lofgren (1988) recently demonstrated this for some *S. saevissima* complex species, and list most of the pertinent literature. Furthermore, they presented data on cuticular hydrocarbon variation and briefly discussed questions concerning species distinctions arising from the chemical studies. In a study by Ross et al. (1987), chemical and morphological phenotype, and genetic (allozymic) characters for recognizing *S. invicta*, *S. richteri*, and their hybrid in North America were shown to be highly correlated.

### *Allozymes*

Ross (1988) discusses use of allozymes for studying systematic problems in complexes of closely related and cryptic species. Genetic characterization of fire ants was initiated by Ross and colleagues (Ross et al., 1987, and included references). Results of a study on the genetics of 6 Argentine taxa of the *S. saevissima* complex will be reported elsewhere (Ross and Trager, 1991). The morphological species concepts presented in this revision are for the most part strongly corroborated by our genetic data, though between 4 and 5% of the 200 samples studied bore such unique allozymes that they could not be placed with any of the larger genetic groupings.

### *Natural history*

A huge body of literature has developed on the biology of fire ants (especially *S. invicta*), but a full accounting of the natural history of these ants is still lacking. Prominent papers on fire ant natural history are those by Tschinkel and coworkers (Tschinkel, 1986, 1988a, b; Porter and Tschinkel, 1988), Vinson and Sorensen (1986), Wojcik (1986), and Porter and Savignano (1990).

Colony foundation is effected by small groups of queens or single individuals following mating flights, which occur under conditions of low wind velocity, either at dusk following rain earlier in the day (*geminata* complex), or in late morning to mid-afternoon following rain the previous day or night (*saevissima* complex). The first brood of a dozen or less workers (more in pleometrotic efforts) is reared out in a month or so. Usually, only one queen survives the colony foundation period, the others being eliminated by the workers. In a year or so, the colony grows to many thousands of individuals. Newly colonized areas may have very high densities of colonies, but through territorial interactions, certain colonies eliminate most of their neighbors as they grow, so that densities in mature populations generally fall into the 30–100 nest/ha range.

Locally, mound densities may be much higher. This is associated with polygyne (multiple queen) colony populations, where densities may be as high as 1,000 mounds/ha, with densities of 300 mounds/ha not uncommon. These arise either by survival of co-foundresses or by adoption of newly mated queens, and are characterized by colonies with several to many hundreds of queens, diminished territoriality and small average worker size. This phenomenon is best known in the North American pop-

ulation of *S. invicta* (Lofgren and Williams, 1984), but I have made several collections from polygyne populations of *S. invicta*, *S. richteri*, and *S. quinquecupis* in Argentina, and of *S. geminata* in Florida. Circumstantial evidence (small worker size, high mound density) points to the occurrence of polygyny in Argentine and Bolivian *S. interrupta* and Brazilian and Bolivian *S. invicta* as well, though conditions were not propitious for me to collect queens from these colonies. Most of the literature on polygyny in fire ants is cited in Glancey and Lofgren (1988) and in Porter and Savignano (1990).

The large workers spend relatively little time away from the nest, but come to the surface readily when the nest is disturbed. Major workers are also important for their food storage capacity, and often have the crop full of oily liquid. Small to medium-size workers forage along both surface and subterranean trails. Food sources are highly varied, but protein and fats from varied invertebrate prey or vertebrate carrion, and carbohydrates from fallen fruits, floral and extrafloral nectaries predominate in the diet of most fire ants. *S. geminata* is unusual in harvesting and milling a large number of seeds, but this behavior occurs in rudimentary fashion in all or most other species.

Fire ants recruit actively to large food sources, and tend to displace other ants from them. Some species of *Pheidole*, *Paratrechina* and other genera tend to find and recruit to such food items more quickly than fire ants, and may be able to carry off the food before fire ant workers are recruited. Once fire ants arrive in great numbers, they drive off other ants by lunging at them, or more often by wagging their gasters, sting exposed and bearing a droplet of venom, near the other ants. The latter are usually so repelled by the volatile components of the venom that they offer little resistance.

Nests are most often in moist sites, such as river banks, pond edges, swales and swampy areas, and their man made analogues, watered lawns and highway rights of way. In areas with argillaceous soils, a conical or domose mound up to a meter across and nearly as high may be a nearly permanent sign of the nest of species of the *saevissima* complex. When colonies die or move out, these mounds may be colonized by other colonies or nest-founding queens, including species of other genera. Occasionally, portions of active fire ant mounds may be occupied by other ants (e.g., *Acromyrmex* or *Paratrechina*) or by termites. In sandy areas, fire ant mounds collapse through disuse in dry, and especially in hot weather. In species inhabiting xeric areas mounds may be built up only during the peak mating flight period.

KEY TO MAJOR WORKERS OF *SOLENOPSIS* WESTWOOD;  
SPECIES OF THE *GEMINATA* GROUP (SENSU EMERY, 1925)

NOTE: This key is not designed for identification of minor workers. Workers of the *tridens* complex are similar in morphology to the minors of other species, but can be recognized by their unique propodeal structure. See Carlton (1987) for a key allowing separation of minor workers of eastern North American species.

- |    |  |   |
|----|--|---|
| 1. | North American species (Panama to southern United States, Antilles, one sp. introduced in tropical Asia, Africa) ..... | 2 |
| –  | South American species (continent-wide, except the coldest and highest parts, also Galápagos) .....                    | 8 |

2. Clypeus, in full-face view, lacking median tooth, or at most with a small blunt protuberance ..... 3  
 – Clypeus, in full-face view, with a conspicuous, median tooth ..... 7
3. Sides of head subparallel; emargination of posterior border deep, extending toward frons as a median rugose furrow; distinct propodeal carinae originating near junction of propodeal dorsum and declivity and extending forward toward anterior edge of propodeum; petiolar ventral process small, rarely flange-like; coastal plain of the Carolinas and Georgia, Florida west to Texas, Central America, Antilles (also South American, widely introduced in Old World tropics) ..... *geminata*  
 – Sides of head distinctly divergent toward occiput; occipital furrow shallower, not rugose; propodeal carinae lacking or at most developed only at junction of basal and declivous propodeal faces (rarely a lobe- or tooth-like flange at junction of dorsal and declivous faces of propodeum); petiolar ventral process developed as ventral flange or lobe on larger specimens ..... 4
4. Larger specimens with HW > 1.5 mm; in largest workers a pair of short, longitudinal carinae, or flange- or tooth-like dorsolateral lobes near junction of basal and declivous propodeal faces ..... *geminata* × *xyloni*  
 – Largest specimens with maximum HW ≤ 1.48 mm; propodeum always lacking dorsolateral carinae or flanges ..... 5
5. Eye with 70–80 pigmented facets; head and thorax red to dark brown; gaster mostly brownish black except for large spot on first tergite of many specimens; Carolinas to southern Georgia west to California and Mexico ..... *xyloni*  
 – Eye with 40–60 pigmented facets; yellowish red to reddish yellow, tergites may be margined with brown ..... 6
6. In workers with HL > 1.20 mm, clypeal carinae weakly developed, carinal teeth rounded and indistinct or entirely lacking in full-face view; pilosity reduced, often lacking entirely on posterior half of pronotum, mesonotum with 8–15 erect setae; cephalic pilosity mostly arising from very small punctures; anterior ventral process of petiole often nearly as large as eye in largest workers; southern Texas to Arizona, desert and semiarid Mexico ..... *amblychila*  
 – Clypeal carinae projecting as distinct teeth from the clypeal surface even in largest workers, carinal teeth conspicuous in full-face view; pilosity abundant and evenly distributed on pronotal dorsum; mesonotum with 18–30 erect setae; cephalic pilosity arising from conspicuous foveolae; petiolar ventral process usually a longitudinal flange with the ventrally projecting anterior lobe, this notably smaller than eye; southern Texas to California, desert and semiarid Mexico ..... *aurea*
7. Head and scapes brownish black, as dark as gaster or only slightly lighter; elongate triangular mark on frons barely or not at all visible; yellowish tergal spot with a definite posterior border usually present; head subelliptical to weakly ovate and relatively narrow in frontal view (Fig. 54), CI 90–96 in largest workers; pronotal dorsum medially concave; pronotum with humeral bosses; northern Mississippi, northwestern Alabama ..... *richteri*  
 – Head, scapes and thorax reddish brown, distinctly lighter than gaster; elongate triangular mark on frons conspicuous, dark brown to black; spot on first tergite lacking, or if present, spot dusky reddish and grading indistinctly into darker posterior band; head ovate to weakly cordate and broader in frontal view (Fig. 50), CI 95–100 in largest workers; humeral bosses lacking or indistinct, anterior portion of pronotum evenly rounded when viewed dorsally; SE U.S., Puerto Rico ..... *invicta*
- 7c. Intermediate in some of the characters in 7a and 7b; most often with the basic color pattern of a “washed out” *S. richteri*, head and thorax more brownish or mottled than gaster; gaster spot dusky with posterior margin indistinct; elongate triangular

- streak on frons visible, and head ovate to weakly cordate; northeastern Mississippi, northern Alabama and northwestern Georgia ..... *richteri* × *invicta*
8. Monomorphic, CI  $\leq$  90 in all workers, AL of largest workers rarely exceeding 1.3 mm; (if values of CI and/or AL larger, postpetiole globular and notably higher and broader than petiole) ..... 9
- Polymorphic, large series from mature colonies always containing some workers with CI  $\geq$  90 (head of *S. weyrauchi* from the mountains of Peru often not so broad); AL of largest workers 1.3–2.0 mm ..... 11
9. Eyes small, with 6–7 facets in greatest diameter; postpetiole as high or higher than petiole in profile, globular and notably broader than petiole; head, thorax, and appendages uniform straw yellow, gaster sometimes with faint brownish banding at posterior edge of tergites; Amazonian forest ..... *virulens*
- Eyes larger, with 8–10 facets in greatest diameter; post petiole notably lower than petiole in profile, little or not at all broader than petiole; color various; catinga and cerrado regions of eastern and central Brazil ..... 10
10. Propodeum, aside from dorsolateral carinae, weakly sculptured and somewhat shining; color nearly uniform brownish black; northeastern Brazil ..... *tridens*
- Propodeum, in addition to dorsolateral carinae, densely sculptured and matt, especially laterally; head and thorax yellowish red to dark brown; gaster brownish black; cerrados, open woodlands and disturbed sandy soil areas of central and southern Brazil ..... *substituta*
11. Head of major subquadrate or weakly trapezoidal (head may be wider in front of eyes, flaring near base of mandibles); posterior border deeply emarginate with strongly convex “temples”; with median rugose furrow extending forward to frons; emargination of posterior border extending to frons as a rugose furrow; propodeum of large and some smaller workers with distinct dorsolateral carinae and other dorsal sculpture; Venezuela to Peru, western Amazonia, Caribbean and Atlantic coastal region south to Bahia, Brazil, also Galápagos Islands (introduced?) ..... *geminata*
- Head of major ovate or cordate, or even if subquadrate, with at most a weakly emarginate posterior border, and never with rugose furrow extending forward to frons; propodeum of even largest workers without longitudinal carinae dorsally, at most with bosses at meeting of dorsal and declivous faces ..... 12
12. Scapes of any size worker notably failing to reach posterior border of head; species of western South American coastal region ..... 13
- Scapes of small and media workers easily reaching or exceeding posterior border of head; species occurring east of the Andes from Guianas, Venezuela to Argentina, (one species from grasslands above 2,000 m elevation in the Peruvian Andes) ..... 14
13. Eyes of major with 50–60 facets (minors have 40 or fewer); color mostly dark brown; Chile to southern Peru (introduced in Colombia?) ..... *gayi*
- Eyes of major with 70–90 facets (minors have 50 or more); color usually uniform reddish; Peru ..... *bruesi*
14. Larger species, AL exceeding 1.75 mm (up to over 2.0 mm) in largest workers of most series ..... 15
- Smaller species, AL rarely in excess of 1.7 mm in even largest workers of most series (rarely up to 1.80 mm) ..... 18
15. Color of major workers mainly brown to nearly black ..... 16
- Color of major mainly yellowish or reddish, often with only the gaster notably darker ..... 17
16. Smaller species, HL of majors 1.45–1.55 mm, but eye of largest workers relatively (and often absolutely) larger, OI 18–20 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; Buenos Aires and La Pampa Provinces, Argentina, Uruguay, north to Santa Catarina, Brazil ..... *quinquecuspis*
- Larger species, HL 1.6–1.75 mm in largest workers, but eye of largest workers relatively (and often absolutely) smaller than above species, OI 16–18 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; southeastern Brazil ..... *megegates*
17. Median ocellus usually lacking; outer surface of mandible weakly shining (“sericeous”) at low magnification due to close-set longitudinal costulae; thorax pilosity yellowish, the longest setae over 3× as long as the shortest, the longest setae curved; sculpture on rear face of postpetiole including transverse striae or rugulae, at least mesially, dorsal surface of postpetiole usually shiny; western Argentina, Bolivia . . . . . *interrupta*
- Median ocellus often present; outer surface of mandible usually shining mesially, costulae obsolescent; thorax pilosity usually flattened basally, reddish, not curved; on largest majors, the longest setae usually little or no more than 2× the length of the shortest (less often but not uncommonly longer); sculpture on rear face of postpetiole punctate or shagreened, usually extending onto dorsal surface, lacking transverse striae or rugae, or these faint; native in Uruguay, Entre Rios Province and adjacent parts of bordering provinces in Argentina; apparently introduced at Cochabamba, Bolivia . . . . . *macdonaghi*
18. Pronotum low and nearly flat or weakly convex in profile; gaster black, legs yellow (yellowish brown in darker specimens); head and thorax usually clear yellowish red with some black or brownish black markings in the occipital area, varying to uniformly brownish black (especially in vicinity of Cochabamba, Bolivia); western Argentina and Paraguay, north to Bolivia in Andean foothills . . . . . *electra*
- Pronotum higher, angular or strongly convex in profile; color various but never with all black gaster and yellow legs . . . . . 19
19. Area immediately behind and above metapleural spiracle finely punctate or striate-punctate; southern half of Mato Grosso, Mato Grosso do Sul, Brazil . . . . . *pusillignis*
- Area surrounding metapleural spiracle shining and smooth . . . . . 20
20. Pronotal dorsum in posterodorsal view mesially concave; anterolateral bosses giving a squared-off appearance to anterodorsal rim of pronotum; head uniformly brownish black; mandibles usually brownish yellow; frons without dark median streak or this barely distinct from remainder of frons; gaster usually with a distinct brownish yellow spot on tergite I; SE Brazil to E-central Argentina . . . . . *richteri*
- Pronotal dorsum in posterodorsal view usually flat or weakly convex; pronotum lacking anterolateral bosses; or if these present, head yellowish, at least near mandibular bases and clypeus and often more extensively . . . . . 21
21. Dark median frontal streak usually lacking, but even when present, sculpture on rear face of postpetiole limited to lower ½ of its surface and usually poorly developed, typically with interstitial spaces shiny . . . . . 22
- Dark median frontal streak present, but even when inconspicuous, sculpture on rear face of postpetiole of large workers covering at least lower half, often lower ¾ or more, consisting of transverse rugose striae with variably developed interstitial punctation obscuring the shininess of interstitial spaces . . . . . 23
22. Larger species, AL 1.4–1.6 mm (rarely 1.7 mm) in large workers; piligerous foveolae usually very small, inconspicuous; Orinoco drainage, Guianas, Amazonia and along rivers in bordering regions, also southeastern Brazil (Cephalic pilosity of queen about

- 0.3–0.33 mm long; queens with gaster pilosity arising from small, inconspicuous foveolae) ..... *saevissima*
- Smaller (and much rarer) species; AL < 1.4 mm in even the largest workers; piligerous foveolae on head and pronotum of some workers conspicuous, 5–10× as wide as base of seta; Mato Grosso do Sul to southeastern Brazil and Misiones, Argentina
  - (Cephalic pilosity of queen about 0.15–0.2 mm long; gaster pilosity arising from conspicuous foveolae nearly or indeed as large as those of head and thorax) ... *pythia*
23. Head narrow, CI of even the largest known workers around 90; Peruvian Andes, 2,000–3,500 m elevation ..... *weyrauchi*
- Head broader, CI 95–100 in large workers; lowland species, western Amazonia, south through Mato Grosso, eastern Bolivia, Paraguay and southeastern Brazil to Santa Fé Province, Argentina ..... *invicta*

### Species descriptions

The species descriptions include synonymy, measurements and indices, worker diagnosis, notes (discussion) and distribution. The notes section presents taxonomic and natural history information. Distribution is summarized by representative collection localities delimiting the known extremes of the geographic range of each species.

#### VIRULENS COMPLEX

A single Amazonian and Brazilian coastal forest species constitutes this complex, which is probably not a true member of the *S. geminata* group. It is characterized by monomorphic, yellowish workers with small eyes, long scapes, and inflated post-petiole. This species is compared to the minor workers of the polymorphic species in the following diagnosis.

#### *Solenopsis virulens*, New Status

Figs. 25–27

*Myrmica virulens* Fred. Smith, 1858:132. Syntype workers. BRAZIL. Amazonas. Ega (=Tefe). Bates. (BMNH, examined.)

*Solenopsis bondari* Santschi, 1925:236. Syntype workers. BRAZIL. Bahia. 891 (=1891?). Bondar. (NMB, examined.) NEW SYNONYMY.

*S. bondari*: Kempf and Brown, 1968:99.

