

## Worldwide spread of the membraniferous dacetine ant, *Strumigenys membranifera* (Hymenoptera: Formicidae)

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### Abstract

*Strumigenys membranifera* EMERY, 1869 (tribe Dacetini) is a tiny predatory ant that has spread around the world through human commerce. To examine the worldwide distribution of *S. membranifera*, I compiled specimen records from > 300 sites. I documented the earliest known *S. membranifera* records for 74 geographic areas (countries, island groups, major Caribbean islands, and US states), including many areas for which I found no previously published records: Arizona, Arkansas, Barbados, Barbuda, Bonaire, British Virgin Islands, Comoro Islands, Dominica, Dominican Republic, Haiti, Îles Éparses, India, Madagascar, Montserrat, Nevis, St Kitts, St Lucia, St Martin, Tobago, Trinidad, and Turks & Caicos Islands.

*Strumigenys membranifera* is one of three Old World dacetine ants, along with *Strumigenys rogeri* EMERY, 1890 and *Strumigenys emmae* (EMERY, 1890), with widespread records in both the Old World and the New World. Whereas *S. rogeri* and *S. emmae* are almost exclusively tropical, *S. membranifera* has spread to higher latitudes. *Strumigenys membranifera* is the only one of the three species with outdoor populations in Europe, e.g., *S. membranifera* is common in urban parks of southern Spain. In the continental US, *S. membranifera* has been found in 12 southern states, whereas *S. rogeri* and *S. emmae* have outdoor populations only in peninsular Florida. *Strumigenys membranifera* occurs in a broad range of habitats, including dense forest, cultivated fields, urban lawns, and gardens. Although predators often act as "keystone" species, having a disproportionate impact on the make up of the community, there is no information on what impact *S. membranifera* may be having on the native fauna in its native or exotic range.

**Key words:** Biogeography, biological invasion, exotic species, invasive species.

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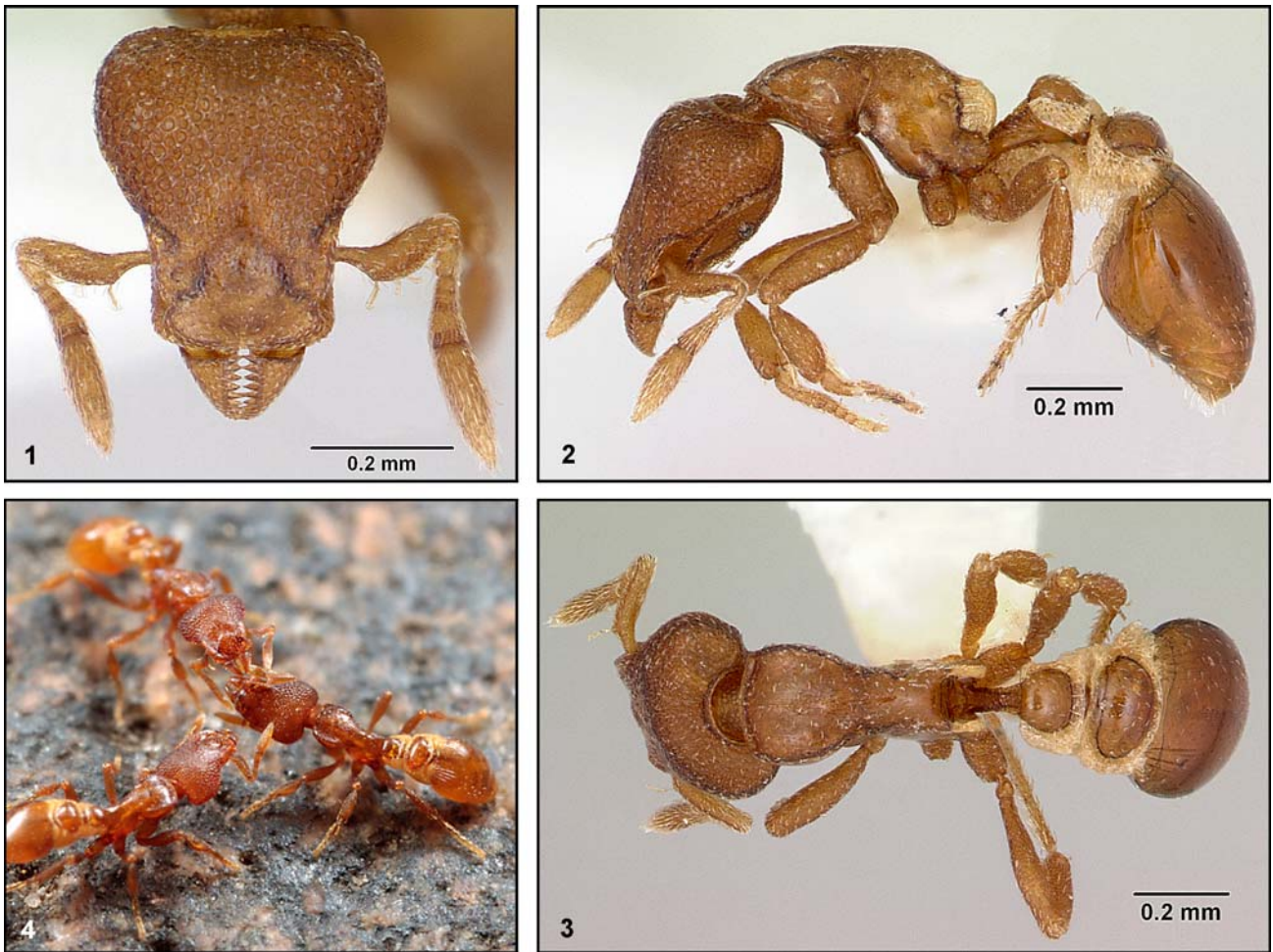
### Introduction

