

WORLDWIDE SPREAD OF THE GRACEFUL TWIG ANT, *PSEUDOMYRMEX GRACILIS* (HYMENOPTERA: FORMICIDAE)

JAMES K. WETTERER

Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, FL 33458

ABSTRACT

Pseudomyrmex gracilis is a large, slender arboreal ant with a painful sting. This species has a broad native range spanning much of the New World tropics and subtropics. In addition, *P. gracilis* has established exotic populations, notably in Florida and Hawaii. Here, I compiled and mapped records of *P. gracilis* from >1500 sites in 32 geographic areas (countries and US states) to evaluate its worldwide distribution and update information on its recent spread. *Pseudomyrmex gracilis* has an essentially continuous distribution ranging from southern Uruguay (~34.9°S) and central Argentina (~34.5°S), through much of South and Central America, to southern Texas (~31.3°N), with recent records (all since 1995) in southern Louisiana (29.9-31.3°N). Populations of *P. gracilis* were first discovered in southeast Florida in 1960. Since then, *P. gracilis* populations have expanded northward in Florida, up to ~30.8°N. In 2009, a *P. gracilis* population was discovered in Mississippi (~30.6°N). Genetic analyses are needed to determine whether the recent appearance of *P. gracilis* in Louisiana and Mississippi has resulted from this species expanding its range eastward out of Texas or westward out of Florida. Exotic populations of *P. gracilis* in Hawaii were first found on Oahu in 1976. There are now >20 reports of *P. gracilis* from Oahu, Kaho'olawe, and Maui, suggesting that the Hawaiian populations are expanding. Finally, there are a few exotic records of *P. gracilis* from the West Indies: Barbados, Guadeloupe, and Jamaica. It remains to be seen whether or not the wide-ranging *P. gracilis*, which has become so well established across Florida, will show comparable success in Hawaii and other regions it has invaded.

Key Words: arboreal ants, exotic species, Hawaii, Florida, Louisiana, Mississippi, Neotropics, pest ants

RESUMEN

Pseudomyrmex gracilis es una hormiga delgada arborea que tiene una picadura dolorosa. Esta especie tiene un rango nativo amplio que se extiende por muchos de las áreas trópicas y subtropical del Mundo Nuevo. Además, *P. gracilis* ha establecido poblaciones exóticas, notablemente en la Florida y Hawaii. Aquí, compilé y trazé un mapa de los registros de *P. gracilis* de >1500 sitios en 32 áreas geográficas (condados y estados de los EEUU) para evaluar su distribución mundial y actualizar información basada en su extensión reciente. Esencialmente, *Pseudomyrmex gracilis* tiene una distribución continua desde el sur de Uruguay (~34.9°S) y el centro de Argentina (~34.5°S), a través de Sudamérica y Centroamérica, hasta la parte sur de Texas (~31.3°N), y con registros recientes (todos desde 1995) en el sur de Louisiana (29.9-31.3°N). Poblaciones de *P. gracilis* fueron descubiertas por primera vez en el sureste de Florida en 1960. Desde entonces, poblaciones de *P. gracilis* se han extendido hacia el norte de la Florida, hasta ~30.8°N. En 2009, una población de *P. gracilis* fue descubierta en Mississippi (~30.6°N). Se necesitan análisis genéticos para determinar si la apariencia reciente de *P. gracilis* en Louisiana y Mississippi es el resultado que esta especie haya extendido su rango hacia el este proveniente del estado de Texas o hacia el oeste y proveniente de la Florida. Poblaciones exóticas de *P. gracilis* en Hawaii fueron encontradas por primera vez en Oahu en 1976. Ahora hay > 20 registros de *P. gracilis* en Oahu, Kaho'olawe, y Maui, que indica que las poblaciones en Hawaii están extendiéndose. Por último, hay pocos registros exóticos de *P. gracilis* en las Antillas: Barbados, Guadeloupe y Jamaica. Queda por ver si *P. gracilis*, con su amplio rango de distribución que esta bien establecida a través de la Florida, demostrara un éxito comparable en Hawaii y otras regiones donde haya invadido.