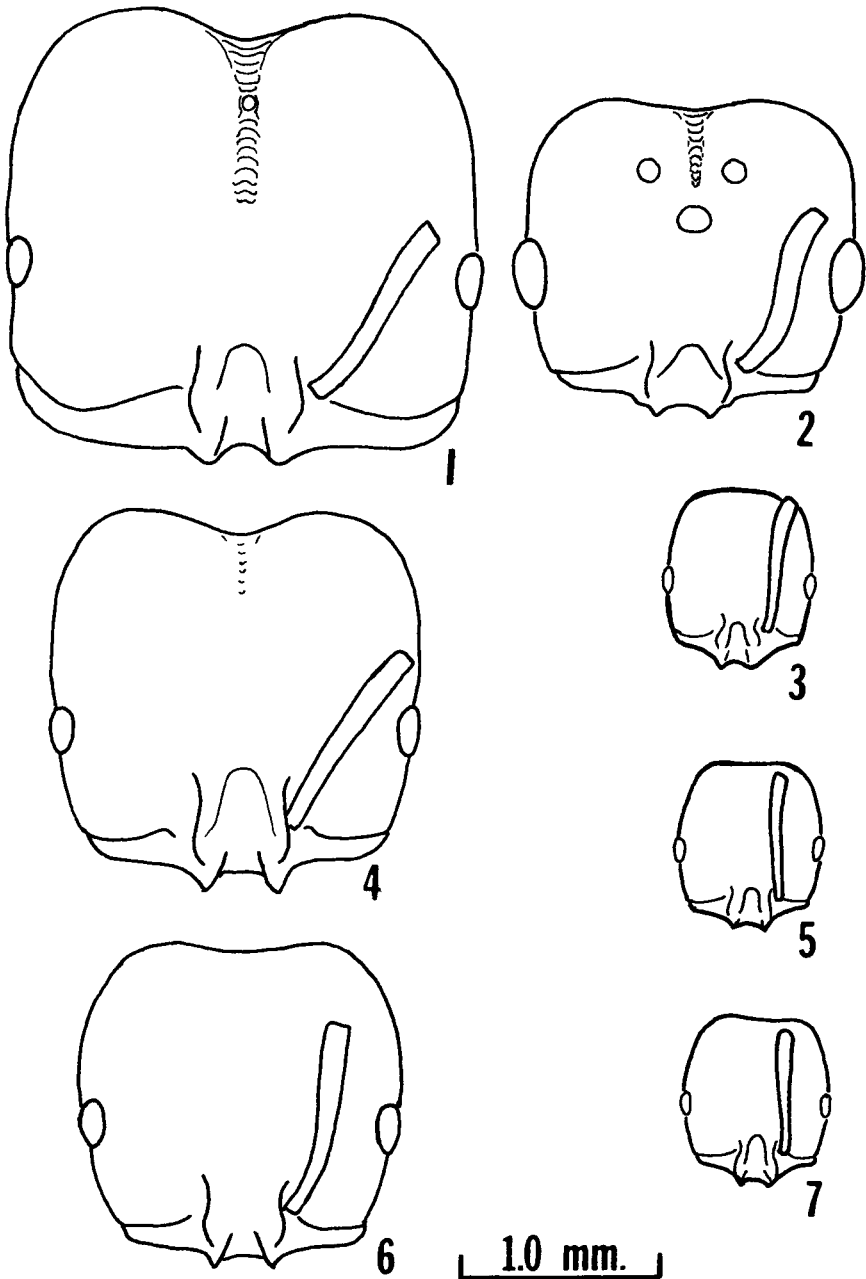
*S. virulens*: Kempf and Brown, 1968:99. (Apparently first used in this combination by these authors, it was treated as *nomen oblitum* by them. Dr. Brown now agrees that the older name should stand.)

*S. (Solenopsis) bondari*: Creighton, 1930:46. Description of workers Creighton considered “cotypes” from Kartabo, British Guiana. (NMB?, not examined.)

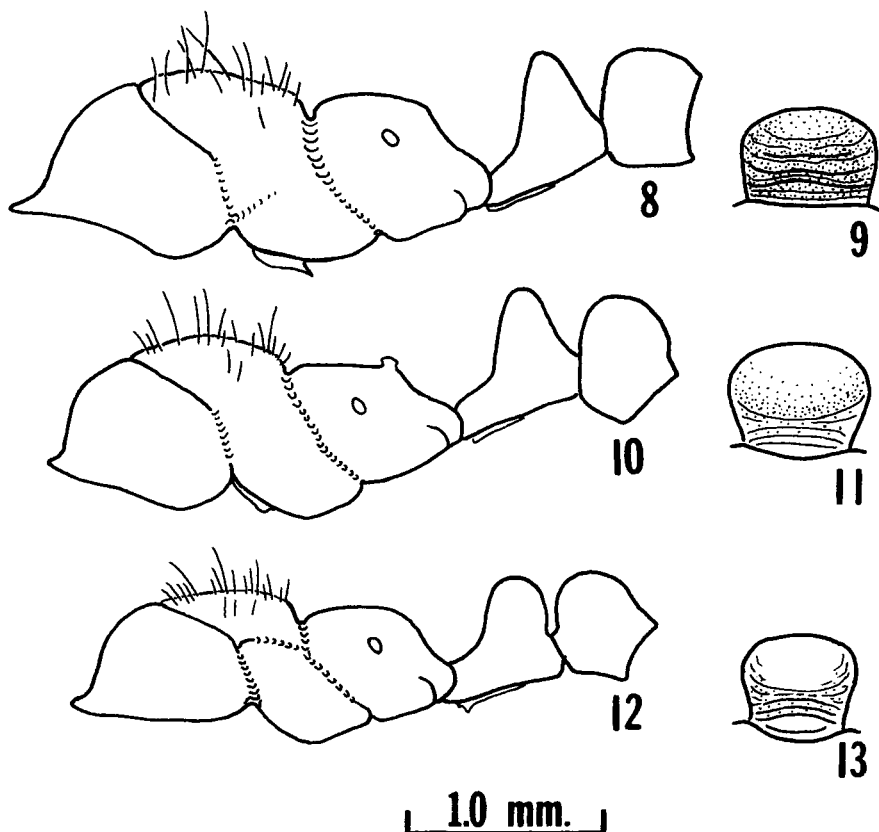
MEASUREMENTS AND INDICES: HL 0.78–1.00, HW 0.68–0.93, SL 0.68–0.88, EL 0.11–0.14 (0.15), PW 0.45–0.60, AL 0.98–1.34, CI 86–95 (97), SI 91–104, OI 13–15 (16). N = 25.

WORKER DIAGNOSIS. Monomorphic. Head (ffv) elliptical, with sides more convex than in minors of other species; posterior border weakly concave, concavity





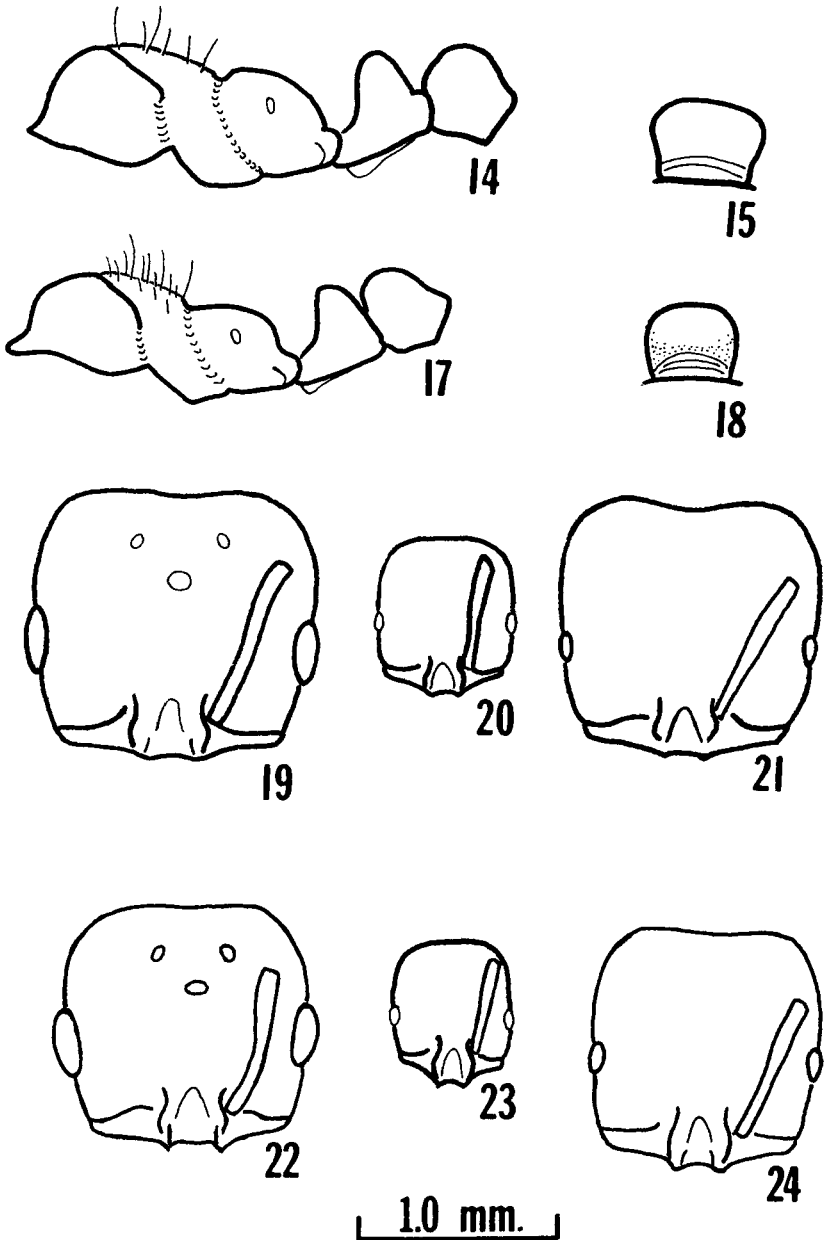
Figs. 1-6. North American *Solenopsis* heads, full face view. 1-3. *S. geminata*; major, queen and minor. 4-5. *S. geminata* × *xyloni*; major and minor. 6-7. *S. xyloni*; major and minor.



Figs. 8–13. North American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 8–9. *S. geminata*. 10–11. *S. geminata* × *xyloani*. 12–13. *S. xyloani*.

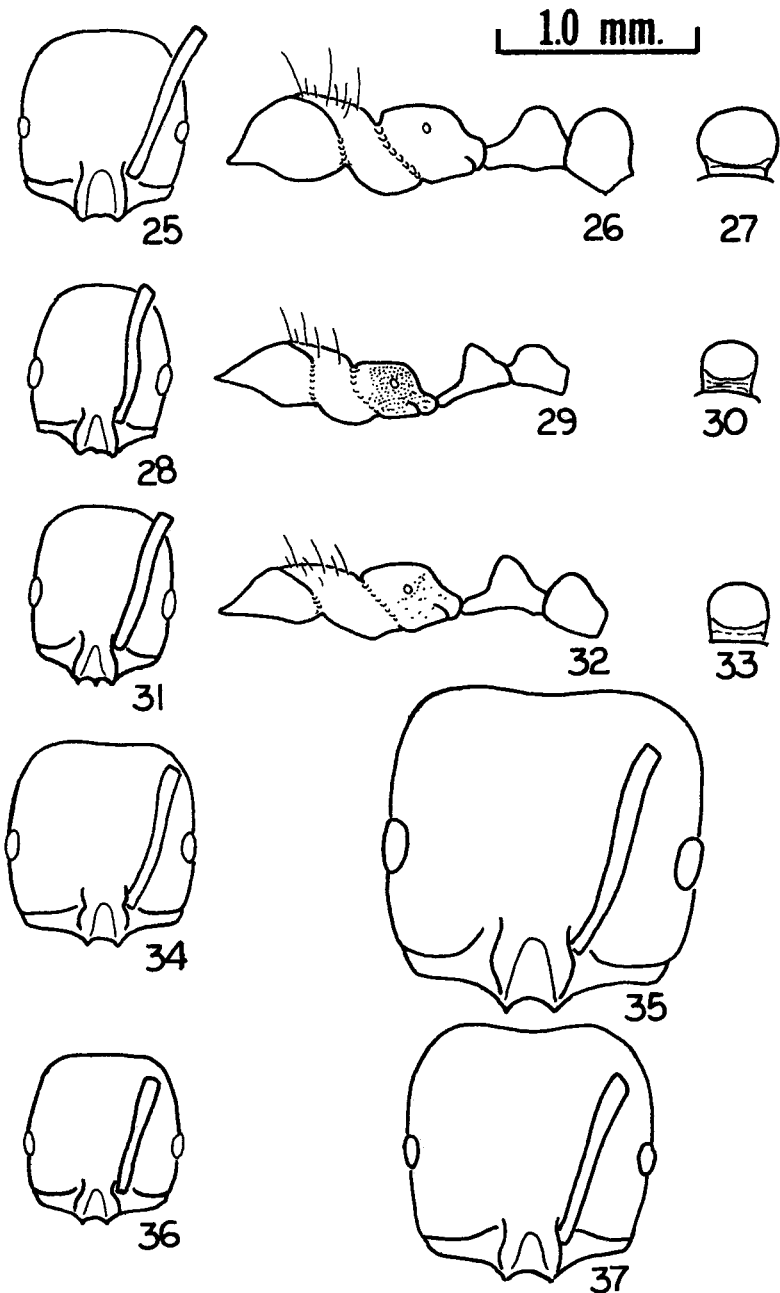
about as wide as distance between frontal lobes (usually) or less; median clypeal tooth poorly developed, or lacking altogether; clypeal carinae weakly produced distally as a pair of (usually) blunt, short teeth; mandibles narrow and weakly curved, less curved than in minors of other species; mandibular costulae well-developed; eye (lv) small, greatest diameter with 5–6 facets, least diameter with 4; scapes (ffv) long, even compared to minor workers of most polymorphic species, scape length exceeding distance between base of scape and occipital corners by 1.3–2.0 × apical diameter of scape; anterior pronotal border (pdv) convex, anterolateral angles distinct but lacking humeral bosses; promesonotal suture obsolete or at most indicated by a shallow, acute-angular impression (not visible in lv); petiolar peduncle longer than base of node, straight to weakly concave ventrally; profile of petiolar node with moderately sharp crest; outline of petiolar node (pdv) globular with shallow median concavity; profile of postpetiolar node in profile globular, as high as that of petiole; postpetiole (pdv) 1.25–1.33 × as wide as petiole.

Piligerous foveolae of head and thoracic dorsum conspicuous, 0.006–0.013 mm



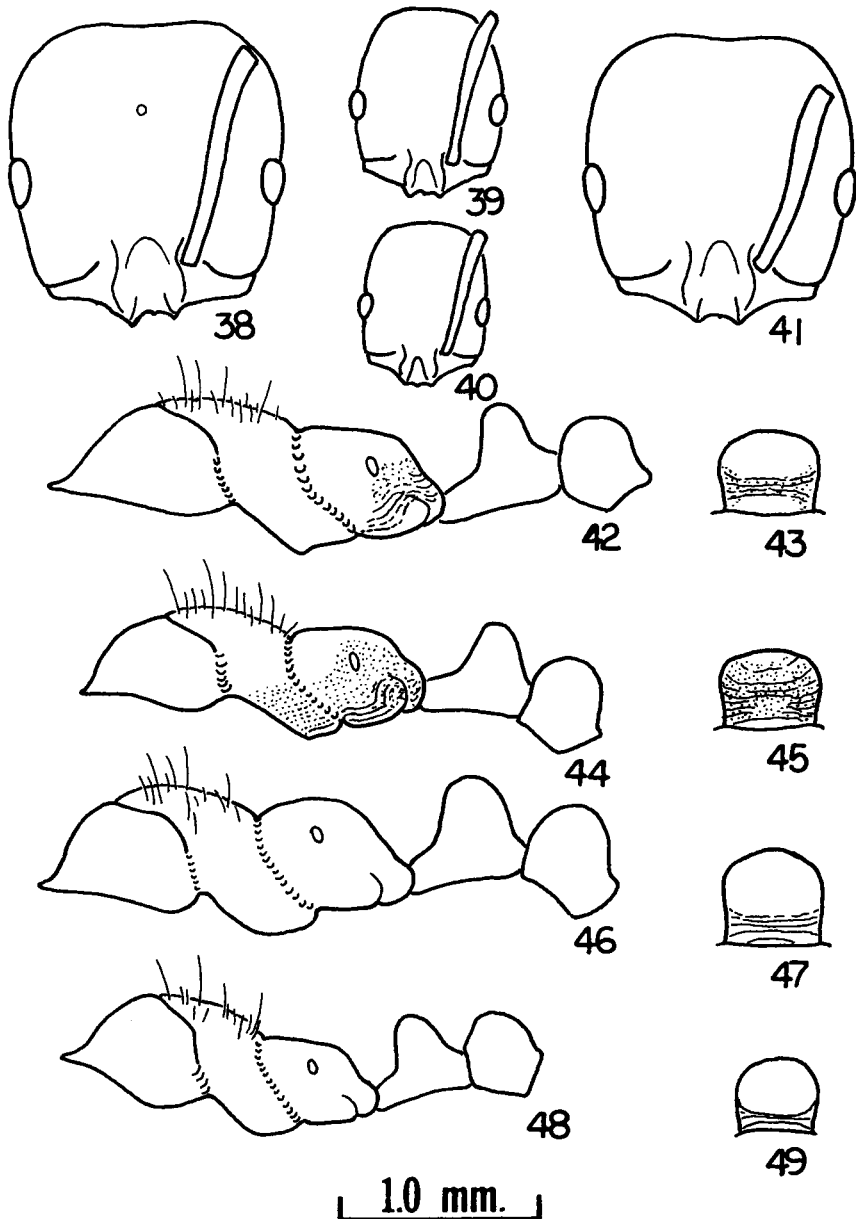
Figs. 14–18. North American desert *Solenopsis* trunk profiles and postpetiole rear views of major workers. 14–15. *S. amblychila*. (16 deleted.) 17–18. *S. aurea*.

Figs. 19–24. North American desert *Solenopsis* heads, full face view. 19–21. *S. amblychila*; queen, minor and major. 22–24. *S. aurea*; queen, minor and major.



Figs. 25–33. Monomorphic *S. geminata* group species; heads, full face view, trunk profiles, and postpetiole rear views. 25–27. *S. virulens*. 28–30. *S. substituta*. 31–33. *S. tridens*.

Figs. 34–37. Trans-Andean western South American *Solenopsis* heads, full face view. 34–35. *S. bruesi*, 36–37. *S. gayi*, minor and major.



Figs. 38–41. Cis-Andean western South American *Solenopsis* heads, full face view. 38–39. *S. electra*; major and minor. 40–41. *S. pusillignis*; minor and major.

