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Distribution and biological notes of *Strumigenys margaritae* (Hymenoptera: Formicidae: Dacetini)

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Summary
Strumigenys margaritae Forel, 1893 (Tribe Dacetini) is a tiny predatory ant native to the New World. It is known from northern South America, Central America, Mexico, the West Indies, and the southeastern US from Texas to Florida. To evaluate the geographic range of *S. margaritae*, we compiled and mapped specimen records from >200 sites. We found *S. margaritae* records for 38 geographic areas (countries, island groups, major islands, and US states), including several locales for which we found no previously published records: Anguilla, Barbados, Barbuda, British Virgin Islands, Dutch Caribbean, Grenada, Honduras, Nevis, Nicaragua, St Kitts, St Lucia, St Martin, Tobago, US Virgin Islands, and Venezuela.

Keywords
Dacetine ants; biogeography; exotic species; non-native species

Introduction

Dacetines (Tribe Dacetini) are predatory ants that generally feed on tiny soil arthropods (Wilson, 1953). Most dacetines are small, cryptically colored, rarely forage openly above ground, are slow moving, and become motionless when disturbed. A few species are arboreal and likewise cryptic in their behavior (Chen et al., 2012). As a result, most people, including field biologists, remain unaware of their presence even in areas where they are common.

Deyrup and Cover (2009) listed nine species of non-native *Strumigenys* that have spread to the southeastern US through human commerce, four Old World (*S. membranifera* Emery, 1869, *S. rogeri* Emery, 1890, *S. emmae* (Emery, 1890), and *S. hexamera* (Brown, 1958)) and five New World species (*S. eggersi* Emery, 1890, *S. gundlachi* (Roger, 1863), *S. lanuginosa* Wheeler, 1905, *Strumigenys silvestrii* Emery, 1906 and *S. margaritae* Forel, 1893). MacGown and Hill (2010) described *Strumigenys subnuda* (as *Pyramica*

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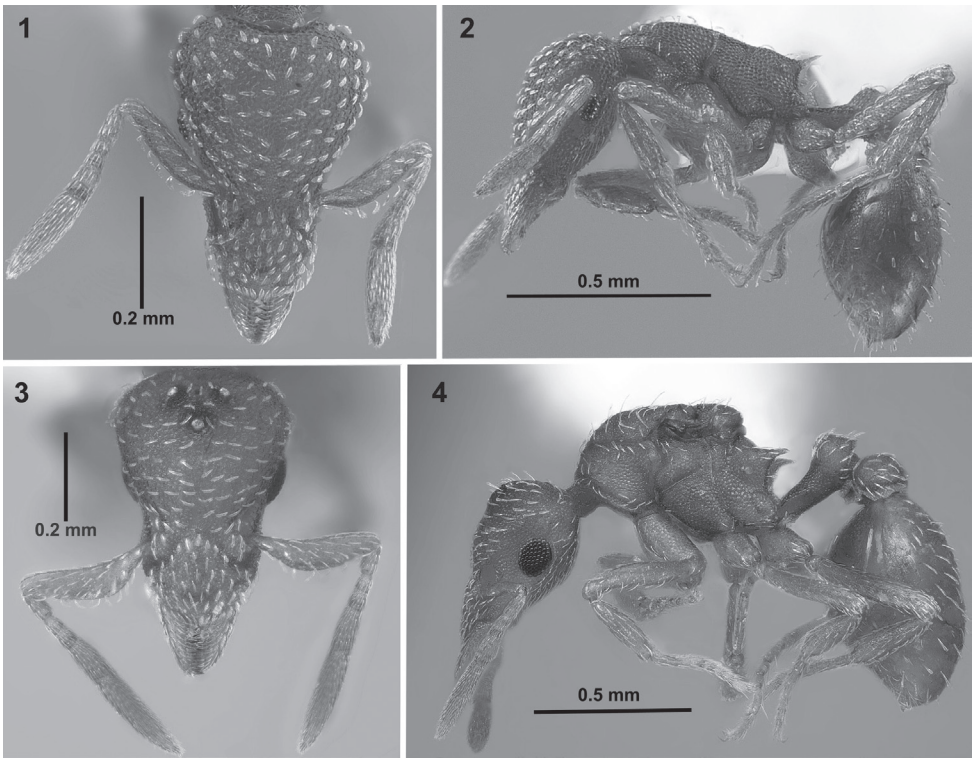
subnuda) as a new species in the *schulzi* group from specimens collected in Mississippi. They proposed *S. subnuda* was most likely an exotic species in North America and native to the New World tropics where it has yet to be discovered. Chen et al. (2012) recently reported another exotic New World species in the same group, *S. epinotalis* Weber, 1934, from Louisiana and Florida. Three of the Old World species have achieved broad distributions in both the Old World and the New World: *Strumigenys membranifera*, *S. rogeri*, and *S. emmae* (Wetterer, 2011, 2012a, 2012b). The fourth, *S. hexamera* originally from East Asia, has begun to spread in the southeastern US, with records from Alabama, Florida, Louisiana, and Mississippi (MacGown and Wetterer, 2012). Three of the five new world species (*S. eggersi* Emery, *S. gundlachi,* and *S. lanuginosa*) reported by Deyrup and Cover (2009) are known to occur in the US only in Florida. *Strumigenys silvestrii* has become much more widespread and is found throughout much of the Southeast, and has been reported from Texas and California (MacGown et al., 2012). The remaining New World species, *S. margaritae,* is also well established in the southeastern US. Here we compiled and mapped specimen records for *S. margaritae* to evaluate the extent of its range.