Dacetines (Tribe Dacetini) are predatory ants that generally feed on springtails (Collembola) and other tiny soil arthropods (WILSON 1953). Most dacetine ants live in the soil and leaf litter and rarely forage openly above ground. They are generally very small, cryptically colored, and slow-moving, becoming motionless when disturbed. As a result, dacetine ants can be easily overlooked. Most people, including field biologists, remain unaware of their presence. BOLTON (2000) recognized 872 species of dacetine ants, placing 90% in two genera, *Strumigenys* (466 species = 53%) and *Pyramica* (324 species = 37%), now combined within *Strumigenys* (BARONI URBANI & DE ANDRADE 2007). Most dacetine species are recently described and known only from their original descriptions, e.g., BOLTON (2000) alone described 303 new *Strumigenys* species and 135 new *Pyramica* (= *Strumigenys*, in part) species.

Three dacetine species have achieved broad distributions in both the Old World and the New World, spread through human commerce: *Strumigenys rogeri* EMERY, 1890, *Strumigenys emmae* (EMERY, 1890), and *Strumigenys membranifera* EMERY, 1869. The workers of these three species differ greatly in morphology. Of these tiny invaders, the workers of *S. rogeri* are the largest (total length = 2.3 - 2.8 mm), those of *S. emmae* are the smallest (1.5 - 1.9 mm),

and *S. membranifera* workers are intermediate in size (1.9 - 2.1 mm). The mandibles are long and linear in *S. rogeri*, sickle-shaped in *S. emmae*, and triangular in *S. membranifera*. DEYRUP & TRAGER (1984) and DEYRUP & DEYRUP (1999) examined the biology of *S. rogeri* and *S. emmae* in the context of their invasions of Florida. Here, I take a closer look at *S. membranifera* (Figs. 1 - 4).

Whereas *Strumigenys rogeri* and *S. emmae* have long teeth on their mandibles used for impaling prey, *S. membranifera* has tiny teeth on pliers-like mandibles that can clamp down and hold prey. WILSON (1953) described the hunting technique of *S. membranifera*: "as soon as the worker becomes aware of the presence of a collembolan, it "freezes" in a lowered, crouching posture and holds this stance briefly. If the collembolan is to her back or side, the worker now turns very slowly to face it. Once it is aligned with the collembolan, it begins a forward movement so extraordinarily slow that it can be detected only by persistent and careful observation. Several minutes may pass before the ant finally maneuvers over less than a millimeter's distance to come into a striking position, and she may remain in this position for as much as a minute or more ... Tactile labral hairs are present and eventually come to touch the prey. The mandibular strike is as sudden as that of the



Figs. 1 - 4: *Strumigenys membranifera*. (1) Head of a worker from the Galapagos; (2) lateral view of the same worker; (3) dorsal view of the same worker; (4) workers in Tucson, Arizona (photos 1 - 3 by A. Nobile; copyright Antweb.org; photo 4 by A. Wild).