The graceful twig ant, *Pseudomyrmex gracilis* Fabricius, is a slender arboreal ant. Workers are usually found foraging solitarily on vegetation, buildings, and other structures. They have large, oval eyes, and apparently have excellent vision that often allows them to detect and escape from predators and ant collectors by dropping to the

ground (pers. obs.). Workers have a painful sting, but are not aggressive, and generally sting only if trapped under clothing or swatted.

Pseudomyrmex gracilis has a native range spanning much of the New World tropics and subtropics. Recently, it has become a common exotic in Florida. Whitcomb et al. (1972) reported that *P.*

gracilis was first found in southeast Florida in 1960, and that this species “has spread steadily in Florida. In 1964, it was found in Broward County on the East Coast and in Pinellas County on the Gulf Coast. By 1970, it had spread to the counties of Palm Beach and Glades. It now appears to be abundant in all southeast Florida from West Palm Beach southward. In Texas, it also appears to have moved northward and eastward; at present it is not uncommon in the Houston area.”

Pseudomyrmex gracilis commonly nests in hollow branches, twigs, and stems, as well as in building crevices (Whitcomb et al. 1972; and pers. obs.). *Pseudomyrmex gracilis* opportunistically nests in ant-acacias, but provides little or no defense for the trees. Wheeler (1942) found that *P. gracilis*, “though a very frequent tenant of dead twigs and *Cordia domatia* in regions where there are no Acacias, nevertheless exhibits a strong proclivity not only to inhabit the spines of these plants [ant-acacias], wherever they are available, but also to perforate them at the same point, to visit the foliar nectaries and to collect food-bodies.” Wetterer & Wetterer (2003) reported *P. gracilis* nesting in the thorns of an exotic ant-acacia in West Palm Beach, Florida, the reconstitution in an exotic locale of a facultative symbiosis evolved in the Neotropics.

Deyrup et al. (2000) categorized *P. gracilis* as a “possible ecological villain” in Florida, writing: “This species is much larger than any of the seven native species of *Pseudomyrmex*. It might compete with these native species for food, but seems to nest in larger diameter holes in twigs and stems. It is more likely to exclude various native carpenter ants: *Camponotus decipiens* Emery, *C. snellingi* Bolton, *C. impressus* (Roger), *C. nearcticus* Emery, *C. discolor* (Buckley). It is a very abundant species in south and central Florida, and does not seem to distinguish between disturbed and undisturbed habitats. Aside from competition with native arboreal ants, this species could affect native phytophagous species, especially butterflies and moths. The buildup of populations of *P. gracilis* in Florida make it highly probable that it will be accidentally introduced into the West Indies, where it could have greater impact than in Florida.”

Here, I evaluate the worldwide distribution of *P. gracilis* and provide an update on the continued spread of exotic populations.

Taxonomy

Fabricius (1804) described *P. gracilis* from South America. Across South and Central America, *P. gracilis* shows much variation in color, and many color variants have been described. Ward (1993) determined many of described taxa to be junior synonyms of *P. gracilis* (type locality in parentheses): *Pseudomyrma bicolor* Guérin-Méne-

ille (Colombia), *Pseudomyrma sericata* Smith (Brazil), *Pseudomyrma dimidiata* Roger (Colombia), *Pseudomyrma mexicana* Roger (Mexico), *Pseudomyrma volatilis* Smith (Mexico), *Pseudomyrma canescens* Smith (Brazil), *Pseudomyrma variabilis* Smith (Barbados), *Pseudomyrma pilosula* Smith (Barbados), *Pseudomyrma gracilis* subsp. *mexicana* var. *guayaquilensis* (Ecuador), *Pseudomyrma gracilis* var. *glabriventris* Santschi (Bolivia), *Pseudomyrma gracilis* var. *velifera* Stitz (Guatemala), and *Pseudomyrma gracilis* var. *longinoda* Enzmann (Peru).