Taxonomy and identification

Forel (1893) described *Strumigenys margaritae* from three sites on the West Indian island of St. Vincent. Bolton (1999) transferred *S. margaritae* to *Pyramica*. Baroni Urbani and De Andrade (2007) later synonymized *Pyramica* with *Strumigenys*.

Strumigenys margaritae (Figs 1-4) can be differentiated from other US dacetine species by the following combination of features: relatively short triangular mandibles with teeth along entire inner borders; presence of reticulate-punctate sculpture on the entire side of the mesosoma; elongate, acute tipped propodeal spines directed posteriorly and slightly upward; lack of spongiform tissue beneath the petiole and base of gaster; and first gastral tergite with rough, grainy, shagreened sculpture. Two similar species in the same species group (*schulzi* group), *S. epinotalis* and *S. subnuda,* were recently reported from the US (Chen et al., 2012, MacGown and Hill, 2010). *Strumigenys epinotalis* is the only other US species with short mandibles that has dense reticulate-punctate sculpture on the entire head and body. It differs from *S. margaritae* by having a curved row of spoon-shaped hairs present on the pronotal dorsum; a distinct, wide, convexly curved propodeal lamella; a ventral spongiform crest on the petiole; fan-shaped patches of spongiform tissue on the petiole and postpetiole; and shorter propodeal spines that are directed upward. *Strumigenys subnuda,* only known from queens, differs by having sparser, less erect, and narrower setation; sculpture lacking on mesopleuron and dorsum of petiole and being shiny in appearance; dentiform propodeal spines; and weakly roughened, somewhat shiny first gastral tergite. *Strumigenys inopina* is the only other US species with short mandibles that lacks spongiform tissue beneath the petiole. This species is easily separated from *S. margaritae* by its more narrowly triangular shaped head (in frontal view); the entire side of the mesosoma being shiny; presence of dense, elongate setae on the entire body; and the complete lack of spongiform tissue or lamella-like structures on the waist and gaster.



Figures 1-4. *Strumigenys margaritae.* (1) Head of a worker, (2) lateral view of worker, (3) head of female, and (4) lateral view of dealate female. These figures are published in color in the online version.

Materials and methods

Using published and unpublished records, we documented the known range of *S. margaritae.* We obtained unpublished site records from museum specimens in the collections of Archbold Biological Station (ABS, identified by M. Deyrup), the Museum of Comparative Zoology (MCZ, identified by S. Cover), University of Georgia Collection (UGC, identified by D. Booher and corroborated by J. MacGown), the Louisiana State Arthropod Museum (LSAM, identified by J. MacGown), the Mississippi Entomological Museum (MEM, identified by J. MacGown), and the Smithsonian Institution (USNM, identified by B. Bolton). In addition, we used on-line databases with collection information on specimens by Antweb (www.antweb .org).

We obtained geo-coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, www.tageo.com, and www.fallingrain.com). If a site record listed a geographic region rather than a "point locale," and we had no other record for this region, we used the coordinates of the largest town within the region or, in the case of small islands and natural areas, the center of the region.

Results and discussion

A summary of the compiled data from >200 sites is presented in Fig. 5 (map of the global distribution of *S. margaritae*) and Tables 1-3. We documented the earliest known *S. margaritae* records for 38 geographic areas (countries, island groups, major islands, and US states), including several areas for which we found no previously published records: Anguilla, Barbados, Barbuda, British Virgin Islands, Dutch Caribbean, Grenada, Honduras, Nevis, Nicaragua, St. Kitts, St. Lucia, St Martin, Tobago, US Virgin Islands, and Venezuela.