*Strumigenys*, but since it is usually directed at an appendage, it does not have the same stunning effect on the collembolan. The insect often struggles violently to escape, but the worker is very tenacious and retains a fast grip until she can sting her prey into immobility."

Although *Strumigenys membranifera* is tiny, its impact on other tiny soil arthropods could be substantial. Predators often act as "keystone" species, having a disproportionate impact on the make up of the community. Invasive predatory ants can be particularly efficient at exterminating local arthropod species. For example, ZIMMERMAN (1970) wrote: "the greatest single known tragedy to have befallen the Hawaiian insect fauna was the early introduction of the widespread big-headed ant, *Pheidole megacephala* (FABRICIUS). Few are the endemic insects which can withstand its rapacity for long." Unfortunately, the almost microscopic organisms of the soil mesofauna community remain largely undescribed in most parts of the world. Mass extinctions among the native mesofauna may be rampant, but simply going on undocumented and unappreciated.

#### Taxonomy and geographic origin

EMERY (1869) described *Strumigenys membranifera* from Italy, placing it in a new subgenus, *Trichoscapa*. Junior synonyms of *S. membranifera*, all synonymized by BROWN

(1948), include: *Strumigenys membranifera simillima* EMERY, 1890 (from St Thomas), *Strumigenys membranifera santschii* FOREL, 1904 (from Tunisia), *Strumigenys vitiensis* MANN, 1921 (from Fiji), *Strumigenys foochowensis* WHEELER, 1928 (from China), *Strumigenys silvestriana* WHEELER, 1928 (from Macao), *Strumigenys membranifera marioni* WHEELER, 1933 (from Mississippi), and *Strumigenys membranifera williamsi* WHEELER, 1933 (from Hawaii). BROWN (1948) raised *Trichoscapa* to genus level. BARONI URBANI & DE ANDRADE (1994), however, transferred all *Trichoscapa* to *Strumigenys*. BOLTON (1999) moved *Trichoscapa* to *Pyramica*. Most recently, BARONI URBANI & DE ANDRADE (2007) transferred all *Pyramica* to *Strumigenys*. Many researchers, however, have continued to use the name *Pyramica* (e.g., FELLNER & al. 2009, BEZDĚČKA & BEZDĚČKOVÁ 2010).

There has been much speculation on which species are most closely related to *Strumigenys membranifera*. After considering several possibilities in earlier papers (e.g., BROWN & WILSON 1959), BROWN (1973) placed *S. membranifera* closest to members of the genus *Miccostruma* (= *Strumigenys*, in part), which at the time included three taxa restricted to sub-Saharan Africa (distributions from BOLTON 2000): *Miccostruma mandibularis* (SZABÓ, 1909) (= *Strumigenys mandibularis*) known from Tanzania, South