MATERIALS AND METHODS

To document the worldwide geographic distribution of *P. gracilis*, I used both published and unpublished records. I obtained unpublished site records from specimens in the collections of Archbold Biological Station (ABS), the British Museum of Natural History (BMNH), and the Museum of Comparative Zoology (MCZ). Philip S. Ward provided a database of *P. gracilis* specimens that he examined in the collections of many other institutions, including the Cornell University Insect Collection (CUIC), the Florida State Collection of Arthropods (FSCA), the Los Angeles County Museum (LACM), the Museo Civico di Storia Naturale “Giacomo Doria” (MCSN), the Muséum National d’Histoire Naturelle (MNHN), and the Smithsonian Institution (SI) (see Ward 1989 for a comprehensive list of ant collections he examined). I also received unpublished records from N. J. Reimer (Hawaii), Z. Prusak (Florida), J. Ott (Mississippi), J. MacGown (Florida, Georgia), M. Leong (Hawaii), B. R. Kumashiro (Hawaii), S. Dash (Louisiana), S. Chamberlain (Mexico), and M. B. Bartosik (Texas). In addition, I included my own published and unpublished records of *P. gracilis* from Florida, Tobago, and Trinidad (e.g., Wetterer & Wetterer 2003).

I obtained the 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). I grouped records according currently defined geographic borders, e.g., I included *P. gracilis* records from Territoire Contesté and “Rivière Lunier” (the name for a tributary of the Rio Carsevenne Basin, coined by the collector, F. Geay, and not used by anyone else) in the Brazilian state of Amapá, although in 1899 when the specimens were collected, the French considered these areas to be part of French Guiana. 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 *P. gracilis* found on boats or in-

tercepted in transit by quarantine inspectors. For example, I did not include *P. gracilis* specimens reportedly from Haiti, collected in quarantine in Pennsylvania, because it is unclear whether the ants actually came from Haiti.

RESULTS

I compiled and mapped >1500 published and unpublished site records of *P. gracilis* records from 32 geographic areas (countries and US States), including every country in South and Central America except Chile (Tables 1 and 2; Fig. 1).

Pseudomyrmex gracilis has a broad, seemingly continuous distribution ranging in the south from southern Uruguay (34.9°S; Montevideo; Berry; SI) and central Argentina (34.5°S; Buenos Aires; A. Zotta; SI), though Kusnezov (1978) listed the latitudinal limit of *P. gracilis* in Argentina as 35°S. These included 9 South American records at latitudes higher than 31.3°S: from Argentina (4), Brazil (1), and Uruguay (4). *Pseudomyrmex gracilis* has been recorded throughout much of South and Central America, north to southern Texas (~31.3°N; Houston County; O'Keefe et al 2000) and southern Louisiana (31.3°N; Pineville; Dash 2004).

In Louisiana, *P. gracilis* was first collected in Lake Charles, Calcasieu Parish in 1995 (Table 2), and has now been collected in 9 Parishes in southern half of the state: Ascension, Calcasieu, East

Baton Rouge, Iberia, Jefferson, Jefferson Davis, Orleans, Rapides, and St. Martin.

Pseudomyrmex gracilis was first found in Florida in 1960 and has become common from the Florida Keys north through much of the state, surpassing 30°N in Bay, Duval, Escambia, Jackson, Leon, and Liberty Counties. In total, I found records from 40 Florida counties: Alachua, Brevard, Broward, Charlotte, Clay, Collier, Desoto, Duval, Escambia, Glades, Hardee, Hendry, Hernando, Highlands, Hillsborough, Indian River, Jackson, Lake, Lee, Leon, Liberty, Manatee, Marion, Martin, Miami-Dade, Monroe, Okeechobee, Orange, Osceola, Palm Beach, Pasco, Pinellas, Polk, Putnam, Sarasota, Seminole, St. Johns, St. Lucie, Sumter, and Volusia.

Based on photographs by J. Ott, S. Cover (pers. comm.) confirmed a 2009-record of *P. gracilis* from Picayune, Pearl River County, Mississippi (~30.6°N). I found no records of *P. gracilis* from Alabama or Georgia, though I expect that it occurs in southernmost parts of both states.