Figs. 42–49. Western South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 42–43. *S. electra*. 44–45. *S. pusillignis*. 46–47. *S. bruesi*. 48–49. *S. gayi*.

in diameter; sculpture of mesometapleuron (lv) consisting of longitudinal rugae with interstitial punctation dulling the interrugal spaces; dorsum of propodeum unsculptured; area surrounding propodeal spiracle unsculptured; ventral process consisting of 1–3 small tooth-like projections; dorsum of petiolar node unsculptured; posterior face of petiolar node unsculptured or with faint areolation on the lower portion; node of postpetiole unsculptured.

Pilosity of head and promesonotum, 0.1–0.36 mm in length.

Color pale yellow; sometimes with posterior portions of gastral tergites slightly brownish.

NOTES. This species may have an origin independent of the *S. geminata* group from *S. globularia*-like ancestors. Its sting is reputed to cause a reaction much more painful than that of typical fire ants. Although common and much collected, sexuals of this species are not known.

DISTRIBUTION. *S. virulens* inhabits all of northern South America in forested areas from the base of the Andes to the Atlantic coast, south to Bolivia and Bahia, Brazil.

#### TRIDENS COMPLEX

This is a small complex of 2 species from the cerrado and catinga vegetation of central and northeastern South America. Both species have monomorphic workers with long scapes, well developed propodeal carinae and an elongate petiolar peduncle.

#### *Solenopsis substituta*, New Status

Figs. 28–30

*Solenopsis tridens* var. *substituta* Santschi, 1925:236. 1 worker, 2 queen syntypes.

BRAZIL. São Paulo. Pitangueiras. Luederwaldt. (NHM, examined.)

*S. (Solenopsis) tridens* var. *substituta*: Creighton, 1930:95. Worker, queen.

MEASUREMENTS AND INDICES: HL 0.71–0.82, HW 0.59–0.69, SL 0.63–0.70, EL 0.13–0.15, PW 0.39–0.51, AL 0.94–1.12, CI 80–86, SI 100–107, OI 17–20. N = 20.

WORKER DIAGNOSIS. Monomorphic. Head (ffv) obovate (broader anteriorly), with sides straight to weakly convex anterior to eye; convex and converging posteriad behind eye; posterior border convex, median concavity lacking; median clypeal tooth well-developed, truncate or acuminate, protruding nearly or indeed as far as carinal teeth; clypeal carinae prominent, sharp-crested, produced distally as a pair of sharp teeth; mandibular costulae weakly developed, 4–5 in number when visible; eye (lv) relatively large, greatest diameter with 9–10 facets, least diameter with 6–7; scapes (ffv) long, SL exceeding distance between base of scape and occipital corner by 0.8–1.5× apical diameter of scape; anterior pronotal border (pdv) with anterolateral corners distinct, bearing small, smooth bosses; promesonotum (lv) without anterior declivity mesially, dorsum a continuous convexity from base of cervical collar to mesothoracic declivity; propodeal dorsum convex, sloping, descending through right, or weakly obtuse angles to declivous face; petiolar peduncle longer than base of node, ventrally concave; profile of petiolar node cuneate with dorsum truncate; postpetiole 1.1–1.2× as wide as petiole.

Integument mostly smooth; piligerous foveolae of head and thoracic dorsum mostly

minute, not readily visible, but a few on vertex up to 0.008 mm in diameter; dorsum of propodeum with lateral carinae, with faint areolation between them; area surrounding propodeal spiracle matt, sculptured as adjacent metapleuron; declivous face of propodeum with transverse striae and areolation contiguous with those of metapleuron, but of larger "mesh"; petiolar peduncle dorsally areolate; venter of petiole concave, with ventral process consisting of concavity between 2 blunt protuberances; petiolar node and entire postpetiole unsculptured.

Pilosity of head and promesonotum 0.08–0.25 mm in length.

Bicolored; head, thorax, waist and appendages brownish-red, gaster dark brown to black.

NOTES. *S. substituta* is found nesting in sandy, or less often, gravelly soils in cerrado vegetation. It seems to prefer sites where there has been grazing or foot traffic.

It is not certain that this taxon will continue to be recognized as a distinct species when further samples are studied coming from the area between that from which it is now known and that from which its sister species *S. tridens* is known. I have separated the 2 taxa in the light of their apparently disjunct ranges and distinct sculpture and color.

DISTRIBUTION. The types (examined) were collected at Pitangueira, São Paulo, Brazil. Other specimens studied come from Brazil, namely vicinity of Cuiabá, Mato Grosso and various locations in São Paulo State.

*Solenopsis tridens*

Figs. 31–33

*Solenopsis tridens* Forel, 1911:298. 5 syntype workers. BRAZIL. Bahia. Villa Nova (=Vila Nova). Garve (MHNG, examined).

*S. (Solenopsis) tridens*: Creighton, 1930:94. (No specimens examined; translation of Forel's original description.)

MEASUREMENTS AND INDICES: HL 0.73–0.80, HW 0.61–0.66, SL 0.65–0.69, EL 0.13–0.14, PW 0.42–0.45, AL 1.04–1.06, CI 81–85, SI 103–107, OI 18 (all). N = 4.

WORKER DIAGNOSIS. Monomorphic. Closely resembling *S. substituta*, but differing as follows: mandibular costulae better developed, especially basally, usually 5 in number, obsolescent in distal 1/3 to 1/2 in some specimens; dorsum of propodeum with ridge-like bosses at juncture of dorsal and declivous propodeal faces, but area between bosses smooth, shining; area surrounding propodeal spiracle unsculptured below, unsculptured to weakly striate above spiracle; declivous face of propodeum unsculptured; venter of petiolar peduncle with longitudinal median carina weakly developed and this only anteriorly, ventral process obsolete.

Color uniform blackish brown, with somewhat lighter appendages.

NOTES. The biology of *S. tridens* is unknown. This species may be the northern part of clinal variation that includes what I have called *S. substituta*, but I have seen no intermediate specimens. DISTRIBUTION. The types (examined) were collected at Villa Nova (now spelled Vila Nova), Bahia, Brazil.

GEMINATA COMPLEX

This complex contains 3 subcomplexes collectively distinguished by their peripheral (northern and western) distribution, strongly-developed polymorphism, rela-

tively short scapes, often well developed inferior petiolar process, and by the reduction or loss of at least the median clypeal tooth.

The *geminata* subcomplex apparently contains one highly variable species ranging from northern South America to southeastern United States. This species has a characteristic hypertrophied major worker head, with thick, strongly curved mandibles whose teeth are often worn off by milling seeds.

The *xyloni* subcomplex comprises 3 species from Mexico and the southern United States. Major workers usually have a conspicuous, transparent flange on the ventral process of the petiolar peduncle. The demonstration of hybridization between *S. geminata* and *S. xyloni* (Hung and Vinson, 1977) has been corroborated morphologically in this study and is evidence for the close relationship of the *xyloni* and *geminata* subcomplexes, their disparate morphological features notwithstanding.

Finally, *S. bruesi* of western South America is reminiscent of the *xyloni* subcomplex of North America in its relative tolerance for drier and cooler climates, and in the reduction or absence of the median clypeal tooth. *S. gayi* sometimes has a well developed petiolar ventral process as in some North American species. Here, the 2 species are called the *gayi* subcomplex.

#### GEMINATA SUBCOMPLEX

##### *Solenopsis geminata*

Figs. 1–3, 8, 9

NOTE: All synonymies listed below which are not attributed to any other author are based on the treatment of this species by Creighton (1930). These synonymies are accepted based on the overall strength of Dr. Creighton's study, even though the specimens were not examined in this study.

*Atta geminata* Fabricius, 1804:423. Queen. South America. (Not examined.)

*Solenopsis mandibularis* Westwood, 1841:87. Worker. (Not examined.)

*Atta rufa* Jerdon 1852:106. Worker. India. (Not examined.) (Synonymy by Ettershank (1966:136).)

*Solenopsis cephalotes* F. Smith, 1858:149. Worker. (Not examined.)

*Atta clypeata* F. Smith, 1858:169. Queen, male. (Not examined.)

*Crematogaster laboriosus* F. Smith, 1860:109. Worker. (Not examined.)

*Diplorhoptum drewseni* Mayr, 1861:71. Worker. (Not examined.)

*Myrmica glaber* F. Smith, 1862:34. Worker. Guiana. (BMNH, examined.)

*Myrmica polita* F. Smith, 1862:34. Worker (minims). Guiana. (BMNH, examined.)

*Solenopsis saevissima*: Mayr, 1862:751. MISIDENTIFICATION.

?*Atta Lincecumii* Buckley, 1867:344. Worker. USA. Texas. (Not examined.)

?*A. coloradensis* Buckley, 1867:346. Worker. USA. Texas. (Not examined.)

*Solenopsis geminata*: Mayr, 1867:109; Forel, 1881:10; Wheeler, 1908:424; Forel, 1909:268; Ettershank, 1966:136, Figs. 95–99.

*S. geminata* var. *rufa*: Wheeler, 1907:272. Forel, 1909:268. Bingham, 1903:158.

*S. geminata* var. *diabola* Wheeler, 1908:424. Worker. Syntype workers. USA. Texas. Austin. Wheeler. (MCZ, examined.)

*S. geminata* var. *nigra* Forel, 1908:45. Syntype workers. Costa Rica. Biolley. (MNHG, examined.); Forel, 1909:268; Forel, 1913:23. (Synonymy by Ettershank, 1966:136.)

*S. eduardi* Forel, 1912:12. Worker. COLOMBIA. Magdalena. Rio Frio. (MHNG, examined.) (Synonymy by Ettershank, 1966:136.)



- S. geminata* var. *innota* Santschi, 1915:257. Worker, queen and male syntypes. GABON. 1909 (workers) and 1914 (alates). F. Faure. (NMB, examined.) (Synonymy by Ettershank, 1966:136.)
- S. geminata medusa* Mann, 1916:447. Syntype workers. BRAZIL. Rio Grande do Norte. Ceará-Mirim. Mann. (MCZ, examined.) (Synonymy by Ettershank, 1966:136.)
- S. geminata galapageia* Wheeler, 1919:272. Worker, queen syntypes. ECUADOR. Galapagos Islands. Santa Cruz Isl. (Charles or Indefatigable.) (MCZ, LACM, examined.) (Synonymy by Ettershank, 1966:136.)
- S. eduardi*: Santschi, 1924:13. (Not examined.) (Synonymy by Ettershank, 1966:136.)
- S. eduardi* var. *perversa* Santschi, 1924:13. Syntype workers. BRAZIL. Pernambuco. Tapeza. Guenther. (NHMB, examined.) (Synonymy by Ettershank, 1966:136.)
- S. eduardi* var. *bahiaensis* Santschi, 1925:236. Syntype workers. BRAZIL. Bahia. 892 (=1892). Bondar. (NMB, examined.) (Synonymy by Ettershank, 1966:136.)
- S. (Solenopsis) geminata*: Creighton, 1930:59. Worker, queen, male.
- S. (Solenopsis) geminata galapageia*: Creighton, 1930:65. Worker, queen.
- S. (Solenopsis) geminata rufa*: Creighton, 1930:66. Worker, queen, male.
- S. (Solenopsis) geminata eduardi*: Creighton, 1930:67. Worker.
- S. (Solenopsis) geminata medusa*: Creighton, 1930:68. Worker, queen.

MEASUREMENTS AND INDICES: HL 1.06–2.20, HW 0.98–2.33, SL 0.78–1.14, EL 0.15–0.29, PW 0.57–1.06, AL 1.18–2.08, CI 92–108, SI 47–84, OI 11–16. N = 34.

WORKER DIAGNOSIS. Head (ffv) subquadrate to subtrapezoidal (sides often divergent or flaring anteriorly, especially in specimens from southern Central America and eastern South America), with sides straight to weakly convex and parallel to weakly divergent anteriorly (sides weakly convergent anteriorly in specimens from southern Texas), often slightly indented just anterior to eyes; posterior border with deep angular median emargination between two nearly hemispherical lobes ("temples"); emargination 1.0–1.5× as wide as distance between apices of frontal lobes; median clypeal tooth lacking or (rarely) rudimentary; carinal teeth thick at base, strongly protruding, clypeal border between them concave; mandibles thick and strongly curved mesad, especially in largest individuals; mandibular teeth present in all individuals upon eclosion, but often worn off through seed-milling by larger individuals, such that apices dulled or flattened; mandibular costulae complete in smaller majors, to irregular and largely obsolete in larger majors; eye (lv) appearing small relative to hypertrophied head, greatest diameter with 9–11 facets, least diameter with 7–9; largest majors rarely with median ocellus more or less well developed; scapes (ffv) short, curved, scape failing to reach apices of occipital lobes by 0.3–0.5× SL; pronotum with rounded, at most faintly angular anterolateral corners; promesonotal suture conspicuous, approximately right-angular to weakly obtuse-angular, raised as a small boss at most anterior point; promesonotal profile (lv) formed of 2 convexities meeting at anterior mesonotal boss, pronotal profile more strongly convex and at most feebly angular; anteroventral border of mesopleuron thickened, often bearing one or more spine-like, triangular, lobate or rectangular projecting flanges; metanotal impression marked, set off by a ridge at its juncture with propodeum; propodeal

profile more or less diamond-shaped, with dorsum flat to weakly concave; descending though obtuse, carinate angles to weakly convex declivous face; petiolar peduncle as long as or a little longer than base of node; profile of petiolar node cuneate with a relatively sharp crest; postpetiole  $1.02\text{--}1.08\times$  as wide as petiole.

Piligerous foveolae of head and thoracic dorsum conspicuous and abundant,  $0.025$  or more in diameter, those near mouthparts and on sides of head sometimes elongate; on larger specimens, mesopleuron largely unsculptured to feebly rugose, but coarsely rugose along pleural suture and near edges of sclerite, especially anteroventrally (in smaller specimens, mesopleuron striate-punctate to coarsely rugose); dorsum of propodeum with a pair of irregular dorsolateral carinae, these best developed at juncture of dorsal and declivous faces; posteriorly, transverse striae or rugae may occur on dorsal, concave surface between carinae; area surrounding propodeal spiracle encircled by coarse, irregular rugosity; declivous face of propodeum with transverse rugae contiguous with those of metapleuron on lower portion, but on upper part more neatly aligned than, and not always contiguous with those on side of propodeum; lateral carinae usually obsolescent on all but uppermost portion of propodeal declivous face; petiolar peduncle transversely striate; base of node areolate-punctate; petiolar ventral process consisting of 1 or 2 small teeth, or rarely, a very narrow, transparent flange; dorsum and anterior face of petiolar node sparsely punctate-foveolate, sometimes dorsum with transverse striation like that on posterior face, dorsal margin weakly scalloped; posterior face of petiolar node transversely striate to weakly rugose-areolate below, sparsely sculptured, or less often sculptured as below near top, though less coarsely; sides of postpetiole rugose-punctate; venter of postpetiole dull, coarsely punctate; dorsum of postpetiole weakly scalloped, usually shiny and unsculptured or with a weaker version of sculpture below; posterior face of postpetiole transversely rugose-punctate.

Pilosity of head and promesonotum abundant,  $0.13\text{--}0.37$  mm in length; some pilosity often present on meso- and metapleuron.

Color highly variable, though generally fairly consistent within a colony; ranging from concolorous orange-red with only posterior portion of gaster dark brown (var. *rufa*), to nearly concolorous brownish black with only head near base of mandibles and appendages (especially distally) reddish-brown (var. *nigra*). Smaller workers tend to be darker and more uniformly colored than bigger ones. Darker *S. geminata* are possibly limited to or at least prefer more humid microhabitats, and ecological conditions during rearing may be at least partly responsible for adult coloration, but this needs study. Redder variants often are, or at least appear less sculptured than darker forms, but are more likely to have mesopleural flanges. However, I have studied samples from single colonies with virtually the entire range of color and sculpture described above, and *S. geminata* individuals may have any possible combination of color and sculpture.

NOTES. The distinctive morphology of the major of *S. geminata* is associated with its granivorous habits. It is not unusual to find caches of small seeds, in the nests of this species. In Florida at least, the seeds are usually those of panicoid grasses. The teeth of the majors, which do most of the seed milling, are usually worn off shortly after eclosion, yielding the flat-ended mandibles typical of this species. Unlike the majors of other species, those of *S. geminata* are rather slow-moving and unaggressive.

*S. geminata* has been introduced into both tropical Asia and Africa. The first of these populations is now distributed from Taiwan and India in the north, throughout the Malay archipelago and Polynesia in the south, but the population is highly uniform throughout this vast range, with the light reddish coloration, relatively weak sculpture, and well-developed mesopleural process typical of the form *rufa*, and may result from the successful spread of a single original introduction. The African population is less well known, but is found in tropical west Africa. It resembles the black form found in Georgia, Florida and the Antilles. The being said, it is important to point out that these color and sculpture variants do not hold up as distinct entities in their native America, where there is great variability both within and among localities.

The only population which might, in my opinion, be a distinct species among the material called *S. geminata* here is the western South American population of Colombia and Peru. This form averages smaller in all castes than *S. geminata* from elsewhere, and its sting is reputed to be more painful and to cause a pustule as do stings of the *S. saevissima* complex. The western population is apparently the source of the rather small *S. geminata* typical of the Galápagos Islands. I have been unable to find any morphological differences other than size between this form and the remainder of what I call *S. geminata*, but further study is necessary to resolve the issue.

*S. geminata* × *xyloni* hybrids (Figs. 4, 5, 10, 11) were confirmed by Hung and Vinson (1977) in an early use of allozymes to tackle a problem in ant systematics. They made the interesting observation that while workers were intermediate between the parent species in allozyme electrophoretic banding patterns, winged queens from the same colony showed only the *S. xyloni* pattern. I have examined a few series of this hybrid from Texas, and can confirm that winged queens from such series usually resemble *S. xyloni* morphologically, as well, though one appeared intermediate. It is possible that the generally weaker sculpture and somewhat anteriorly convergent major worker head of Texas *S. geminata* result from introgression of characteristics from *S. xyloni*.