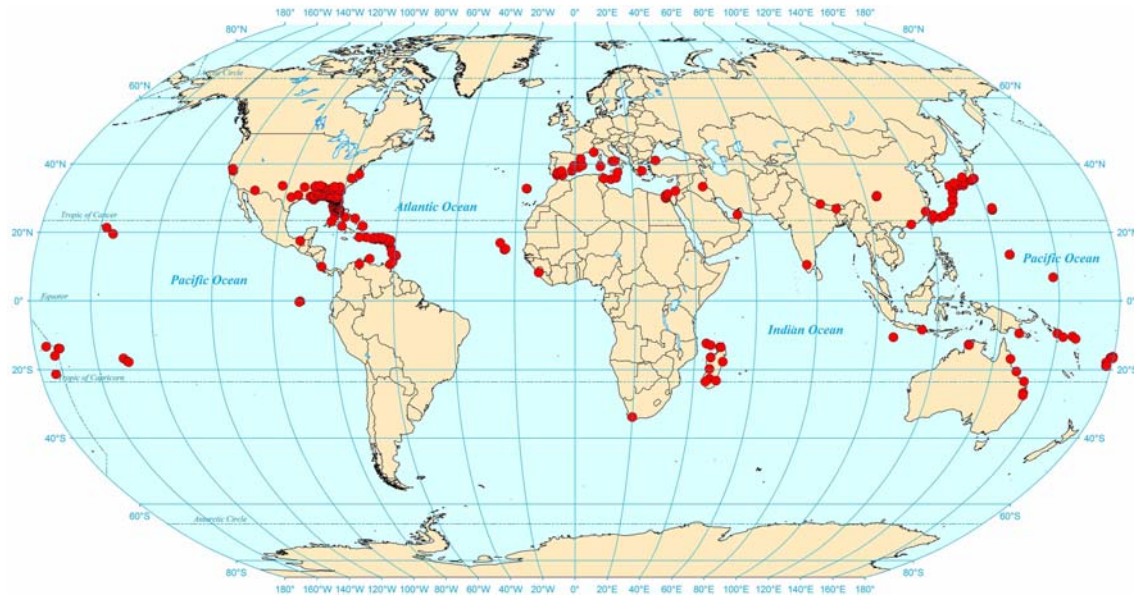


Fig. 5: Worldwide distribution records of *Strumigenys membranifera*.

Africa, and Madagascar; *Miccostruma marginata* (SANT-SCHI, 1914) (= *Strumigenys marginata*) known from Kenya, Ivory Coast, Tanzania, Ghana, and South Africa; and *Miccostruma tigrilla* BROWN, 1973 (= *Strumigenys tigrilla*) known from Ivory Coast, Ghana, and Gabon. BOLTON (1983) subsequently moved all three of these species to *Smithistruma* (= *Strumigenys*, in part), and wrote that *S. membranifera* "is very close to *Smithistruma*, being separated only by the differently constructed mandibles." BOLTON (1999, 2000) designated both *Miccostruma* and *Smithistruma* to be junior synonyms of *Pyramica* (= *Strumigenys*, in part). BOLTON (2000) assigned *S. membranifera* to the monotypic *membranifera*-group within *Pyramica* (= *Strumigenys*, in part).

### Common name

DEYRUP (1997) reported that *S. membranifera* has little hair "except for a pair of small scale-like hairs on the head, and hairs on the antennae, legs, and tip of the gaster." Based on this, DEYRUP (1997) called *S. membranifera* the "bare snap-trap ant," and DEYRUP & al. (2000) called this species the "bare pygmy snapping ant." However, high-resolution photographs of *S. membranifera* workers reveal tiny hairs over much of the body (Figs. 2 - 3). I have used the name "membraniferous dacetine ant," based on the short skirt of membranous "spongiform tissue" surrounding the waist (petiole and post-petiole) of this ant, no doubt the basis of the name "*membranifera*," Latin for "membrane bearing." Although many dacetine ants have membranous skirts, it is particularly well developed in *S. membranifera*. These tissues, also called "spongiform appendages" or "spongiform masses," are "thin, complicated and involuted lamelliform structures on the sides of the pedicellar nodes" (BROWN 1953). The adaptive function of these tissues remains unknown. One possibility may be protection of the ant's narrow waist, making this vulnerable area more difficult for a predator and other enemies to grasp and sever.

### Materials and methods

Using published and unpublished records, I documented the worldwide range of *Strumigenys membranifera*. I ob-

tained unpublished site records from museum specimens in the collections of Archbold Biological Station (ABS; identified by M. Deyrup), the Illinois Natural History Survey (INHS; identified by J. Trager), the Museum of Comparative Zoology (MCZ; identified by S. Cover), and the Smithsonian Institution (SI; identified by J.K. Wetterer, using the key in BOLTON 2000). In addition, I used on-line databases with collection information on specimens (including ant.edb.miyakyo-u.ac.jp, www.antweb.org, antbase.org/ants/africa, formicidae.org, and www.gbif.org). Finally, I collected *S. membranifera* specimens on numerous Atlantic and West Indian Islands.

I obtained geographic 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 I had no other record for this region, I 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. I did not map records of *S. membranifera* found in newly imported goods or intercepted in transit by quarantine inspectors. Published records usually included collection dates. In a number of cases, publications did not include the collection dates for specimens, but I was able to determine the approximate date based on information on the collector's travel dates or limit the date by the collector's date of death.