Kempf (1972) listed *S. margaritae* from the Guianas, but this would appear to refer to the one record from Suriname (Kempf, 1961). Sosa-Calvo et al. (2010) did not record *S. margaritae* in Guyana.

Longino (2012) listed the range of *S. margaritae* as "Southern U.S. to Guianas." It is unclear whether continental populations of *S. margaritae* are continuous through this range. There are significant gaps in its known distribution, e.g., no records from South Texas, or Guyana. These gaps may be due to inadequate sampling and more specifically the use of sampling techniques that fail to capture this small, cryptic, and sometimes rare species. Typical methods for collecting dacetine ants utilizing litter and soil extraction techniques may not be ideal for collection of this species in some habitats because *Strumigenys margaritae,* similar to many members of the *schulzi* species

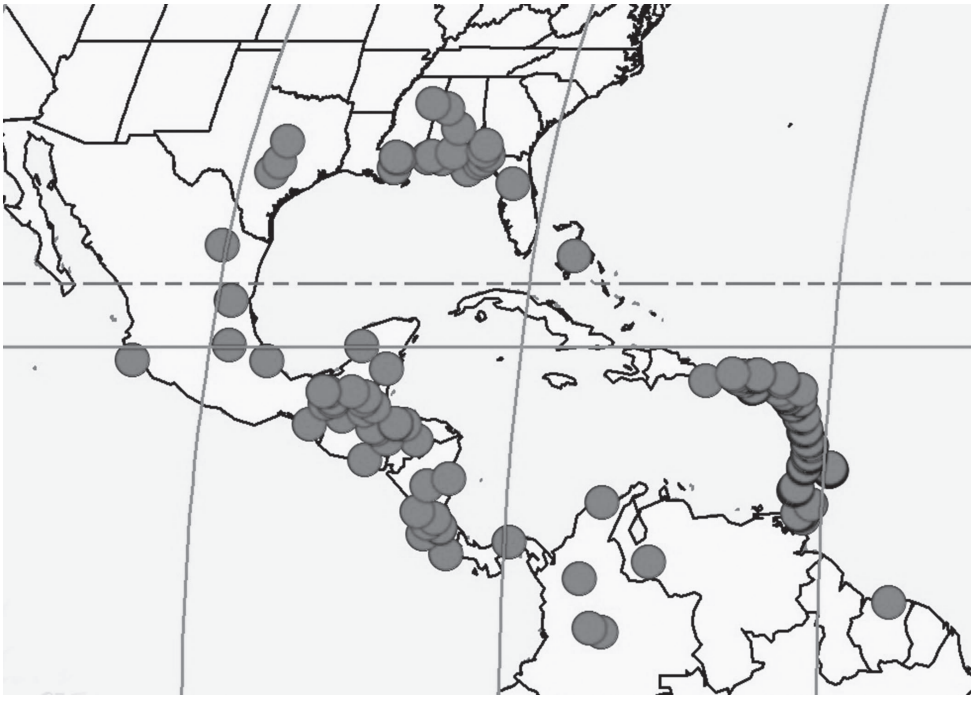


Figure 5. Map showing the worldwide distribution of *Strumigenys margaritae*. This figure is published in color in the online version.

Table 1. Earliest known records of *Strumigenys margaritae* from South and Central America. The "+" symbol indicates new records for that region.

Region	Earliest record
Colombia	1938 (N.A. Weber, MCZ): Rio Porce
Mexico	1949 (C.J. Goodnight, MCZ): Palenque Ruins
Suriname	1959 (Kempf, 1961)
El Salvador	1963 (Bolton 2000)
Panama	1979 (W.L. Brown, MCZ): 14 km W Panama City
Costa RicaVenezuela	1980 (J.T. Longino, MCZ): Sirena1983 (P.S. Ward, antweb)
Belize	1996 (Bolton 2000)
Guatemala	1999 (Bestelmeyer et al. 2000)
+ Honduras	2009 (J.T. Longino, antweb): 14km WSW Catacamas
+ Nicaragua	2011 (J.T. Longino, antweb): 2.5km NE Santo Domingo

Table 2. Earliest known records of *Strumigenys margaritae* from the West Indies. The "+" symbol indicates new records for that region.