**DISTRIBUTION.** *S. geminata* is apparently native from the southeast coastal plain and Florida to Texas (lacking in Alabama, Mississippi and Louisiana?) south through Central America to northern South America, including the coastal areas of northeastern Brazil, west through the Guianas to the Orinoco Basin, the western Amazon Basin and coastal areas of Peru. Populations of the Antilles and Galápagos (and possibly the southeastern U.S.A.) are probably introduced, but have been in these areas for several centuries.

#### XYLONI SUBCOMPLEX

##### *Solenopsis xyloni*

Figs. 6, 7, 12, 13

*Solenopsis xyloni* MacCook 1879:188. Worker, queen. (No types designated. Specimens studied by MacCook from Alabama, now at USNM, examined.)

*S. pylades* Forel 1904:172. Queen. Mexico. **NEW SYNONYMY.** (Examined by W. F. Buren.) (All later references to this taxon, including those by Forel, concern members of the *saevissima* complex, and not Forel's Mexican species.)

*S. geminata xyloni*: Wheeler 1915:395.

*S. geminata maniosa*: Wheeler 1915:396. Syntype workers. USA. California, Santa Barbara. (Synonymy by Creighton, 1950:232–233.) (To my knowledge, no specimens from Santa Barbara, dead or alive, have been seen since! Specimens labeled cotypes by Wheeler from various California localities were examined.)

*S. (Solenopsis) xyloni*: Creighton 1930:99. Worker, queen, male. Smith 1947:568.

*S. (Solenopsis) xyloni* var. *maniosa*: Creighton 1930:102. *Solenopsis maniosa*: Snelling 1963:9. (Invalid resurrection of taxon.)

?*Myrmica (Atta) sabeana* Buckley 1866:343. Worker. (No types.)

?*Atta brazoensis* Buckley 1866:345. Worker. (No types.)

MEASUREMENTS AND INDICES: HL 1.00–1.50 (1.57), HW 0.89–1.53 (1.58), SL 0.73–0.95, EL 0.16–0.25 (0.29), PW 0.51–0.84 (0.88), AL 1.10–1.75 (1.80), CI 89–102, SI 59–82, OI 14–19 (20). N = 38.

WORKER DIAGNOSIS. Head (ffv) weakly to distinctly cordate, with sides convex; posterior border with a concave median impression, the concavity about  $1.5\times$  or more as wide as distance between apices of frontal lobes; median clypeal tooth lacking; median clypeal seta sometimes lacking or displaced off center; clypeal carinae conspicuous, projecting apically as short, rounded teeth, the clypeal border between them straight to concave, or wavy in outline; mandibles with the usual curvature; mandibular costulae 6–7 in number, complete of obsolete mesially near inner border; eye (lv) ovate, greatest diameter with 9–11 facets, least diameter with 7–9, southwestern specimens (Mexico, Arizona, California) often have the outer ring of facets depigmented, making the eye appear smaller; scapes (ffv) short, distance between tip of scape and occipital corner about  $0.25\text{--}0.45\times$  scape length in major workers, even in smallest workers scape apex fails to reach posterior border by almost  $2\times$  apical width of scape (scape reaching or exceeding posterior border in minors of all other species except *S. amblychila* and *S. aurea*); anterolateral pronotal corners (pdv) rounded, lacking protruding angles; distal border of mesopleuron thickened, flange-like, turned outward; metanotal impression conspicuous; propodeal profile with anterior declivity usually concave, often set off from propodeal dorsum by sharp anterior border, dorsum weakly convex, descending through rounded angles to declivous face; petiolar peduncle a little shorter to slightly longer than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) globular, or especially in larger workers with dorsal face convex, and lateral faces straight, convergent ventrad; postpetiole  $1.05\text{--}1.2\times$  as wide as petiole.

Piligerous foveolae of head and thoracic dorsum 0.01–0.02 mm in diameter; sculpture of mesometapleuron (lv) consisting of fine longitudinal rugae or striae with interstitial punctation or areolation, sculpture lacking on episternal (anteroventral) portion of mesopleuron; surface of mesopleural marginal flange roughened; dorsum of propodeum unsculptured; area surrounding propodeal spiracle usually unsculptured, or with some faint semicircular rugae behind and/or above spiracle; declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle and base of node weakly areolate; venter of petiole with longitudinal median carina and ventral process consisting of a more or less triangular, transparent, jagged edged flange, this always significantly smaller than eye, sometimes narrow

flange continues backward along median carina; petiolar node largely unsculptured except piligerous foveolae; dorsum of postpetiole unsculptured other than piligerous foveolae, or rarely weakly transversely striate-punctate; posterior face of postpetiole mostly shiny above, shiny to transversely rugose below.

Pilosity of head and promesonotum abundant, 0.08–0.35 mm in length; some pilosity often present on meso- and metapleuron.

Color highly variable, though generally fairly consistent within a colony; ranging from concolorous orange-red (var. *maniosa*) with only posterior portion of gaster dark brown, to nearly concolorous brownish black with only head near base of mandibles, and appendages (especially distally) brownish-red. Smaller workers, unlike those of *S. geminata*, tend to be colored like larger workers of the same colony. The darkest color variants occur interspersed among redder ones from Texas to Arizona, south into Mexico. The former are possibly limited to or at least prefer more humid microhabitats (Dr. M. J. Plagens, Phoenix, Arizona, pers. comm.) as in *S. geminata*; the reddest ones occur in the deserts of California.

NOTES. The pale California desert samples of *S. xyloni* are barely distinguishable from *S. aurea*, and single individuals will probably be impossible to determine with certainty. The form *maniosa* (which includes these desert samples) is no more than a slightly smaller variant of *S. xyloni*, at least morphologically. Future studies of the biochemistry or genetics of *S. xyloni* may reveal some cryptic speciation in this taxon, but I have been unable to find any morphological justification for separating the form *maniosa*. The variation in *S. xyloni* is no greater than the sort seen in other widely distributed, abundant species of fire ants.

See notes on *S. geminata* for discussion of hybridization with *S. geminata*.

No type locality (nor any type specimens) were designated in the original description of this species. I have designated a worker from Baton Rouge, Louisiana as holotype, and the remainder of the accompanying series with the same collection data as paratypes. The specimens are housed in the USNM.

DISTRIBUTION. *S. xyloni* is found across the southern United States from the Carolinas and Georgia, through lowland Tennessee, south central Kansas and southern Nevada to the Pacific coast of California. In Mexico, it seems to be limited to dry subtropical areas. In the southeastern U.S., *S. xyloni* has been largely eliminated from areas within the current range of the imported fire ant species, *S. invicta* and *S. richteri*. There is no evidence that *S. xyloni* ever inhabited any portion of Florida, and it is very rare or absent right along the Gulf Coast.

### *Solenopsis amblychila*, New Status

Figs. 14, 15, 19–21

*Solenopsis aurea amblychila* Wheeler 1915:394. Syntype workers, queens, males.

USA. Arizona. Huachuca Mts., Ramsey Canyon. (MCZ, LACM, examined.)

*S. (Solenopsis) xyloni amblychila*: Creighton 1930:104. Worker, queen, male.

*S. aurea amblychila*: Creighton 1950:230.

*S. aurea*: Snelling 1963:7. (In part.)

MEASUREMENTS AND INDICES: HL 1.01–1.30 (1.35), HW 0.95–1.40, SL 0.65–0.78 (0.80), EL 0.15–0.19 (0.20), PW 0.55–0.75 (0.80), AL 1.15–1.50 (1.60), CI 93–104, SI 57–72, OI 12–16. N = 24.

**WORKER DIAGNOSIS.** Resembling a small, yellowish *S. xyloni* and very closely resembling *S. aurea* from which only queens and major workers can be distinguished with certainty; differing from the latter as follows: head (ffv) broader, more cordate; median clypeal seta sometimes displaced off center; clypeal carinae short and blunt, or obsolete, little projecting apically, the clypeal border between them straight to weakly concave; mandibular costulae complete, 6–7 in number; eye (lv) small, ovate, greatest diameter with 8–9 (rarely 10) facets, least diameter with 6–7, at least a portion of outer ring of facets depigmented and often distorted, making the eye appear smaller; anterolateral pronotal corners (pdv) usually with small protruding bosses at angles; postpetiole 1.08–1.19 × as wide as petiole.

Sculpture less pronounced than in *S. xyloni* and *S. aurea*, shinier than these species, further distinguished by the following; piligerous foveolae of head, thorax and postpetiole small and inconspicuous, rarely exceeding 0.005 mm in diameter, placed 0.08–0.20 mm apart; flange of petiolar ventral process larger, diameter of ventrally projecting portion of this flange usually greater than half length of eye, in large workers nearly as long as EL.

Pilosity of head and promesonotum less abundant than in any other fire ant, mesonotum with 8–15 erect setae.

Color reddish yellow, generally of a shade a little darker than that of *S. aurea*, and less often with posterior margins of tergites infuscated.

**NOTES.** Queens from the western part the range of this species may easily be distinguished from those of *S. aurea* by the same characters as the major workers, namely the broad and blunt, or missing clypeal teeth, reduced pilosity, inconspicuous piligerous punctures, and especially by their broader head, CI 108–118 (105 or less in *S. aurea*). Queens from Texas have less conspicuously broad heads, but these are still above the range of *S. aurea*.

The minor, and even submajor workers of *S. amblychila* are difficult or impossible to distinguish from those of *S. aurea*, but the former are less pilose in general, as noted in the description of the major. The consistently different queens and large majors of these forms argue for their being distinct species. There is also an ecological difference, in that in the mountains of southern New Mexico and Arizona at least, *S. amblychila* is found at elevations of about 1,500–2,500 m, while *S. aurea* is found at elevations no higher than 2000 m, and usually much below this. I have not seen any samples of the 2 species collected from exactly the same locality.

**DISTRIBUTION.** The types (examined) were collected in Ramsey Canyon, in the Huachuca Mountains of southern Arizona. Other specimens examined hail from the Doña Ana Mountains of New Mexico, Davis Mountains of Texas, and locations of unspecified elevation in the Mexican states of Guadalajara, Nuevo Leon, Durango, Zacatecas, and Baja California. I have not seen *S. amblychila* specimens from California, U.S.A.

*Solenopsis aurea*  
Figs. 17, 18, 22–24

*Solenopsis geminata* var. *aurea* Wheeler 1906:336. Syntype workers, queen. USA.

Texas. Austin. (MCZ, LACM examined); Wheeler 1908:425.

*S. aurea*: Forel 1909:269; Creighton; Snelling 1963:7 (in part).

*S. huachucana* Wheeler 1915:393. Syntype workers, queen. USA. Arizona. Huachuca Mts., Miller Canyon. (Examined.) NEW SYNONYMY.

*S. (Solenopsis) xyloni aurea*: Creighton 1930:103. Worker, queen, male.

*S. (Euopthalma) huachucana*: Creighton 1930:118. Worker, queen.

MEASUREMENTS AND INDICES: HL 1.00–1.28 (1.35), HW 0.93–1.23 (1.34), SL 0.63–0.75 (0.79), EL 0.15–0.18 (0.19), PW 0.55–0.75 (0.83), AL 1.10–1.49 (1.58), CI 91–100, SI 56–73, OI 13–15 (17). N = 19.

WORKER DIAGNOSIS. Resembling a small, yellowish *S. xyloni*, but differing as follows: head (ffv) narrower, weakly cordate or weakly trapezoidal (converging anteriad) as in smaller *S. xyloni*; median clypeal seta sometimes displaced off center; clypeal carinae conspicuous, projecting apically as conspicuous, isosceles-triangular teeth, the clypeal border between them straight to convex or broadly angular; mandibular costulae complete, 6–7 in number; eye (lv) small, ovate, greatest diameter with 8–9 (rarely 10) facets, least diameter with 6–7, at least a portion of outer ring of facets depigmented and often distorted, making the eye appear smaller; antero-lateral pronotal corners (pdv) usually with small protruding bosses at angles; post-petiole 1.08–1.19× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum 0.01–0.02 mm in diameter and mostly between 0.05–0.10 mm apart; venter of petiole with longitudinal median carina and ventral process consisting of a transparent triangular or subrectangular, jagged edged flange, diameter of ventrally projecting portion of this flange usually less than half the length of greatest diameter of eye.

Pilosity of head and promesonotum abundant, 0.08–0.30 mm in length; mesonotum with 18–30 erect setae.

Color light reddish yellow, with posterior margins of tergites brown to dark brown.

NOTES. As indicated in the discussion of *S. amblychila*, *S. aurea* occurs at lower elevations than the former, and indeed may be found below sea level in the deserts of California.

DISTRIBUTION. The types (examined) were collected at Austin, Texas. The range extends west to inland California and south into northern Mexico, mainly in desert and dry grassland regions.

GAYI SUBCOMPLEX

*Solenopsis gayi*

Figs. 36, 37, 48, 49

*Myrmica gayi* Spinola 1851:242. Syntype workers, queen, male. CHILE. Santiago. (Not examined.)

*Pogonomyrmex gayi*: Mayr 1868:170.

*Solenopsis gayi*: Mayr 1870:971–972. Worker; Snelling and Hunt 1975:84–85. Worker, queen, male (illustrated). (Various Chilean localities, examined.)

*Solenopsis geminata gayi*: Emery 1895.

*Solenopsis (Solenopsis) gayi*: Creighton 1930:48–51.

*Solenopsis gayi* var. *fazi* Santschi 1923. Syntype workers, queens. CHILE. Santiago. (NMB, examined.) *Solenopsis gayi* var. *fazi*: Creighton 1930. (Synonymy by Snelling and Hunt, 1975.)

MEASUREMENTS AND INDICES: HL 1.00–1.23, HW 0.94–1.26, SL 0.73–0.86, EL 0.15–0.20, PW 0.51–0.69, AL 1.24–1.51, CI 94–103, SI 68–80, OI 14–16. N = 10.

WORKER DIAGNOSIS. The smallest South American fire ant and the only one found in Chile, distinguished as follows: head (ffv) subrectangular, except in largest workers in which it may be convergent anterior to eyes; sides straight to weakly convex; posterior border straight or with a broad, shallow concave median impression, concavity occupying nearly entire breadth of the posterior borders; median clypeal tooth lacking; clypeal carinae conspicuous, close-set, projecting apically as long, blunt teeth; clypeal border between carinal teeth strongly concave; distance between teeth a little over  $\frac{1}{2} \times$  distance between apices of frontal lobes (about  $\frac{3}{4}$  this distance in most species outside *gayi* subcomplex); mandibles straight near base, then curving mesad as in media workers of *S. geminata*; mandibular costulae 6–7 in number, complete and well developed; eye (lv) ovate, greatest diameter with 8–9 facets, least diameter with 6–7 (facet count 40 or less in minors); scapes (ffv) in majors failing to reach rear border of head by 3–5  $\times$  greatest scape width, and even in small minors, distance between tip of scape and occipital corner about 1–2  $\times$  apical width of scape (scape reaching or exceeding posterior border in minors of all other species except *xyloni* complex), stated otherwise, CI varied less with size than in other species; anterolateral pronotal corners (pdv) rounded; metanotal impression conspicuous, but shallow and weakly sculptured compared to other species besides *S. bruesi*; propodeal profile with anterior declivity obsolete, grading insensibly into weakly convex dorsum, the latter ranging from distinctly sloped to little or not at all sloping posteriad; dorsal face of propodeum meeting rear face through rounded-off obtuse to right angles; petiolar peduncle a little shorter to slightly longer than base of node; postpetiolar node in profile lower than petiole, globular; outline of postpetiolar node (pdv) globular and little or not at all wider than petiole.

Piligerous foveolae of head and thoracic dorsum small, 0.003–0.005 mm in diameter; sculpture of mesometapleuron (lv) normal or sometimes reduced, with longitudinal rugae and interstitial punctation largely obsolete; area surrounding propodeal spiracle shining, unsculptured; declivous face of propodeum with transverse striae below, contiguous with those of metapleuron; petiolar peduncle and base of node weakly areolate; venter of petiole with longitudinal median carina and ventral process consisting of at most a small protuberance; petiolar and postpetiolar nodes largely unsculptured, shining and globular as in *S. virulens*, except for faint transverse rugae at base of rear face of postpetiole in some specimens.

Pilosity of head and promesonotum as in *S. aurea*.

Color uniform dark reddish brown with the gaster slightly darker; many specimens have at least part of the clypeus, frons, sides of head in front of eyes, and a triangular area that would have its corners approximately at the positions of the ocelli if these were present, lighter reddish or even yellowish; the lightest specimens may have a distinct yellowish brown spot on the first tergite.

NOTES. Snelling and Hunt (1975) state that *S. gayi* "is one of the commonest ants in Chile, and is the most widely distributed." In southern Peru, *S. gayi* is sympatric with *S. bruesi*, but is apparently limited to low elevations (up to 500 m).

DISTRIBUTION. The types of *S. gayi* (not examined, but certainly belonging to this, the only fire ant species in Chile) were described from Santiago, Chile. It occurs



from as far south as Malleco province, Chile north to southern Peru. I have seen a sample from Villavicencio, Meta, Colombia, which may represent an introduction.

*Solenopsis bruesi*, New Status

Figs. 34, 35, 46, 47

*Solenopsis (Solenopsis) gayi bruesi* Creighton 1930:52–53. Syntype workers. PERU. Chosica Canyon (near Lima). C. T. Brues. (MCZ, LACM, examined.)

MEASUREMENTS AND INDICES: HL 1.00–1.47, HW 0.92–1.47, SL 0.73–0.98, EL 0.16–0.24, PW 0.51–0.80, AL 1.16–1.73, CI 91–106, SI 66–83, OI 14–19. N = 16.

WORKER DIAGNOSIS. Closely resembling a large, reddish *S. gayi* in morphology, with the following characteristics like those of the latter: head (ffv) subrectangular, except in largest workers in which it may be convergent anterior to eyes; sides straight to weakly convex; posterior border straight or with a broad, shallow concave median impression, concavity occupying nearly entire breadth of the posterior borders; median clypeal tooth lacking; clypeal carinae conspicuous, close-set, projecting apically as long, blunt teeth; clypeal border between carinal teeth strongly concave; distance between teeth a little over  $\frac{1}{2} \times$  distance between apices of frontal lobes (about  $\frac{3}{4}$  this distance in most species outside *gayi* subcomplex); scapes (ffv) short in majors, failing to reach rear border of head by  $3\text{--}5 \times$  greatest width of scape, and even in small minors, distance between tip of scape and rear corner of head about  $1\text{--}2 \times$  scape widths (scape reaching or exceeding posterior border in minors of all other species except *xyloni* complex), stated otherwise, CI varies less with size than in other species; outline of postpetiolar node (pdv) globular and little or not at all wider than petiole.