### Results

I compiled *Strumigenys membranifera* specimen records from > 300 sites worldwide (Fig. 5). I documented the earliest known *S. membranifera* records for 74 geographic areas (countries, island groups, major Caribbean islands, and US states; Tabs. 1 - 4), including many locales for which I found no previously published records: Arizona, Arkansas, Barbados, Barbuda, Bonaire, British Virgin Islands, Comoros, Dominica, Dominican Republic, Haiti, Îles Éparses, India, Madagascar, Montserrat, Nevis, St Kitts, St Lucia, St Martin, Tobago, Trinidad, and Turks & Caicos Islands.

Tab. 1: Earliest known records of *Strumigenys membranifera* from Europe, Africa, the Middle East, and neighboring islands. CAS = California Academy of Sciences.

	Earliest record
Italy	1868 (EMERY 1869, type locality)
Tunisia	≤ 1904 (FOREL 1904 as <i>S. membranifera santschii</i> )
Egypt	1933 (FINZI 1936 as <i>S. membranifera santschii</i> )
Iraq	1950 (WEBER 1952)
France	1962 (HERVÉ 1969)
Malta	1975 (SCHEMBRI & COLLINGWOOD 1995)
Spain	1975 (ESPADALER 1979)
Sierra Leone	≤ 1983 (BOLTON 1983)
Greece	1987 (AGOSTI & COLLINGWOOD 1987)
Israel	≤ 1988 (KUGLER 1988)
Turkey	≤ 1988 (KUGLER 1988)
Cape Verde	≤ 1993 (COLLINGWOOD & VAN HARTEN 1993)
+ Madagascar	1993 (A. Pauley, CAS): Mahavelona
Sardinia	≤ 1994 (POLDI & al. 1995)
Sicily	≤ 1994 (POLDI & al. 1995)
South Africa	≤ 2000 (BOLTON 2000)
United Arab Emirates	≤ 2000 (BOLTON 2000)
Madeira	2002 (WETTERER & al. 2007)
+ Îles Éparses	2007 (B.L. Fisher & al., CAS): Mont Benara, Mayotte
+ Comoros	2009 (B.L. Fisher & al., CAS): Ouallah

## Discussion

There are three truly cosmopolitan dacetine species, *Strumigenys rogeri*, *S. emmae*, and *S. membranifera*, all originating in the Old World. Of these three species, *S. membranifera* has spread to the highest latitudes in both the Old World and New World. For example, in Southern Europe, *S. membranifera* is the only one of the three species with outdoor colonies. In the continental US, *S. membranifera* is found in 12 southern states, whereas *S. rogeri* and *S. emmae* have outdoor populations only in peninsular Florida. In Florida, ~ 70% of *S. membranifera* records I found came from north of 29° N, but all *S. rogeri* and *S. emmae* records were from south of 29° N.

WILSON & HUNT (1967) wrote that *Strumigenys membranifera* "has proven to be ecologically the most variable of the dacetine ants, nesting in rotting log and soil in both moist (mesophytic) forest and moderately dry, open cultivated fields." DEYRUP (1997) wrote that *S. membranifera*

Tab. 2: Earliest known records of *Strumigenys membranifera* from Asia and the Pacific. MCZ = Museum of Comparative Zoology.

	Earliest record
Fiji	1915 - 1916 (MANN 1921 as <i>S. vitiensis</i> )
Samoa	1923 (WILSON & TAYLOR 1967)
China	≤ 1928 (WHEELER 1928 as <i>S. silvestriana</i> & <i>S. fochowensis</i> )
Hawaii	1932 (WHEELER 1933 as <i>S. membranifera williamsi</i> )
Mariana Islands	1945 (CLOUSE 2007)
Japan	1953 (S. Miyamoto, MCZ): Nakano-shima
Solomon Islands	1964 (BOLTON 2000)
Wallis & Futuna	1965 (WILSON & HUNT 1967)
Tonga	1971 (WETTERER 2002)
+ India	1972 (B. Lobi Mussard, MCZ): near Aliyar Dam
Taiwan	1981 (TERAYAMA & KUBOTA 1989)
Papua New Guinea	1984 (BOLTON 2000)
Society Islands	≤ 1987 (PERRAULT 1988)
Christmas Island	≤ 1990 (TAYLOR 1990 in FRAMENAU & THOMAS 2008)
Federated States of Micronesia	1995 (CLOUSE 2007)
Indonesia	≤ 2000 (BOLTON 2000)
Bhutan	≤ 2000 (BOLTON 2000)
Nepal	≤ 2000 (BOLTON 2000)
Australia	2003 (BURWELL & al. 2010)