Region	Earliest record
St Vincent	≤ 1893 (Forel, 1893)
Bahamas	1917-1918 (Mann, 1920)
Montserrat	1934 (N.A. Weber, MCZ): site unknown
Puerto Rico	1951 (Bolton 2000)
Antigua	≤ 1949 (N.A. Weber, MCZ): site unknown
Martinique	≤ 1972 (Kempf, 1972)
Dominica	1976 (N.L.H. Krauss, SI): Roseau
Guadeloupe	1989 (J.P.E.C. Darlington, MCZ): Bouillante
Trinidad	1994 (L.R. Davis et al., MCZ): Mt. St. Benedict
+ Barbados	1998 (E.O. Wilson and S.P. Cover, MCZ): Casuarina Beach Club
+ Grenada	2003 (J.K. Wetterer, MCZ): Annandale Waterfall
+ Tobago	2003 (J.K. Wetterer, MCZ): Mason Hall
+ St Lucia	2003 (J.K. Wetterer, MCZ): Mount Parasol
+ British Virgin Is.	2005 (J.K. Wetterer, MCZ): Smuggler's Cove, Tortola
+ US Virgin Islands	2005 (J.K. Wetterer, MCZ): West end Creque Dam Road, St Croix
+ Anguilla	2006 (J.K. Wetterer, MCZ): Katouche Valley
+ St Martin	2006 (J.K. Wetterer, MCZ): road to Mt Fortune
+ St Kitts	2007 (J.K. Wetterer, MCZ): Rawlins
+ Barbuda	2007 (J.K. Wetterer, MCZ): Codrington
+ Nevis	2007 (J.K. Wetterer, MCZ): Hog Valley Estate
+ Dutch Caribbean	2008 (G.D. Alpert, MCZ): Old Booby Hill, Saba

group, may be semi-arboreal to arboreal. Longino (2012) wrote that he never collected this species by sifting litter in Costa Rica, and only rarely collected it on shoots of plants or in sweep net samples. The large compound eyes of this species (and others in this group), attest to its above ground foraging tendencies, as compared to the minute eyes of its hypogeic and epigeic relatives.

Table 3. Earliest known records of *Strumigenys margaritae* from the US.

Region	Earliest record
Texas	1901 (W.M. Wheeler, MCZ): New Braunfels
Alabama	1947 (E.O. Wilson, MCZ): Deer River
Georgia	1953 (Brown, 1964)
Louisiana	1996 (D. Colby, LSAM): Lake Ramsey Savannah WMA
Florida	1983 (Deyrup et al., 1989)
Mississippi	2009 (MacGown and Hill 2010)

The first records of *S. margaritae* from many of the West Indies presented here also indicate that *S. margaritae* occurs on most major islands of the Lesser Antilles, as well as Puerto Rico.

In the southern part of its range, *Strumigenys margaritae* has been collected most commonly in lowland wet forests, tropical moist forests, mesophil forests, lowland rainforests, tropical rainforests, and montane rainforests (AntWeb data); whereas in the US, it has been most often collected in drier, more open areas such as prairie remnants, pine savannas, scrub, and open disturbed sites (JAM). It has been collected most often from litter samples using Winkler sacks and Berlese funnel extractions, but also by beating or sweeping vegetation, baiting, visual searches, in flight interception traps, and in malaise traps (AntWeb data). On semi-arid Anguilla and St Martin, JKW found *S. margaritae* only in one area of each island: the sole remnants of intact closed-canopy forest (two sites in Katouche Valley and two sites on the south flank of Mt. Fortune, respectively). Longino (2012) reported that Costa Rican specimens were found in open, disturbed habitats in Pacific lowlands and Meseta Central. Longino (2012) also observed this species visiting extrafloral nectaries of *Passiflora pittieri* Mast. (Passifloraceae). Specimens from Alabama and Mississippi were collected in Black Belt Prairie remnants by sweeping native vegetation or sifting dead native grasses (JAM). Numerous specimens were collected from southern Louisiana from pitfall traps located in longleaf pine savanna habitat with open grassy understories (JAM). This species has been collected in deep pine and oak litter in waterway scrub in Florida (AntWeb data). Unlike some of its *schulzi* group relatives that may actually nest in trees (i.e., *S. epinotalis*, Chen et al., 2012), *S. margaritae* appears to prefer lower vegetation (Longino, 2012), and although specimens may be collected while foraging in litter, perhaps sweep samples would yield more specimens.