Differing from *S. gayi* in the following: larger, about the size of *S. invicta*; blade of mandible broader, mandibular costulae finer and more numerous, 8–9 in number, complete and well developed; eye (lv) larger, greatest diameter with 9–12 facets, least diameter with 7–8 (facet count 50 or more in minors).

Piligerous foveolae of head and thoracic dorsum smaller than those of *S. gayi*, rarely in excess of 0.003 mm in diameter; all other sculpture reduced, often lacking altogether, yielding a generally quite shiny ant.

Pilosity of head and promesonotum of the usual sort for the *saevissima* complex, though a little less abundant than in other species, mesonotal dorsum with about 20 erect setae (25 or more in most other species).

Color uniform reddish brown to light reddish, with the gaster slightly darker; triangular area that would have its corners approximately at the positions of the ocelli if these were present, distinctly darker than surrounding area (lighter reddish or yellowish in *S. gayi*).

NOTES. Creighton described *S. bruesi* from media workers, stating that their features “might be considered sufficient to entitle it to specific status, [but] the question turns upon the character of the [as yet uncollected] sexual forms.” While the latter remain unknown, the major worker specimens collected by Weyrauch leave no doubt in my mind that this is a distinct species. The majors resemble nothing so much as submajors of *S. geminata* from which all the sculpture has been polished off. From label information, we gather *S. bruesi* occurs in wild areas, including sand deserts and canyons, but also occurs in urban areas.

**DISTRIBUTION.** The types (examined) came from Chosica Canyon, (near Lima), Peru. Additional localities are Trujillo, and others in the vicinity of Lima.

*SAEVISSIMA* COMPLEX

This complex contains 2 subcomplexes. While it is fairly certain that the *saevissima* subcomplex is monophyletic, this is less certain for the *electra* subcomplex. As a complex, all the species are characterized by their cis-Andean South American distribution (except *S. weyrauchi* may be found in the Pacific drainage), polymorphism of the workers, long scapes of the minor, weak sculpture, and a small or absent ventral process on the petiolar pedicel.

The *electra* subcomplex contains two species, *S. electra* and *S. pusillignis*, found in the dry western portion of South America east of the Andes. Both have small sexual forms, and the head shape of the majors is similar. They are described near the end of this paper.

The remaining species form the *saevissima* subcomplex. They inhabit grasslands and forest openings (usually near water, often in seasonally flooded habitats) in tropical to warm temperate lowland South America. An interesting exception is *S. weyrauchi* which lives in the cool bunch grass habitats of the Andean uplands of Peru. These are relatively large species, with long scapes, and in every case known, their venoms cause pustules on the skin of human victims of their stings. *S. invicta* is intermediate in size and sculpture between the "extreme" species of the subcomplex, *S. saevissima* and *S. macdonaghi*, and is used as the "standard" to which most other species are compared in the following treatment. The parasites of the *S. daguerrei* group all live with species of the *saevissima* subcomplex, and are apparently derived from it.

*SAEVISSIMA* SUBCOMPLEX

*Solenopsis invicta*

Figs. 50, 51, 56, 57

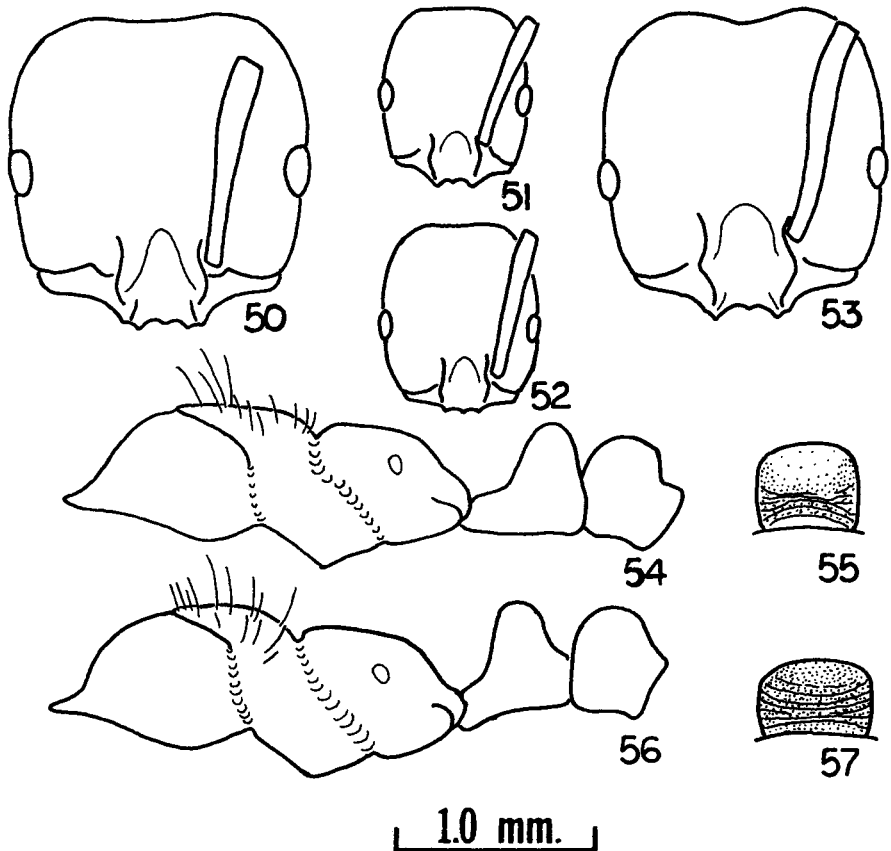
*Solenopsis saevissima saevissima* cline *S. saevissima richteri* ("light red phase" and probably also "subsp. *electra*"): Wilson 1952:65. Workers from USA. Alabama, Mississippi. (MCZ, examined.) (Synonymy by Ettershank, 1966:136.)

*S. invicta* Buren 1972:9. Worker, queen, male. (This name was misspelled as "*invica*" at the head of the species description in Buren's paper, but it is clear from the rest of the paper and the etymology of the name, not to mention a huge body of subsequent usage, that *invicta* was the intended spelling.)

*S. quinquecupis*: Buren 1972:17-19. (Numerous workers in WFB, examined.) MISIDENTIFICATION.

(But not *Solenopsis pylades* var. *quinquecupis* Forel 1913:224, which is a valid, distinct species.)

*S. saevissima electra* var. *wagneri* Santschi 1916:380. Syntype worker. ARGENTINA. Santiago de Estero. Near Icano. Wagner. (NMB, examined. Other specimens probably exist in the Paris Museum, but were not examined.) NOT AVAILABLE; Santschi 1923:266. Creighton, 1930:94. (In part only, since Santschi's types were included among the localities.)



Figs. 50–53. South American *Solenopsis* heads, full face view. 50–51. *S. invicta*; major and minor. 52–53. *S. richteri*; minor and major.

Figs. 54–57. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 54–55. *S. richteri*. 56–57. *S. invicta*.

NOTE: Though it has priority over Buren's name, *wagneri* is not an available name, as it has never been used above infrasubspecific rank. Uses of the name since Santschi have not been associated with specimens and thus are, in effect, nomina nuda.

MEASUREMENTS AND INDICES: HL 1.00–1.47 (1.49), HW 0.90–1.42 (1.49), SL 0.80–1.06, EL 0.18–0.26 (0.27), PW 0.55–0.90, AL 1.26–1.90, CI 89–99 (101), SI 70–92, OI 15–18 (19). N = 40.

WORKER DIAGNOSIS. Head (ffv) subquadrate to weakly cordate (occasionally broader and more cordate in particularly large individuals), with sides convex; posterior border with a shallow concave median impression, the concavity about 1.5× or more as wide as distance between apices of frontal lobes; median clypeal tooth well-developed, usually sharp and about 0.5× as long as lateral teeth, sometimes

displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth, or curved mesad and faintly falcate; space between clypeal carinae concave, except near base of median tooth; mandibles with the usual curvature; mandibular costulae mostly obsolete except distally and near base along outer border, rarely one or more of the median intercostular furrows extends length of mandible; eye (lv) ovate, greatest diameter with 11–14 (rarely less) facets, least diameter with 8–10, often outer ring of facets depigmented, especially anteriorly; distance between tip of scape and occipital corner about  $0.08\text{--}0.15 \times$  scape length in major workers, (ffv) in smallest workers scape apex easily reaches or slightly exceeds posterior border; anterolateral pronotal corners (pdv) rounded to weakly angular, especially in smaller workers, but only very rarely with a protruding humeral boss; anteroventral border of mesopleuron with a seam-like flange separating its lateral portion from the ventral concavity in which the procoxa fits at rest, though often this seam obsolete anteriorly or absent altogether; metanotal impression conspicuous; propodeal profile with anterior declivity short, convex, set off from propodeal dorsum by a rounded angle; propodeal dorsum weakly convex, descending through rounded angles to declivous face, or rarely forming a continuous convexity with the declivous face, in which case both surfaces more rounded than usual; petiolar peduncle notably to slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subrectangular to subtrapezoidal, with dorsal outline weakly convex, and lateral faces straight, parallel to convergent ventrad; postpetiole  $1.04\text{--}1.15 \times$  as wide as petiole.

Piligerous foveolae of head and thoracic dorsum typically small, round and inconspicuous, mostly  $0.003\text{--}0.005$  mm in diameter, but occasionally up to  $0.01$  mm and slightly elongate, especially in darker color variants from southeastern part of range (SE Brazil, Uruguay, Argentina); sculpture of mesometapleuron (lv) consisting of fine longitudinal striae or rugose striae, often with interstitial punctation or areolation; sculpture often weakened or obsolete on mesial and/or anteroventral portion of mesopleuron; surface of mesopleural marginal flange, when present, roughened; dorsum of propodeum unsculptured; area surrounding propodeal spiracle usually unsculptured, except frequently some semicircular rugae behind, and rarely above, spiracle, but these separated from spiracle by a smooth, shiny area; declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle, and sometimes base of node, weakly areolate; venter of petiole with longitudinal median carina and ventral process obsolete or consisting of a small truncate projection; petiolar node largely unsculptured except piligerous foveolae, and perhaps a few shallow longitudinal furrows; dorsum of postpetiole unsculptured other than piligerous foveolae, or rarely weakly transversely striate-punctate; posterior face of postpetiole mostly shiny near top, transversely rugose or punctate-rugose on lower  $\frac{2}{3}$  or more.

Pilosity of head and promesonotum abundant,  $0.08\text{--}0.33$  mm in length; 2–8 erect setae also present on mesopleuron and 1 or 2 on metapleuron, gaster pilosity normal.

Color variable, though generally fairly consistent within a colony; bicolored, with head and thorax ranging from concolorous yellowish-red to dark reddish brown, gaster brown with a large spot the color of the foreparts of tergite I to nearly con-

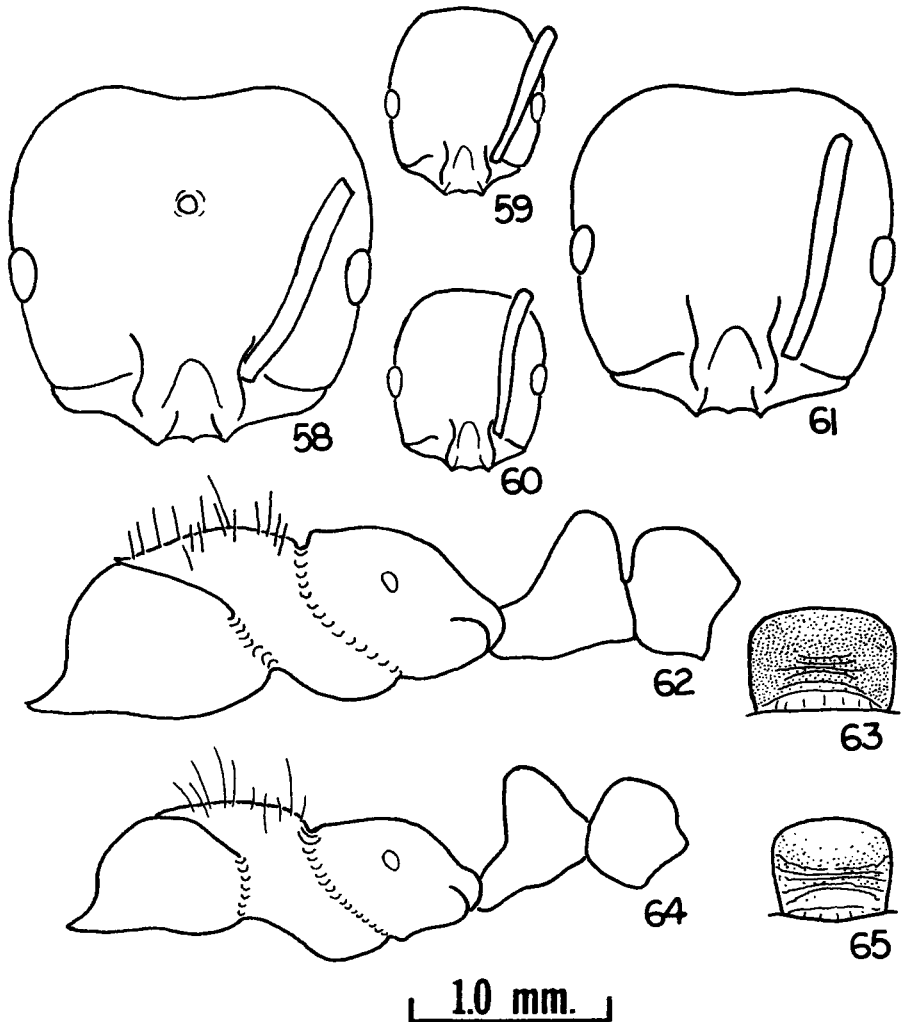
colorous brownish black; head of darker variants often concolorous except for dark frontal streak (not usually conspicuously lighter near base of mandibles and on clypeus as in the related *S. quinquecupis*); frontal triangle and narrow median impression behind it notably darker than surrounding area in most specimens of all sizes, except in the brightest red specimens from the northern and western parts of the range. Smaller workers tend to be colored darker than larger workers of the same colony. The darkest color variants are most common from southeastern Brazil to east-central Argentina (but can be found locally as far west and north as Mato Grosso), interspersed among redder colonies, or in more uniformly dark local demes. A pale, honey colored form occurs locally in the pantanal of Mato Grosso, and rarely elsewhere.

NOTES. This is the infamous red imported fire ant of the southeastern U.S.A. The North American population appears to have originated in the Paraguay River drainage of South America, where at least the majority of ants among the South American *S. invicta* thus far studied most closely resemble the North American population in venom chemistry (Vander Meer, unpubl. data), allozyme allele frequencies (Ross and Trager, 1991) and color and morphology (this study). The area in question includes southern Mato Grosso and Mato Grosso do Sul, Brazil, all of Paraguay and northern Argentina. Buren's (1972) selection of Cuiabá as the type locality is thus close to the mark in terms of selecting an area in South America from which the specimens would be representative of both the North American and South American populations. However, in terms of shipping routes and practices in the late 1930's, I believe it more likely that *S. invicta* arrived with cattle from northern Argentina or Paraguay.

Of the 2 imported fire ant species, *S. invicta* has been much more successful in North America than *S. richteri*, as evidenced by the now much retracted range of the latter there. The hybrid population resulting from the crossing of these two species (and subsequent reproduction within the hybrid population) has also retreated in the face of the spread of *S. invicta*, though the mechanism (competitive displacement, genetic swamping, other?) is unclear. See the notes on *S. richteri* for further information relevant to hybrid imported fire ants.

In the light of the fertility and evident viability of the hybrid, one may legitimately question my maintenance of these forms as distinct species. I base this upon the behavior of the species in South America. In the small area in Argentina where they are sympatric, available evidence of introgression between *S. invicta* and *S. richteri* indicates that it occurs only at a very low rate (Ross and Trager, 1991). Several features of the North American populations of both species indicate that they originated far from the zone of natural sympatry in South America, and it is not unreasonable to hypothesize that the North American populations of *S. invicta* and *S. richteri* came from populations that either had lost or never had whatever isolating mechanisms exist in the area of sympatry.

DISTRIBUTION. The types (examined) are from Cuiabá, Mato Grosso, Brazil. In North America, *S. invicta* occurs from the Carolinas to Florida west to Texas. Isolated populations have been found somewhat to the north of this area, and have also been found in New Mexico, Arizona and California, where they arrived with sod or nursery stock from the southeast. These outlier populations were quickly eliminated shortly after their discovery. In South America, *S. invicta* is found from northern Mato Grosso west to Peru and Bolivia, south to Santiago del Estero and



Figs. 58–61. South American *Solenopsis* heads, full face view. 58–59. *S. macdonaghi*; major and minor. 60–61. *S. interrupta*; minor and major.

Figs. 62–65. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 62–63. *S. macdonaghi*. 64–65. *S. interrupta*.

Santa Fé provinces in Argentina and northeast through Uruguay and southern Brazil to São Paulo state.

*Solenopsis interrupta*

Figs. 60, 61, 64, 65

*Solenopsis saevissima* var. *interrupta* Santschi 1916:397. Syntype (?) workers (see discussion). ARGENTINA. La Rioja. Bajo Hondo. (USNM, examined; NMB, not examined.)

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

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

(*S. interrupta*: Buren 1972:22 is in the synonymy of *S. macdonaghi*. Buren recognized the true *S. interrupta* as a distinct species, but assigned the name incorrectly (Buren, pers. comm.).)

MEASUREMENTS AND INDICES: HL 1.19–1.60, HW 1.05–1.53 (1.61), SL 0.90–1.15, EL 0.20–0.28, PW 0.63–0.90 (0.95), AL 1.35–1.89 (2.00), CI 88–99 (101), SI 66–90, OI 15–19. N = 22.