"often occurs in disturbed open areas, such as lawns and pastures." On Caribbean islands, I most often found *S. membranifera* in urban gardens, although I also found it in some forest areas, e.g., in the Forest Reserve on Tobago. On Atlantic Islands, I collected *S. membranifera* at three sites in Cape Verde and two sites in Madeira; all five sites were urban flower gardens. ORDÓÑEZ-URBANO & al. (2008) found *S. membranifera* in 21 of 32 urban parks (66%) in southern Spain surveyed using pitfall traps. Although earlier studies considered this species to be rare in Spain, ORDÓÑEZ-URBANO & al. (2008) concluded that *S. membranifera* is common in southern Spain, but simply overlooked by researchers using other methods for collecting ants. In my recent collections in the West Indies, I recorded *S. membranifera* for the first time from many different islands (Tab. 3). Most often I collected *S. membranifera* from leaf litter using a Davis sifter (a screen-bottom tray fitted over a white sorting tray). These new West Indian records, how-

Tab. 3: Earliest known records of *Strumigenys membranifera* from the Neotropics. INHS = Illinois Natural History Survey, MCZ = Museum of Comparative Zoology.

	Earliest record
US Virgin Islands	1890 (EMERY 1890 as <i>S. membranifera simillima</i> )
Puerto Rico	1914 (WEBER 1934)
Cuba	≤ 1918 (BOLTON 2000)
Venezuela	≤ 1948 (BROWN 1949)
+ Dominica	1935 (N.A. Weber, MCZ): site unknown
+ Haiti	1950 (H.B. Mills, INHS): Port-au-Prince
Costa Rica	≤ 1972 (KEMPF 1972)
Mexico	1988 (MACKAY & al. 1991)
Galapagos	1998 (HERRERA & ROQUE-ALBELA 2007)
+ Barbados	1998 (S.P. Cover & E.O. Wilson, MCZ): Barbados Wildlife Preserve
+ Dominican Republic	2003 (M. Deyrup, MCZ): Santo Domingo Botanical Garden
+ Trinidad	2003 (J.K. Wetterer, MCZ): Charlieville
+ Tobago	2003 (J.K. Wetterer, MCZ): Forest Reserve
+ British Virgin Islands	2005 (J.K. Wetterer, MCZ): Road Town
+ St Lucia	2006 (J.K. Wetterer, MCZ): St Urbain
+ St Martin	2006 (J.K. Wetterer, MCZ): Fond Mahaut
+ Barbuda	2007 (J.K. Wetterer, MCZ): Codrington
+ Montserrat	2007 (J.K. Wetterer, MCZ): Brades
+ Nevis	2007 (J.K. Wetterer, MCZ): Montpelier
+ St Kitts	2007 (J.K. Wetterer, MCZ): Romney's
+ Bonaire	2008 (J.K. Wetterer, MCZ): Fontein
+ Turks & Caicos Islands	2010 (J.K. Wetterer, MCZ): Graceway, Providenciales

ever, are probably indicative not of recent arrival, but rather are simply due to this inconspicuous species having eluded detection by earlier collectors.

The ecological significance of *Strumigenys membranifera* has also largely escaped study. There is no information on what impact *S. membranifera* may be having on other species in its native or exotic range. Certainly more research is warranted to evaluate the ecological importance of *S. membranifera* and other tiny dacetine ants.

### Geographic origin

The geographic origin of *Strumigenys membranifera* remains unclear. BROWN & WILSON (1959) concluded that

Tab. 4: Earliest known records of *Strumigenys membranifera* from the US and Bahamas. MCZ = Museum of Comparative Zoology, SI = Smithsonian Institution.