Various morphological features of *S. margaritae* and other members of the schulzi group, including the lack of antennal scrobes, greatly reduced spongiform tissue, and enlarged eyes may be related to the arboreal habitat where they are found. For those species living beneath ground in small, tight tunnels and cavities, the ability to fold the antennae into recesses in the head could be a useful function, but unnecessary for arboreal species. The function of spongiform tissue in dacetines is as yet unclear, but based on the fact that most arboreal species lack or only have reduced spongiform tissue, it seems likely this extracuticular tissue serves some purpose not needed above ground. Large compound eyes would be an obvious advantage to the more arboreal

S. margaritae as compared to the minute eyes of its subterranean relatives. Deyrup and Cover (1998) proposed that some of these features may have evolved "based on some degree of dependence on other species, especially for defense." In Trinidad, Deyrup and Cover (1998) observed workers of *S. margaritae* intermingled in foraging columns of *Wasmannia auropunctata* (Roger, 1863), an often dominant Neotropical species, on three consecutive days. Mixed foraging columns also were observed on a return trip to the same site two years later (Deyrup and Cover, 1998). Wetterer (JKW) found *Strumigenys margaritae* on Anguilla and St Martin in the same forests where he found *W. auropunctata.* In many parts of both these forests, *W. auropunctata* attained very high densities. Similarly, on part of the southern waterfront of Capesterre Belle Eau, Guadeloupe overrun with *W. auropunctata*, the only other ant species collected was *S. margaritae*. A perhaps similar coexistence has been noted for *W. auropunctata* and *Cyphomyrmex* species (Grangier et al., 2007). As they noted, "This tolerance is surprising given the usually high interspecific aggressiveness of *W. auropunctata* when dominant." Perhaps some degree of protection is offered by being in the presence of the aggressive *W. auropunctata* that allows *S. margaritae* to forage openly. Further work is needed to evaluate the relationship between *S. margaritae* and *W. auropunctata*. The ecology of *S. margaritae*, as well as that of all other dacetine ants, remains largely unstudied.

Despite it's being described from the Antilles (Forel, 1893) and its having a nearly continuous distribution from northern South America through the US Gulf Coast and the Caribbean region, *S. margaritae* has been considered to be of Neotropical origin. (Deyrup and Cover, 2009, Deyrup et al., 2000). At the time of Deyrup and Cover's most recent publication that mentioned the status of this species as non-native (Deyrup and Cover, 2009), *S. margaritae* was the only member of the *schulzi* species group reported north of Mexico (Bolton, 2000). Several other factors also suggest that *S. margaritae* is non-native in the US and Caribbean. A widespread distribution does not necessarily indicate that a species is native to the entire region where it is found. Other exotic ant species, such as the red imported fire ant *Solenopsis invicta* Buren, have extensive distributions in their non-native range (Peterson and Nakazawa, 2008). The fact that *S. margaritae* has been collected on numerous Caribbean islands may simply attest to its effective dispersal abilities. Alate females of this species often have been collected in flight interception traps. McGlynn (1999) noted that the workers of monomorphic non-native species, including *S. margaritae,* were smaller on average than their native congeners. McGlynn (1999) had several theories to explain this phenomenon such as: smaller ants belong to larger colonies, which give them a competitive edge in interspecific combat; non-native species may not need to be as large in size in non-native regions due to a reduction of interspecific competition; or non-native species may be smaller as a result of the unicoloniality. Collections of *S. margaritae* from the US, Caribbean and some other localities tend to be from open, disturbed habitats; whereas, many collections from the southern portions of its range are from natural wooded habitats. This trend of non-native ant species thriving in disturbed habitats is not unusual and is often an indication that species is exotic to an area (Buczkowski, 2010). However, the "nearly" continuous distribution of this species

from northern South America through southeastern US opens the possibility that *S. margaritae* could be native to the Southeast and Caribbean regions. Longino (2012) reported collecting specimens of this species from its "native" range in Costa Rica in open, disturbed habitats similar to US habitats where it has been collected. This either implies that it is non-native to Costa Rica, or it could indicate that it is more general in its ecological and habitat requirements and can live in a variety of habitat types. Recent reports of two additional species in the *schulzi* species group from the southeastern US, *S. epinotalis* and *S. subnuda,* the former of which has been collected in natural wetland ecosystems throughout its range (Chen et al., 2012) and the latter of which has only been reported from the US (Louisiana and Mississippi) (MacGown and Hill, 2010), make us question our distributional concept of this species group previously only thought to be Neotropical. Tracking the earliest known records of this species from all regions is not helpful in determining the origins of this species either, as the earliest collection dates are from the type locality in St. Vincent (1893), Texas (1901), and the Bahamas (1917) (Tables 1-3). First reports from the Neotropics, where it is thought to be native, were much later, although this is likely a result of inadequate sampling in that region during earlier times. At this time, we cannot say with certainty whether *S. margaritae* is alien or native in regions north of Mexico. Future genetic analyses could help delimit the native and exotic ranges of this species.

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