WORKER DIAGNOSIS. Larger, more yellowish or amber-colored than *S. invicta*, differing additionally as follows: Head (ffv) weakly cordate to strongly cordate, with sides weakly to notably convex; posterior border with a concave median impression about as in *S. invicta*, but tending to be a little narrower and deeper, the concavity less than  $1.5 \times$  distance between apices of frontal lobes; mandibles with the usual curvature; mandibular costulae usually complete and close set, yielding a silky sheen to the mandibular upper surface (rather than highly polished mesial region typical in *S. macdonaghi* and most common in *S. invicta*), costulae rarely partly obsolete mesially; anterolateral pronotal corners (pdv) usually weakly angular, protruding humeral bosses lacking or at most feebly protruding; propodeal profile with anterior declivity of most workers straight, sloped backward, set off from propodeal dorsum by a distinct angle; propodeal dorsum weakly convex, sloping to the rear, descending through rounded angles to declivous face, never forming a continuous convexity with the declivous face; postpetiolar node in profile lower than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subtrapezoidal, with dorsal outline weakly convex, and lateral faces straight or concave, slightly to notably convergent ventrad.

Sculpture as in less heavily sculptured series of *S. invicta*, in particular, *S. interrupta* tends to have the postpetiolar rear face weakly transversely rugose with interrugal punctuation weakly developed, this sculpture rarely reaching postpetiolar dorsum except in some large workers.

Vestiture not appreciably different from that of *S. invicta*, but finer and much more variable in length than in typical specimens of the otherwise somewhat similar *S. macdonaghi*.

Two more or less distinct color forms of *S. interrupta* occur. The most common form has the head predominantly bright reddish or amber yellow; median frontal impression sometimes darkened as in *S. invicta*, but more often not; thorax weakly infuscated dorsally, appendages and rear portion of the head somewhat darker; gaster dark brown with gaster spot occupying at least  $\frac{2}{3}$  of first tergite, this also true of median and many small workers (spot rarely occupies more than  $\frac{1}{2}$  to  $\frac{3}{5}$  of tergite in *S. invicta* and obsolete on smaller workers). A less common form, but one predominating in the vicinity of Santa Cruz, Bolivia and occurring less frequently elsewhere is colored uniform dusky yellowish brown dorsally, fading to yellower on the anterior half of the head, pleura and coxae; median frontal dark streak poorly defined; gaster spot only slightly lighter than remainder of gaster, occupying only about half the tergite and fading gradually into darker area, or even obsolescent.

NOTES. See notes on *S. macdonaghi* for comments on separating these two large and generally brightly colored species.

The darker color form may be difficult to separate from sympatric *S. invicta*, but the latter generally has a more rectangular postpetiolar node, and has a rather distinct median frontal dark streak surrounded by a notably lighter and yellower surrounding region of the frons and clypeus, at least.

Occasional colonies have weakly developed polymorphism as in polygyne colonies of *S. invicta*. Their smaller size and somewhat darker color will probably render them impossible to identify by any other than the most experienced collector of fire ants, unless one resorts to biochemical genetic characters (Ross and Trager, 1991). Polygyny is suspected, but not confirmed in these colonies.

Within the *saevissima* subcomplex, this is certainly the most xerophilic species, and may be found together with *S. electra* in at least the eastern portion of the deserts of northern Argentina and in the dry Andean foothills.

There is some question about the type locality of *S. interrupta*. The original description states that the specimens were from "Bajo Hondo, Argentina," but there are two widely separated localities by this name in Argentina. One is in La Rioja province, well within what I understand to be the normal range of this species, and the other in a portion of Buenos Aires province inhabited, to my knowledge, by only 2 fire ant species, namely *S. quinquecupis* and *S. richteri*. I have not examined types, but a series in USNM has the same locality and collector data, and may be from the same colony. They appear to be typical western Argentine *S. interrupta*, and since the collector (Carette) travelled widely in that region as well as in Buenos Aires, I think it safe to assume that the sample was collected in La Rioja.

**DISTRIBUTION.** The types (not seen, but studied by W. F. Buren) were collected in Bajo Hondo, La Rioja, Argentina. (Mistakenly, I believe, listed as Bajo Hondo, Buenos Aires by Santschi and Creighton. See above.)

The distribution of *S. interrupta* has its southern extremes in Cordoba and Mendoza provinces in west central Argentina, and extends north along the base and foothills of the Andes well into Bolivia.

#### *Solenopsis macdonaghi*, New Status

Figs. 58, 59, 62, 63

*Solenopsis saevissima* var. *macdonaghi* Santschi 1916:397. Syntype workers, queens.

ARGENTINA. Entre Rios. Estación Sosa. MacDonagh. (NMB, examined.)

*S. geminata pylades*: Bruch 1916:313. (Not examined.) (Synonymy by Emery, 1925.)

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

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

*S. interrupta*: Buren 1972:22. MISIDENTIFICATION.

(But not *Solenopsis saevissima* var. *interrupta* Santschi 1916:397, which is a valid, distinct species.)

**MEASUREMENTS AND INDICES:** HL 1.05–1.69 (1.75), HW 0.93–1.73 (1.80), SL 0.80–1.15, EL 0.20–0.33 (0.35), PW 0.58–1.15, AL 1.26–2.10 (2.21), CI 90–102 (103), SI 63–90, OI 16–20. N = 23.

**WORKER DIAGNOSIS.** Most closely resembling *S. interrupta*; larger, more reddish than most *S. invicta*, differing additionally as follows: Head (ffv) broad (often slightly broader than long) cordate, with sides convex; posterior border with a concave



median impression, the concavity about as wide as distance between apices of frontal lobes; median ocellus usually conspicuous and with a clear lens in large and even in some smaller specimens; mandibular costulae mostly obsolete except distally and near base along outer border, less often (especially in series from Paraguay and Bolivia) costulae more or less complete; pronotal profile more arched than in other species; anterolateral pronotal corners (pdv) rounded, weakly angular in smaller workers, but lacking protruding bosses; metanotal impression deep; anterior declivity of propodeum straight, higher than in other species, set off from propodeal dorsum by a more or less rounded angle; anterior portion of propodeal dorsum flat to weakly concave (upturned to meet anterior angle), posterior portion convex and sloping through an even convexity to a low posterior face, or the latter set off by a rounded broadly obtuse angle; petiolar peduncle notably shorter than base of node, the node appearing a little thicker basally than in other species; postpetiolar node (pdv) broad, subrectangular; with dorsal outline weakly convex, lateral faces straight, parallel.

Piligerous foveolae of head and thoracic dorsum typically round and more conspicuous than in *S. interrupta*, about 0.01 in diameter, occasionally larger and slightly elongate; rear face of postpetiole usually lacking or with only very weak transverse rugae except near base, uniformly and densely punctate, the punctuation usually extending onto dorsum of postpetiole.

Pilosity of head and promesonotum abundant, 0.08–0.33 mm in length as in other species, but in most specimens, the majority of setae are of more or less uniform length (0.15–0.25 mm); setae flatter at base, redder in color, and less curved than is typical of other species.

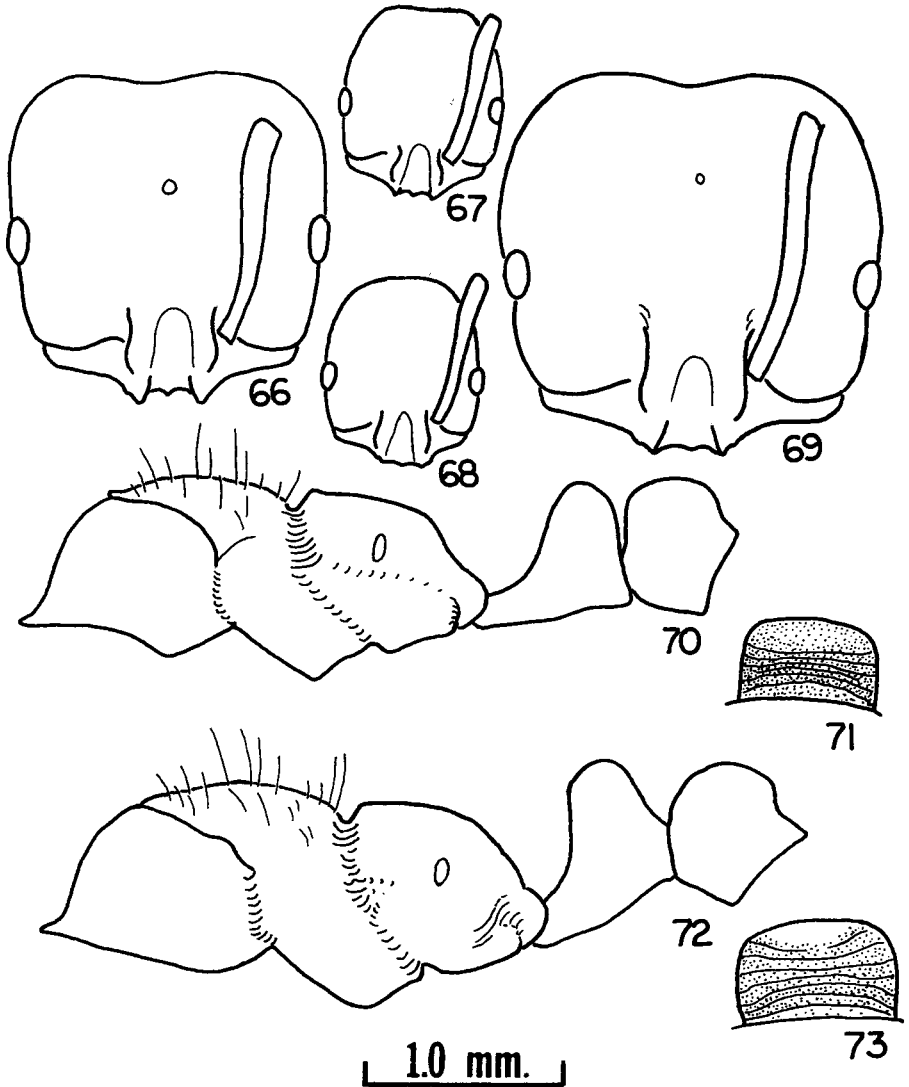
Color reminiscent of that of *S. interrupta*, but usually lacking faint infuscation of head and thorax and of a slightly deeper hue, thus appearing redder in the field, this distinction elusive in pinned specimens. Occasional colonies are darker, closely resembling *S. quinquecupis*.

NOTES. As indicated in the synonymy, this species has been thought by some authors to be the typical *S. interrupta*, or at least part of the normal variation of the latter. *S. macdonaghi* is more eastern in distribution, is redder in color, has mesially obsolete mandibular costulae, usually bears a well developed median ocellus (occasionally even on submajors), has the thoracic dorsum covered with straight reddish pilosity of nearly uniform length on many specimens, and the rear face of the postpetiole is broad and subquadrate and bears dense, punctulate sculpture over all or nearly all of its surface.

Though largely allopatric, *S. interrupta* and *S. macdonaghi* may be found together at least in the vicinity of Cochabamba, Bolivia. Although the Bolivian population often has complete mandibular costulae, the more uniform pilosity length, well-developed ocellus and broader, more sculptured postpetiole of *S. macdonaghi* will distinguish major workers of this population.

The queen of this species may also be recognized by its broad head. The CI of 5 queens measured at random was 101–104, while queens of all other species in the *S. saevissima* complex (including *S. interrupta*) had  $CI \leq 101$ .

DISTRIBUTION. *S. macdonaghi* is characteristic of the vast floodplain of western Uruguay and “mesopotamian” eastern Argentina, and there are a few records from Paraguay. The population at Cochabamba, Bolivia is disjunct and probably introduced.



Figs. 66–69. South American *Solenopsis* heads, full face view. 66–67. *S. quinquecuspis*; major and minor. 68–69. *S. megergates*; minor and major.

Figs. 70–73. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 70–71. *S. quinquecuspis*. 72–73. *S. megergates*.

***Solenopsis megergates*, new species**

Figs. 68, 69, 72, 73

MEASUREMENTS AND INDICES: HL 1.04–1.75, HW 0.90–1.79, SL 0.88–1.30, EL 0.18–0.27 (0.29), PW 0.53–1.10, AL 1.12–2.33, CI 87–106, SI 71–98, OI 14–18. N = 20.

HOLOTYPE MEASUREMENTS: HL 1.69, HW 1.71, SL 1.26, EL 0.26, PW 1.05, AL 2.32, CI 101, SI 74, OI 15.

WORKER DIAGNOSIS. A large, brown species, likely to be confused in appearance only with *S. quinquecupis*, and in size with *S. macdonaghi*, distinguished as follows (compared to *S. quinquecupis*): head broader than long in most large majors (ffv), cordate, with sides convex; posterior border with a concave median impression, the concavity shallower than in *S. quinquecupis*, but about 1.1–1.4× as wide as distance between apices of frontal lobes as in that species; mandibular costulae sometimes obsolescent mesially but most often extend entire length of mandible and broaden mesially; eye (lv) appears and is often, in fact, smaller and less elongate, but with about the same number of somewhat smaller ommatidia, than in *S. quinquecupis*; anterolateral pronotal corners (pdv) rounded to weakly angular, tending toward weakly angular in smaller workers, with anterolateral ridge-like bosses; propodeal profile most often a continuous convexity, with anterior and posterior declivities indistinct, less often the faces distinct and separated by rounded angles as in *S. quinquecupis*; form of petiole and postpetiole as in *S. quinquecupis*.

Piligerous foveolae of head and thoracic dorsum round, conspicuous, about 0.01 mm or more in diameter; sculpture otherwise as in *S. invicta*, i.e., posterior face postpetiole transversely rugose on lower half to  $\frac{3}{4}$ , with weak interrugal punctation, sculpture not usually extending onto dorsum.

Vestiture of the normal sort for the complex; abundant, highly varied in length on head and especially on thoracic dorsum, the longer setae curved.

Weakly bicolored, head, thorax, gaster spot and appendages uniform reddish brown; dorsum of petiole and postpetiole, and remainder of gaster darker brown; median frontal furrow not distinctly colored or at most faintly darker than remainder of frons.

NOTES. *S. megergates* has the largest workers of any fire ant species, hence the name, which is Greek for "large worker." The queens are not especially large, and cannot be readily distinguished from some *S. quinquecupis* or *S. invicta*.

DISTRIBUTION. *S. megergates* is known only from southeastern Brazil, including the states of Paraná, Santa Catarina and Rio Grande do Sul. The type series was collected 4 km N of Curitiba, Paraná, Brazil.

TYPE DEPOSITION. The holotype worker and 20 paratypes will be placed in MZSP. 52 remaining paratypes and numerous other specimens will be divided between AMNH, BMNH, FSCA, LACM, MCZ and MZSP.

### *Solenopsis pythia*

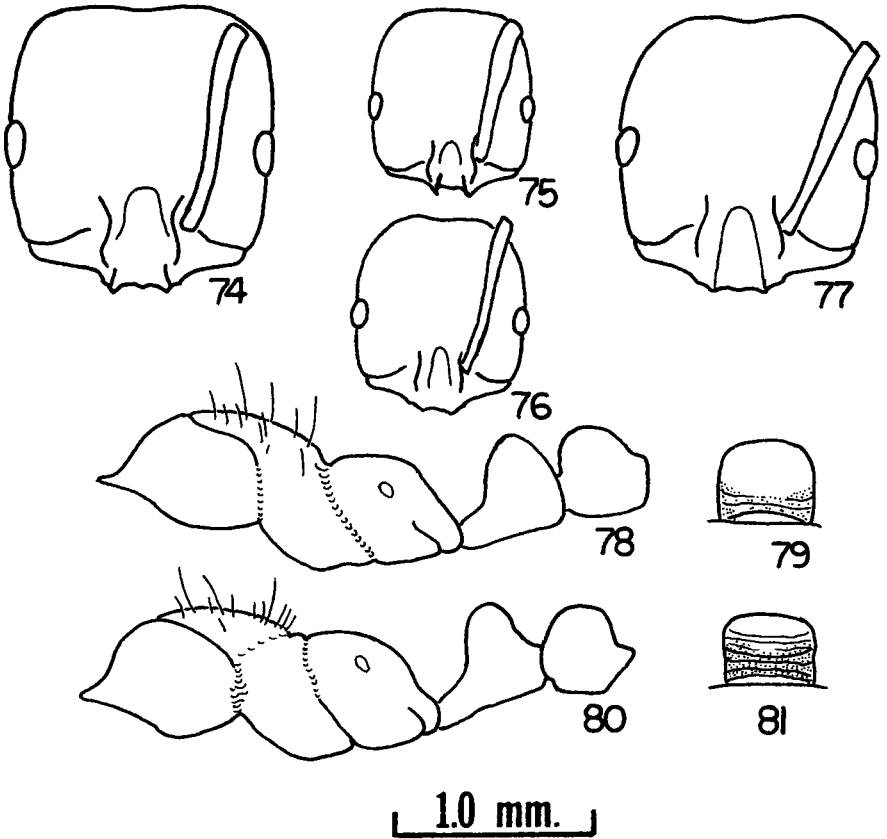
#### Fig. 83

*Solenopsis pythia* Santschi 1934:30. Holotype queen. ARGENTINA. Misiones. Loreto. A. A. Oglobin. (NMB, examined.)

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

MEASUREMENTS AND INDICES: HL 1.00–1.20, HW 0.91–1.14, SL 0.76–0.90, EL 0.17–0.23, PW 0.55–0.65, AL 1.22–1.47, CI 87–96, SI 77–91, OI 16–20. N = 21.