	Earliest record
Louisiana	1914 (J.R. Horton, MCZ & SI): Happy Jack
Mississippi	1929 (H. Dietrich, SI): Avera
Georgia	1936 (W.F. Turner, SI): several sites
Florida	1943 (DEYRUP & al. 2000)
Alabama	1947 (E.O. Wilson, MCZ): Deer River
Virginia	1932 (H.T. Vanderford, SI): Norfolk
South Carolina	1957 - 1960 (VAN PELT 1966)
California	≤ 1967 (SMITH 1967)
North Carolina	1972 - 1973 (NUHN & WRIGHT 1979)
Texas	≤ 1990 (COKENDOLPHER 1990)
Bahamas	1994 (DEYRUP 1997)
+ Arizona	2007 (A.L. Wild, pers. comm.): Tucson
+ Arkansas	2008 (L.C. Thompson, MCZ): Sandhills Natural Area

*S. membranifera* was probably of African origin and I have found no subsequent author who has presented evidence to the contrary. BOLTON (1983, 2000) included *S. membranifera* as a tropical African species. BOLTON (1983) wrote: "BROWN & WILSON (1959) suggested an African origin for the species but at that time no specimens of *membranifera* had been reported from the Afrotropical region. A single series from Sierra Leone (in BMNH) shows that the species does indeed occur in sub-Saharan Africa but whether this continent represents its place of origin remains to be seen, for this series may also represent an introduction." Indeed, this one record from Sierra Leone remains the only tropical African record of *S. membranifera* (Fig. 5), suggesting that this species may not originate in this region.

BOLTON (2000) noted that of the 87 *Pyramica* (= *Strumigenys*, in part) species known at the time from the Afrotropical and Palaearctic regions, "only one, the cosmopolitan tramp-species *membranifera*, is found in both regions." In the Old World, *S. membranifera* records are widespread in three regions: the Mediterranean, Madagascar, and the southern Japanese islands (Fig. 5). Research on the genetic diversity of *S. membranifera* in different parts of the world is needed to evaluate hypotheses concerning the geographic origin of this cosmopolitan species.

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### Zusammenfassung

*Strumigenys membranifera* EMERY, 1869 (Tribus Dacetini) ist eine winzige räuberische Ameisenart, die durch menschliche Handelsaktivitäten global verbreitet wurde. Um die weltweite Verbreitung von *S. membranifera* zu untersuchen, habe ich Nachweise von > 300 Fundorten zusammengetragen. Ich dokumentiere die frühesten bekannten Nachweise der Art für 74 geographische Gebiete (Länder, Inselgruppen, große karibische Inseln und US-Bundesstaaten), einschließlich vieler, für die ich keine bisher veröffentlichten Nachweise gefunden habe: Arizona, Arkansas, Barbados, Barbuda, Bonaire, Britische Jungferninseln, Dominica, Dominikanische Republik, Haiti, Îles Éparses, Indien, Komoren, Madagaskar, Montserrat, Nevis, St. Kitts, St. Lucia, St. Martin, Tobago, Trinidad und Turks- und Caicosinseln.

*Strumigenys membranifera* ist eine von drei Arten der Dacetini aus der Alten Welt, zusammen mit *Strumigenys rogeri* EMERY, 1890 und *Strumigenys emmae* (EMERY, 1890), mit umfassenden Nachweisen aus der Alten und der Neuen Welt. Während *S. rogeri* und *S. emmae* fast ausschließlich tropisch sind, hat sich *S. membranifera* in höhere geographische Breiten ausgebreitet. *Strumigenys membranifera* ist die einzige der drei Arten, die freilebende Populationen in Europa hat; beispielsweise ist *S. membranifera* in städtischen Parkanlagen in Südspanien häufig. In den kontinentalen USA wurde *S. membranifera* in zwölf südlichen Bundesstaaten gefunden, während die freilebenden Populationen von *S. rogeri* und *S. emmae* auf den Halbinselteil Floridas beschränkt sind. *Strumigenys membranifera* kommt in einer großen Bandbreite von Lebensräumen vor, so auch in dichten Wäldern, Ackerland, urbanen Rasenanlagen und Privatgärten. Räuber fungieren oft als "Schlüsselarten", die einen überproportionalen Einfluss auf die Zusammensetzung einer Gemeinschaft haben; über den möglichen Einfluss von *S. membranifera* auf die native Fauna in ihrem nativen und exotischen Verbreitungsgebiet gibt es aber keine Information.

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