WORKER DIAGNOSIS. A species virtually indistinguishable from media and small major workers of the small, brown variety of *S. saevissima* found in southeastern

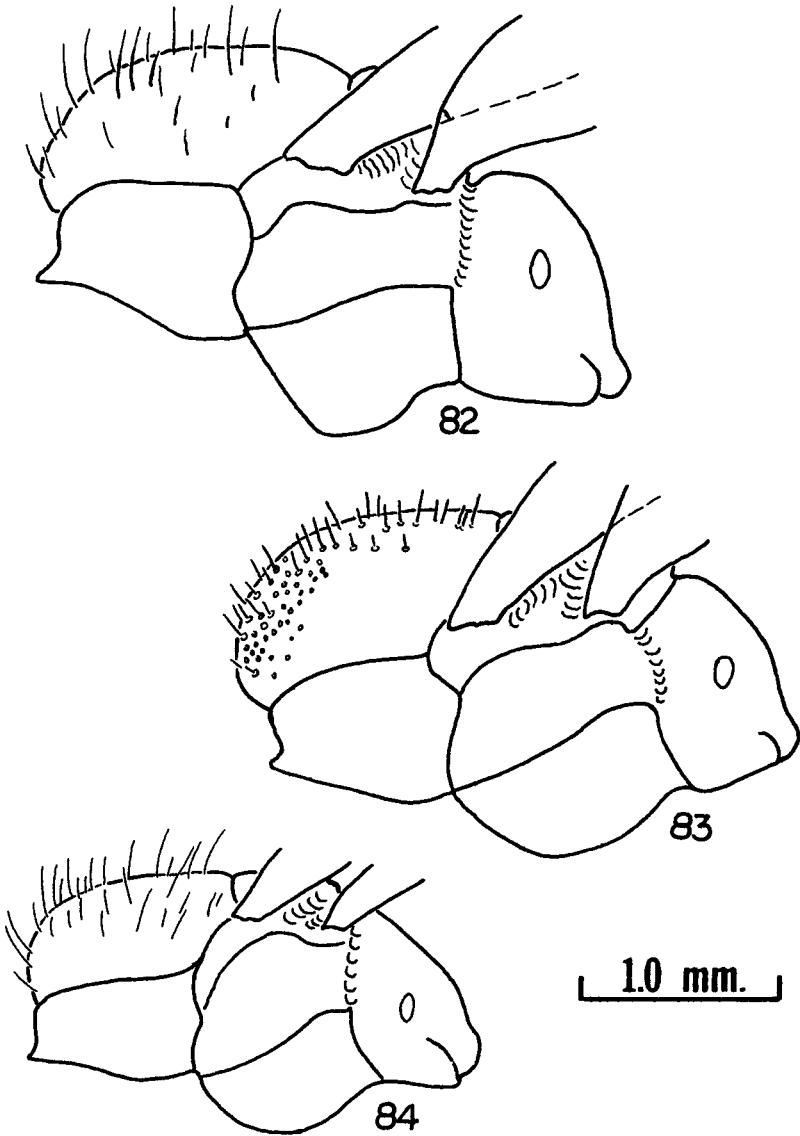


Figs. 74-77. South American *Solenopsis* heads, full face view. 74-75. *S. saevissima*; major and minor. 76-77. *S. weyrauchi*; minor and major.

Figs. 78-81. South American *Solenopsis* trunk profiles and postpetiole rear views of major workers. 78-79. *S. saevissima*. 80-81. *S. weyrauchi*.

Brazil (var. *perfida*), some larger workers have conspicuous piligerous foveolae many of which are 0.01 mm or more in diameter on the head and pronotum (less than 0.01 mm in *S. saevissima*). See queen diagnosis for more certain separatory characters.

**QUEEN DIAGNOSIS.** In color and proportions, resembling a small version of Amazonian *S. saevissima*, but differing conspicuously in pilosity and sculpture: pilosity of entire dorsum relatively uniform in length, 0.15-0.20 mm (many setae over 0.30 mm in all other species), to slightly longer on head, pilosity dense, arising from conspicuous foveolae 0.01-0.15 mm in diameter even on gaster (0.005-0.01 in other species, even smaller on gaster); interfoveolar spaced on much of head (especially frons) and anterior pronotum of most specimens sculptured with fine, weak, confused rugosity (head lacking such sculpture in other species, or at most with faint rugosity on frons); pleura sculptured with longitudinal, slightly irregular striae (pronotum and pleura unsculptured other than piligerous foveolae in other species).



Figs. 82-84. *S. geminata* group queen alitrunk profiles. 82. *S. saevissima*, with "typical" size, sculpture and pilosity. 83. *S. pythia*, with short, bristle-like pilosity and unusually conspicuous piligerous foveolae. 84. *S. pusillignis*, of uniquely small size and slender build.

NOTES. In the original description of *S. pythia*, Santschi stated that the queens have 10-segmented antennae, rather than the usual 11-segmented antennae of fire ant queens. In fact, the queen described by Santschi does have 10-segmented antennae. Of the 6 other specimens I have studied, one has one antenna 10-segmented

and the other 11-segmented, but the remaining 5 specimens have completely unremarkable 11-segmented antennae.

Unassociated workers like those collected with the distinctive queens of *S. pythia* are distinguishable only with great difficulty from *S. saevissima* (especially the variety *perfida*) occurring in the same area. It has occurred to me that the workers collected with *S. pythia* queens may in fact be depauperate workers of *S. saevissima* from colonies parasitized by *S. pythia*, which in its turn may be without a worker caste. Only further study, perhaps including collections of fresh material for biochemical (especially genetic) analysis will resolve this question.

DISTRIBUTION. The types (examined) are from Loreto, Misiones, Argentina. Other specimens studied are from Botucatu, São Paulo, Brazil. The queen with unequal antennae mentioned above has only the number 189 on the label, but has been retained as part of the Buren collection because of her interesting morphology.

*Solenopsis quinquecupis*

Figs. 66, 67, 72, 73

*Solenopsis pylades* var. *quinquecupis* Forel 1913:224. Syntype workers. ARGENTINA. Buenos Aires Prov. Bahia Blanca. 28-X-913 (=1913). Zelenko. (MHNB, examined.)

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

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

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

*S. blumi* Buren 1972:20. Syntype workers. URUGUAY. Colonia Suiza. March 11, 1969. M. S. Blum et al. (WFB, examined.) NEW SYNONYMY.

*S. quinquecupis*: Buren 1972:17. In part. (Also in part *S. invicta*.)

MEASUREMENTS AND INDICES: HL 1.10–1.55, HW 0.98–1.55, SL 0.86–1.14, EL 0.18–0.29, PW 0.59–0.98, AL 1.35–2.12, CI 89–101, SI 71–88, OI 15–20. N = 25.

WORKER DIAGNOSIS. Similar to *S. invicta*, but larger; with head broader, (ffv) cordate, with sides convex; posterior border with a concave median impression, this always deeper than in the nearly similar dark southern *S. invicta*, the concavity about 1.1–1.4× as wide as distance between apices of frontal lobes (narrower than in *S. invicta*); mandibles with the usual curvature; mandibular costulae sometimes obsolete mesially, but most often extend entire length of mandible; eye (lv) appears larger than in other species (especially the somewhat similar *S. megergates*), elliptical or ovate, greatest diameter with 11–14 (rarely less) facets, least diameter with 8–10, outer ring of facets rarely depigmented as is common in some species; distance between tip of scape and occipital corner about 0.08–0.15× scape length in major workers, (ffv) in smallest workers scape apex easily reaches or slightly exceeds posterior border; anterolateral pronotal corners (pdv) rounded to weakly angular, tending toward weakly angular in smaller workers, often with anterolateral bosses; propodeal profile with anterior declivity convex, merging into propodeal dorsum by a rounded angle; propodeal dorsum straight, sloping to the rear, descending through rounded angles to declivous face, never forming a continuous convexity with the declivous face; petiolar peduncle shorter than base of node; postpetiolar node in profile lower

than petiole, globular, sometimes with dorsoposterior face a little more convex than anterior face, outline of postpetiolar node (pdv) subrectangular to subtrapezoidal, with dorsal outline nearly flat to weakly concave, and lateral faces straight or concave, subparallel to convergent ventrad; postpetiole 1.07–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum round, conspicuous, about 0.01 mm or more in diameter (about half or less this in *S. invicta* or, if approaching this size, elliptical in shape, as in darker color variants from southeastern part of range in SE Brazil, Uruguay, Argentina); sculpture otherwise as in *S. invicta* except that of posterior face of petiole and especially postpetiole, which is denser and often extends onto dorsum, especially on transversely rugose-punctate postpetiole.

Pilosity of head and promesonotum abundant, more variable in length than in *S. invicta*, 0.06–0.36 mm; 2–11 erect setae also present on mesopleuron and 1 or 2 on metapleuron, gaster pilosity normal.

Color much less variable than in *S. invicta*, resembling the color of dark *S. invicta*; narrow median frontal impression nearly black, surrounding area dark brown, fading into narrow yellowish surrounding area; clypeus, antennal fossae and sides of head between eye and base of mandible also yellowish; head of less common darker individuals usually concolorous except for dark frontal streak and faintly lighter area near base of mandibles and on clypeus; remainder of head, thorax, propodeum and petiole dark brown, the latter two somewhat lighter ventrally; postpetiole and base of first tergite dusky yellowish to reddish brown; remainder of gaster blackish brown; appendages a little lighter than general color of thorax.

NOTES. The ants that Buren (1972) called *S. quinquecupis* were mostly the dark southern variant of *S. invicta*, but also included were some true *S. quinquecupis* which had the characteristic yellowish gaster spot of the first tergite darker than usual. The type series in the Forel collection contains only dark submajors and smaller workers of the latter sort, but Buren did not see these until 2 years after his 1972 publication, rather basing his concept of *S. quinquecupis* on the description by Creighton (1930). The characters of the mesonotal and propodeal profile presented by Buren for his species *S. blumi* (mesonotum arched, longer than propodeum, the latter with weakly convex dorsal face notably longer than declivous face) are the most common character states in large workers of *S. quinquecupis*, but they are hardly invariant. Furthermore, the variation in shape of these body parts overlaps broadly the typical shape in *S. invicta*, and this is especially true of workers of less than maximum size. In different individuals of a single colony, the entire range of variation may be expressed. Some samples in Buren's collection bear small pencilled labels in Buren's hand "*blumi* or *quinquecupis*?" indicating his own (fully understandable) confusion over the distinction between smaller workers of *S. quinquecupis* and the dark southern *S. invicta*. Metric characters of the largest workers of monogyne colonies may be the only consistent morphological characters for separating in the area where their ranges abut, though genetic and chemical characters seem to provide good separation (Ross and Trager, 1991; Vander Meer, unpubl.).

DISTRIBUTION. The types (examined) of *S. quinquecupis* came from Bahía Blanca, in southern Buenos Aires province, Argentina. This species occurs from the southern tip of Brazil, south through Uruguay into Argentina including all of Buenos Aires province, most of La Pampa province, and the adjacent fringes of Córdoba and Santa Fé provinces.

*Solenopsis richteri*

Figs. 52–55

- Solenopsis pylades* var. *richteri* Forel 1909:267. Syntype workers, queens, male. ARGENTINA. Buenos Aires. Richter. (MHNG, examined.)
- S. pylades* var. *tricuspis* Forel 1912:397. Syntype workers. ARGENTINA. Buenos Aires Prov. La Plata. BRUCH. (MHNG, examined.)
- S. geminata saevissima* var. *richteri*: Wheeler 1915:397.
- S. saevissima* var. *richteri*: Santschi 1916:281.
- S. saevissima* var. *tricuspis*: Santschi 1916:281.
- S. (Solenopsis) saevissima richteri*: Creighton 1930:87; Creighton 1950:232 (In part?).
- S. saevissima* var. *oblongiceps* Santschi 1936:405. Syntype workers. ARGENTINA. Misiones. Loreto. A. A. Oglobin. (NMB, examined.) NEW SYNONYMY.
- S. saevissima richteri*: Wilson 1952:66.
- S. richteri*: Buren 1972:4. Worker, queen, male.

MEASUREMENTS AND INDICES: HL 1.04–1.41, HW 0.87–1.35, SL 0.78–1.13, EL 0.16–0.23, PW 0.55–0.85, AL 1.20–1.84, CI 82–96, SI 77–93, OI 14–17. N = 25.

WORKER DIAGNOSIS. A slender, mostly black species somewhat resembling *S. quinquecupis* or far southern *S. invicta*, but with the following distinctive features: Head (ffv) elliptical (*oblongiceps*) to weakly cordate in largest workers, with sides convex; posterior border with a concave median impression, the concavity deep and about as wide as distance between apices of frontal lobes; median clypeal tooth often shorter and blunter than in *S. quinquecupis* or *S. invicta*, and paracarinal teeth often small or absent (*tricuspis*), but this also true in some specimens of other species; clypeal carinae conspicuous, projecting apically as triangular teeth; mandibles with the usual curvature; in large workers mandibular costulae usually obsolete except distally and near base along outer border; eye (lv) ovate, smaller than in *S. quinquecupis*, often outer ring of facets depigmented, appearing darker than interior facets because of dark background color; anterolateral pronotal corners (pdv) distinctly angular, often with distinct tuberculate or short ridge-like humeral bosses; posterior dorsum usually notably concave mesially (normally convex in all other species); metanotal impression conspicuous; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle, occasionally with a ridge at juncture with dorsal face; propodeal dorsum weakly convex, sloping to rear, forming a continuous convexity with the declivous face, or descending through rounded angles to declivous face; petiolar peduncle notably to slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular, sometimes with dorso-posterior face a little more convex than anterior face, outline of postpetiolar node (pdv) nearly globular to subrectangular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15× as wide as petiole.

Piligerous foveolae of head and thoracic dorsum small, round and inconspicuous, mostly 0.003–0.008 mm in diameter, sculpture otherwise as in *S. invicta*, except postpetiole less sculptured, especially on posterior face, which is transversely rugose on lower third to half, shiny and smooth or faintly tessellate above.

Pilosity as in *S. invicta*.

Color predominantly black with mandibles, lateral lobes of clypeus, antennal fos-



sae, thoracic sutures, tarsi and funiculi, and gaster spot dark brown to yellowish brown; median frontal streak black, but obscured by blackness of surrounding region of many specimens; older preserved material and some fresh specimens paler, with head brown and thorax brown with greater or lesser degree of yellowish mottling.

NOTES. Since I have had the advantage of studying specimens confirmed as hybrids of *S. invicta* and *S. richteri* (through chemical and genetic studies) in order to determine the morphological characteristics of the hybrid, I cannot agree with Buren (1972) that there was little evidence of hybridization among the specimens he studied. In fact, it is clear that much of what he called *S. richteri* was hybrid material, and this from areas along the Gulf Coast from which both *S. richteri* and the hybrid are now completely lacking. It should be noted that specimens of *S. richteri* from some parts of the South American population morphologically resemble hybrids from North America, but other evidence indicates they are not hybrid. "Pure" *S. richteri* from North America is, not surprisingly, less variable morphologically than that from South America.

DISTRIBUTION. The types (examined) were collected in Buenos Aires, Argentina. In the north the limit of the range of *S. richteri* is in southeastern Brazil (Rio Negro, Paraná) and west from there into Misiones province. (Creighton's record from Salta, Argentina, most likely refers to rather dark submajor workers of *S. interrupta*, but I have not seen the specimens he had in mind.) The southern part of the range is delimited by the Atlantic Ocean on the east, and extends west to Mendoza province. In North America, *S. richteri* apparently once occupied much of Alabama and Mississippi, but is now limited to a small portion of northwestern Alabama and northeastern Mississippi. To the south, the current North American range of *S. richteri* is bordered by a broad band of territory occupied by the *S. richteri* × *invicta* hybrid population, encompassing much of northern Alabama and Mississippi and a portion of northwestern Georgia.

*Solenopsis saevissima*

Figs. 74, 75, 78, 79, 82

- Myrmica saevissima* F. Smith 1855:166. (Syn-?) type worker. BRAZIL. Para. Rio Tapajós. Bates. (BMNH, examined.)
- S. moelleri* Forel 1904:174. Syntype workers only. BRAZIL. Santa Catarina. Blumenau. Moeller. (MHNG, examined.) RESTRICTION OF TYPE SERIES. (The male and queen of this taxon are workerless parasites of the *S. daguerrei* group, probably the species known as *S. acuminata*.)
- S. moelleri* var. *gracilior* Forel 1904:174. Syntype workers. BRAZIL. Ceara. Rocha (leg.). #48. (MHNG, examined.) (Synonymy by Ettershank, 1966:136.)
- S. geminata* var. *incrassata* Forel 1908:362. Syntype workers. BRAZIL. São Paulo (state). São Paulo. Ihering. (Synonymy by Ettershank, 1966:136.)
- S. geminata* *pylades* Forel 1909:268. NEW SYNONYMY.  
(But not *S. geminata* *pylades* Forel 1904, described from a single queen from Mexico, which is a synonym of *S. xyloni*.)
- S. pylades*: Forel 1911:279; Forel 1917:723.

- S. geminata saevissima*: Wheeler 1915:397.  
*S. geminata saevissima* var. *incrassata*: Wheeler 1915:397.  
*S. saevissima* var. *incrassata*: Santschi 1916:380.  
*S. saevissima* var. *pylades*: Santschi 1916:380.  
*S. saevissima* var. *morosa* Santschi 1916:380. Worker. (Synonymy by Ettershank, 1966:136.)  
*S. geminata saevissima* var. *picea* Wasmann 1918:212. Worker, NEW SYNONYMY (*picea* not available in any case, as this name is preoccupied for the small Central American *Solenopsis picea* Emery 1896:89.)  
*S. saevissima* var. *perfidata* Santschi 1923:266. Syntype workers. BRAZIL. Minas Gerais. Piracicabo. E. Luja. (NMB, examined.) (Synonymy by Ettershank, 1966:136.)  
*S. (Solenopsis) saevissima saevissima*: Creighton 1930:80–83; Wilson 1952:63.  
*S. saevissima*: Santschi 1916:378–380. Buren 1972:15.  
*S. saevissima* var. *picea*: Kistner 1982:73–74 (Table II). NEW SYNONYMY. (See note on *picea*, above.)

MEASUREMENTS AND INDICES: HL 1.00–1.41, HW 0.85–1.38, SL 0.80–1.13, EL 0.16–0.26, PW 0.55–0.88, AL 1.20–1.83, CI 83–96, SI 76–100, OI 14–18. N = 33.

WORKER DIAGNOSIS. A widely distributed, highly variable species which, like *S. geminata*, could easily be separated into morphological species if only peripheral populations were known. More slender, smaller and more strictly tropical than *S. invicta*, and except in color, most closely resembling *S. richteri*. Distinguished as follows: Head (ffv) weakly trapezoidal (slightly broader anteriorly) or subquadrate to slightly ovate, with sides straight to weakly convex; posterior border with a concave median impression slightly less to a little wider than distance between apices of frontal lobes; median clypeal tooth poorly-developed, broad-based and blunt, often displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth; paracarinial teeth often small or absent, but this also true in some specimens of other species; mandibles with the usual curvature; in large workers mandibular costulae complete or, less often, costulae becoming broader with shallower intercostular furrows on middle, inner portion of upper surface of mandible; eye (lv) ovate, smaller than in *S. quinquecupis*, often outer ring of facets depigmented; anterolateral pronotal corners (pdv) distinctly angular, but lacking distinct humeral bosses, or these merely small tubercles; posterior pronotal dorsum usually notably flat to weakly convex; promesonotal profile more arched than in *S. richteri*; metanotal impression conspicuous; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle, occasionally with a ridge at juncture with dorsal face; propodeal dorsum weakly convex, sloping to rear, forming a continuous convexity with the declivous face, or descending through rounded angles to declivous face; petiolar peduncle notably to slightly shorter than base of node; outline of postpetiolar node (pdv) nearly globular to subrectangular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15 × as wide as petiole.

Piligerous foveolae of head and thoracic dorsum small, round and inconspicuous,

mostly 0.003–0.005 mm in diameter, sculpture otherwise as in *S. invicta*, except postpetiole less sculptured, especially on posterior face, which is transversely rugose on lower third to half, shiny and smooth or faintly tessellate above.

Pilosity as in *S. invicta*.

Color highly variable, the variation partly clinal, with the distribution of color patterns resembling that of *S. invicta*, i.e., predominantly red samples from the north, dark brown samples from the southeast. The following color features may be used in addition to morphology to recognize this species. In western Amazonia (Peru, Rondonia and Acre, Brazil) *S. saevissima* distinguished from sympatric *S. invicta* by lack of median frontal dark streak, and by gaster spot occupying  $\frac{3}{4}$  or more of first tergite. To the south and east, *S. saevissima* specimens are smaller and darker, and most can be distinguished from dark southeastern Brazilian *S. invicta* by the distinctive yellow frons and clypeus (the yellow sometimes extending to include anterior  $\frac{1}{6}$ – $\frac{2}{6}$  of the head) in high contrast to the brown remainder of head, and by the lack of median frontal dark streak on the more or less bright yellow frons.

NOTES. *S. saevissima* as considered in this study, incorporates a great amount of regional variation. When looking only at the type specimens of forms such as *perfida*, *incrassata*, and *saevissima*, one is easily convinced they represent separate species. There is, however, abundant additional material available for study which presents a rather confusing panorama of annectant forms and intracolony variation. From the Brazilian states of Minas Gerais, Goiás and Bahia comes an array of samples including every possible intermediate condition between the typical Amazonian reddish *S. saevissima* and the smaller, darker southern form variously named *incrassata*, *moelleri*, or *morosa*. While these 2 extremes differ in average size and in color, their proportions and morphology are not particularly distinct. The form *perfida* is apparently more distinctive. The types of this taxon were collected in Minas Gerais. They bear little resemblance to typical *S. saevissima*, and in fact, look more like small, dingy *S. invicta*. I include them in *S. saevissima* because many large samples of the latter from the southern end of its range contain at least a few majors with some or all of the features characteristic of *perfida*, namely broader head with rounded sides, somewhat coarser punctures on the head, and lack of distinctly yellower frons and clypeus relative to the rest of the head.

DISTRIBUTION. The types (examined) of *S. saevissima* were collected along the Tapajós river, in the state of Pará, Brazil. The northern, red form is found virtually throughout Amazonia, and in much of this area is the predominant or only fire ant present, but it does not extend much beyond the limit of the Amazon Shield. A dark variant appears sporadically in Amazonia, but begins to predominate at the southeastern edge of the Amazon drainage in the area from Goiás to Bahia. A tongue of territory occupied by the southern form of *S. saevissima* extends south (the ants coming to smaller average size on the way) through São Paulo to southeastern Brazil.

### *Solenopsis weyrauchi*, new species

Figs. 76, 77, 80, 81

MEASUREMENTS AND INDICES: HL 1.02–1.34, HW 0.85–1.18, SL 0.78–1.02, EL 0.14–0.19, PW 0.57–0.75, AL 1.18–1.67, CI 85–92, SI 83–94, OI 13–15. N = 12.

HOLOTYPE MEASUREMENTS: HL 1.34, HW 1.18, SL 0.98, EL 0.19, PW 0.74, AL 1.67, CI 88, SI 83, OI 14.

WORKER DIAGNOSIS. Ecologically unusual within this subcomplex, this species is superficially unremarkable, resembling a slender *S. saevissima*, but distinguished as follows: Head (ffv) elongate, subrectangular, sides straighter than typical for *S. saevissima*; posterior border with a concave median impression somewhat narrower than distance between apices of frontal lobes; median clypeal tooth even more poorly developed than in *S. saevissima*, most often lacking altogether; median clypeal seta conspicuous, arising near apex of median tooth or in middle or clypeal margin, sometimes off-center; clypeal carinae weakly developed, cross section through middle of clypeus a flattened trapezoid without ridges at angles between upper and declivous faces; clypeal carinae developed apically, at margin forming usually very short, acuminate teeth; paracarinal teeth small or absent; mandibles with the usual curvature; in workers of all sizes, mandibular costulae 5–6 (usually 7 or more in other species), costulae becoming broader with shallower intercostular furrows on middle and on upper surface of mandible, obsolescent near base; eye (lv) ovate, smaller than in *S. saevissima*, greatest diameter with 10–11 facets, least diameter with 7–8, often outer ring of facets depigmented; anterolateral pronotal corners (pdv) rounded, never angular, but may bear minute humeral small tubercles; convex; pronotal profile convex, blending insensibly into flatter mesonotal profile; metanotal impression, propodeal profile, and conformation of petiole and postpetiole not appreciably different from those of *S. saevissima*.

Piligerous foveolae of head and thoracic dorsum round, more conspicuous than in *S. saevissima*, mostly 0.005–0.01 mm in diameter, sculpture otherwise as in *S. invicta*, postpetiole more sculptured than *S. saevissima*, especially on posterior face, which is transversely rugose on lower  $\frac{1}{2}$ – $\frac{3}{4}$ , generally smooth with conspicuous piligerous foveolae above.

Pilosity a little more abundant than in *S. saevissima*, mesonotum of large workers with about 30 erect setae, (20–25 in *S. saevissima*).

Color striking, head (at least anterior portion), mesonotum and gaster spot (when present) bright reddish yellow; remainder of gaster blackish brown; propodeum, dorsum of petiole and postpetiole, and sometimes rear portion of head, pronotum and region of frons surrounding median streak yellowish brown with brown spots set off by rather distinct borders from surrounding lighter areas; median frontal streak small, blackish, often formed of 2 elongate dots; gaster spot marked with 2 small anterolateral spots in lighter specimens, or may be reduced to a mere anterior yellowing in darker specimens, which lack a distinct tergal spot.

NOTES. All but one pin of the known specimens of *S. weyrauchi* were collected by the German collector Weyrauch in the early part of this century, hence the name. Weyrauch's specimens were ultimately deposited at the Instituto Miguel Lillo in Tucumán, Argentina, and a few ended up in the USNM and MZSP. It is possible he took duplicate material back to Germany, but I have been unable to locate it.

The queen of this species is not morphologically distinguishable from those of most other *saevissima* subcomplex species, especially *S. invicta* and *S. saevissima*. *S. weyrauchi* queens do, however, share the striking bright yellow ground color and dark brown markings of the worker, including, in all 3 specimens observed, the 2 anterolateral dark spots within the yellow gaster spot on the first tergite.

This species is unusual in that it is apparently restricted to the high altitude grasslands of the Peruvian Andes. According to altitude data on the collection labels, the specimens were collected at altitudes from a moderately surprising 2,500 m to a barely credible 4,300 m.

**DISTRIBUTION.** The types are labelled "Abra Gavilán b. Cajamarca, 2,800 m. PERU. #709. ex. col. Weyrauch." *S. weyrauchi* is known from only a few widely separated localities in the Peruvian Andes. Further collecting may well reveal its occurrence in Andean localities from Colombia to Argentina and Chile.

**TYPE DEPOSITION.** The holotype is the largest of 6 workers mounted on 3 points on a single pin to be deposited at LACM. The remaining 23 paratypes (same collection data) and the other specimens borrowed from IML will be returned there, except for 2 pins bearing a total of 9 specimens which will be sent to LACM and MCZ.

*ELECTRA* SUBCOMPLEX

*Solenopsis electra*, **New Status**

Figs. 38, 39, 42, 43

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

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

*S. saevissima electra*: Santschi 1916:381.

*S. saevissima saevissima* cline *S. saevissima richteri* (Bolivia variant) Wilson 1952:65. (Specimens identified by Wilson in MCZ examined.) **NEW SYNONYMY.**

*S. saevissima saevissima* cline *S. saevissima richteri* subsp. *electra* Wilson 1952:65. (Specimens identified by Wilson in MCZ examined.)

**MEASUREMENTS AND INDICES:** HL 1.05–1.35 (1.40–1.55), HW 0.90–1.23 (1.33–1.48), SL 0.90–1.00 (1.08–1.13), EL 0.19–0.24 (0.25–0.26), PW 0.55–0.68 (0.75–0.85), AL 1.28–1.53 (1.70–1.98), CI 86–95 (91–99), SI 74–100, OI 16–19. N = 23. Values in ( ) are for robust specimens from large colonies from the vicinity of Cochabamba, Bolivia.

**WORKER DIAGNOSIS.** Head (ffv) subovate, with sides convex; posterior border with a concave median impression, concavity shallow and about 1–1.5× or more as wide as distance between apices of frontal lobes; median clypeal tooth well-developed, usually sharp, 0.5–1× as long as lateral teeth, sometimes displaced off center; on some specimens, a smaller second, off-center intercarinal tooth occurs, rarely this and median tooth nearly equal in size; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as acuminate, triangular teeth, or curved mesad and faintly falcate; space between clypeal carinae concave, except near base of median tooth (teeth); mandibles with the usual curvature; mandibular costulae mostly complete, broader and flatter in inner, mesial portion of upper mandibular surface; eye (lv) ovate, greatest diameter with 11–13 (rarely less) facets, least diameter with 8–9, often outer ring of facets depigmented, especially anteriorly; anterolateral pronotal corners (pdv) rounded, lacking protruding angles; this species unique in that in workers of all sizes, pronotal profile a continuous nearly flat to weakly convex surface, rarely with even the least hint of more vertical anterior declivity and more horizontally oriented dorsal surface as found in all other

fire ants; anteroventral border of mesopleuron with a seam-like flange and often a lobate anteroventral projection on lower  $\frac{1}{3}$ – $\frac{1}{2}$ , (unlike projection of *S. geminata*, which is most often placed near middle of mesopleural border; propodeal profile with anterior declivity convex, set off from propodeal dorsum by a rounded angle; propodeal dorsum flat or weakly convex, descending through rounded angles to declivous face, or rarely forming a continuous convexity with the declivous face, latter 2 faces at approximately a right angle; petiolar peduncle slightly shorter than base of node; postpetiolar node in profile lower than petiole, globular; outline of postpetiolar node (pdv) subglobular, with dorsal outline convex, and lateral faces straight, parallel to convergent ventrad; postpetiole 1.04–1.15 $\times$  as wide as petiole.

Piligerous foveolae of head and thoracic dorsum typically small, round and inconspicuous, mostly 0.003–0.005 mm in diameter; sculpture of mesometapleuron (lv) consisting of fine longitudinal rugose striae, often with interstitial punctation or areolation, striation obsolete above leaving only faint punctation; dorsum of propodeum unsculptured; area surrounding propodeal spiracle unsculptured anterodorsally, but behind spiracle, weak irregular punctation often partially obscures sheen of circumspiracular area (though less so than in *S. pusillignis*, where this area is heavily punctate and dull); declivous face of propodeum with transverse striae contiguous with those of metapleuron; petiolar peduncle, and sometimes base of node, weakly areolate; venter of petiole with longitudinal median carina and ventral process obsolete, consisting of a small truncate projection; petiolar node largely unsculptured except piligerous foveolae, and perhaps a few shallow longitudinal furrows; dorsum of postpetiole unsculptured other than piligerous foveolae; posterior face of postpetiole mostly shiny near top, transversely rugose-striate on lower  $\frac{2}{3}$ , with interspersed punctation below.

Pilosity of head and promesonotum moderately abundant to abundant, like that of *S. invicta*.

Color variable, though generally fairly consistent within a colony; most often bicolored with head (except posterior border and a triangular area the apex of which is at the position of the median ocellus, the latter rarely present), legs and antennae reddish yellow; mandibles brown; thorax and gaster darker brown with yellowish areas near sutures and anterior portion of first tergite; less often darker, ranging from dark brown with anterior portion of head, scapes and legs dingy yellow, to uniform brownish black with only frons and legs slightly lighter. The darker forms are more common in Bolivia, the lighter ones to the south.

NOTES. Since *S. electra* is normally bicolored and lives in poorly marked nests in well-drained soil, this species is somewhat reminiscent of a polymorphic *S. substituta*. It has been collected in desert and chaco areas in the lowlands, and occurs in rocky, exposed sites in the Andean foothills.

In the Bolivian part of its range this species is considerably more robust than in Argentina and Paraguay (see measurements and indices). If we knew this ant only from the south, it would be safe to characterize it as a small fire ant, but the major workers of the large northern variant of *S. electra* fall well within the size range of, say, *S. interrupta*, a mid- to large-sized fire ant. As in the related species *S. pusillignis* (see discussion of that species), even where it develops the larger major workers *S. electra* has its characteristic small queens and males.

DISTRIBUTION. *S. electra* was described from Salta, Jujuy, Argentina, approx-

imately in the middle of its range. Specimens I have seen come from Cochabamba and Santa Cruz, Bolivia south to Santiago del Estero province, Argentina. Creighton lists a credible locality in Córdoba, while a sample I examined from Asunción, Paraguay seems to be far east of the normal range, may represent an introduction from the west.

***Solenopsis pusillignis*, new species**

Figs. 40, 41, 44, 45, 84

MEASUREMENTS AND INDICES: HL 1.03–1.33 (1.50–1.60), HW 0.88–1.24 (1.43–1.54), SL 0.80–0.98 (1.00–1.05), EL 0.21–0.26 (0.28–0.29), PW 0.53–0.69 (0.78–0.83), AL 1.20–1.55 (1.63–1.80), CI 85–94 (95–98), SI 77–91 (68–70), OI 18–22. N = 21. Values in ( ) are for 5 large, robust specimens from 2 colonies from the vicinity of Corumbá, Mato Grosso do Sul, Brazil. See discussion.

HOLOTYPE MEASUREMENTS: HL 1.25, HW 1.18, SL 0.98, EL 0.25, PW 0.63, AL 1.45, CI 94, SI 83, OI 20.

WORKER DIAGNOSIS. The smallest fire ant, superficially resembling North American *S. aurea*, but differing as follows: Head (ffv) subovate with shallow median posterior concavity as in *S. electra*, the concavity usually about as wide as distance between apices of frontal lobes; median clypeal tooth always present, usually sharp and  $0.5\times$  (or a little less) as long as lateral teeth, rarely displaced off center; median clypeal seta conspicuous, arising at or near apex of median tooth; clypeal carinae conspicuous, projecting apically as triangular teeth; space between clypeal carinae concave, except near base of median tooth; mandibles with the usual curvature; mandibular costulae complete, configured as in *S. electra*; remainder of head structurally as in *S. electra*; anterolateral pronotal corners (pdv) rounded-angular, with faint ridge-like humeral bosses; propodeal profile like that of *S. electra*, but with dorsal face more often sloping posteriad; remainder of body like a small *S. electra*, except petiolar and postpetiolar node profiles a little thicker.

Piligerous foveolae of head and thoracic dorsum typically small, a little more conspicuous than in *S. electra*, mostly 0.005–0.008 mm in diameter, but occasionally up to 0.01 mm; sculpture of mesometapleuron (lv) unusually well developed, especially for a fire ant of this small size, consisting of fine longitudinal striae or rugose striae, interstitial punctation strongly developed and extending beyond limits of striation dorsad; punctation nearly surrounding and contiguous with propodeal sculpture except for a small shiny area anterior to spiracle; declivous face of propodeum with transverse striae contiguous with those of metapleuron, and with well developed interstitial punctation; petiolar peduncle, and sometimes base of node, weakly areolate; remainder of sculpture as in *S. electra*.

Pilosity as in *S. electra*, of the *S. invicta* type.

Color like that of *S. aurea*, light brownish yellow with brown extremities, to more uniform yellowish brown.

NOTES. The name *pusillignis*, referring to the small size and relatively mild sting, means "little fire."

*S. pusillignis* is known only from the 2 localities mentioned below. Colonies from Corumbá produce workers significantly larger than those in the Cuiabá area, but the sexuals are about the same size. These queens are the smallest of any cis-Andean

fire ant, about the same size as those of *S. gayi*, or of the non-fire ant, *S. wasmanni*. *S. pusillignis* seems truly to be a "cerrado ant," the only fire ant that lives in relatively undisturbed cerrado. It may also be found in disturbed cerrado, but is often displaced by *S. invicta* (or *Paratrechina fulva* in some areas) in cerrados subject to heavy grazing. The preferred habitat seems to be at or near the edges of grassy temporary ponds (campo limpo), but it is also found in better drained sites.

**DISTRIBUTION.** The types were collected in a cerrado remnant (now largely destroyed) on the Federal University campus in Cuiabá, Mato Grosso, Brazil. *S. pusillignis* is so far known only from the vicinity of Cuiabá, Mato Grosso and Corumbá, Mato Grosso do Sul, Brazil.

**TYPE DEPOSITION.** The holotype worker and 5 paratypes (including 2 queens) will be placed in MZSP. Fifteen remaining paratypes and numerous other specimens will be divided between AMNH, BMNH, FSCA, LACM, MCZ and MZSP.

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