In addition, there are a few scattered exotic records of *P. gracilis* from the tropics (Barbados, Guadeloupe, Jamaica, and Hawaii) and indoor records from temperate Europe (England and the Netherlands).

Excluded Records

Although Belt (1874) reported *Pseudomyrmex bicolor* (= *P. gracilis*) in Nicaragua, Ward (1993)

TABLE 1. EARLIEST KNOWN RECORDS FOR *PSEUDOMYRMEX GRACILIS* FROM ITS PRESUMED NATIVE RANGE.

Argentina	1899 (A. Girard; MNHN*): Tucum
Belize	1959 (N. L. H. Krauss; SI*): near Belize City
Bolivia	1891 (L. Balzan; MCSN*): many localities
Brazil	≤1855 (Smith 1855 as <i>P. sericata</i>)
Colombia	≤1844 (Guérin-Méneville 1844 as <i>P. bicolor</i>)
Costa Rica	≤1889 (Emery 1889 as <i>P. mexicana</i>)
Ecuador	1903 (Forel 1907 as <i>P. guayaquilensis</i>)
El Salvador	1958 (O. L. Cartwright; SI*): San Salvador
French Guiana	1914 (R. Benoist; MNHN*): St-Jean du Maroni
Guatemala	≤1899 (Forel 1899)
Guyana	1911 (Wheeler 1916)
Honduras	1916 (F. J. Dyer; SI*): La Ceiba
Mexico	≤1863 (Roger 1863 as <i>P. mexicana</i>)
Nicaragua	≤1899 (Forel 1899)
Panama	≤1861 (Smith 1862 as <i>P. bicolor</i>)
Paraguay	≤1890 (Emery 1890a as <i>P. sericata</i>)
Peru	1920 (Cornell U. Expedition; CUIC*): Colonia Perene
Surinam	1911 (Wheeler 1916)
Tobago	1912 (A. Busck; SI*): locality unknown
Trinidad	1920 (Wheeler 1922)
Texas	1896 (C. L. Marlatt; LACM*): Neuceest (= Nueces?)
Uruguay	1942 (Berry; SI*): Montevideo
Venezuela	1887-1888 (Emery 1890b)

Unpublished records include collector, museum source, and site.

* = data from P.S. Ward. See Methods for museum abbreviations.

TABLE 2. EARLIEST KNOWN RECORDS FOR *PSEUDOMYRMEX GRACILIS* FROM ITS PRESUMED EXOTIC RANGE.

Barbados	≤1877 (Smith 1877 as <i>P. pilosula</i> and <i>P. variabilis</i>)
Jamaica	1909 (Wheeler 1911)
England	1912 (Donisthorpe 1915)
Netherlands	1936 (Boer & Vierbergen 2008)
Florida	1960 (Whitcomb et al. 1972)
Hawaii	1976 (Beardsley 1979 as <i>P. mexicanus</i>)
Guadeloupe	1977 (W.H. Whitcomb; FSCA*): Petit Bourg
Louisiana	1995 (A.R. Kirk; S. Dash pers. comm.): Lake Charles
Mississippi	2009 (J. Ott, pers. comm.): Picayune

Abbreviations as in Table 1.

concluded that Belt (1874) actually was referring to *Pseudomyrmex flavicornis*. Rothney (1892) reported that *Pseudomyrmex bicolor* (= *P. gracilis*) was synonymous with *Sima rufonigra* (= *Tetraponera rufonigra*) and was common in Barrackpore, India. Rothney (1903), however, reported only *T. rufonigra* from Barrackpore, indicating that the earlier evaluation was an error. Ward (1992) listed *P. gracilis* from Hispanola, but based on the database he provided to me, this record appears to be based on specimens intercepted by quarantine (see Methods).

DISCUSSION

Pseudomyrmex gracilis has an essentially continuous distribution from Uruguay and Argentina in the south to Texas in the north, with several recent records (all since 1995) across southern Louisiana. Populations of *P. gracilis* extend to

higher latitudes in South America (34.9°S) than they do in North America (31.3°N), suggesting that North American populations may still have potential to expand further northward. Alternatively, the highest latitude populations in South America may have greater climatic tolerance than populations in North America.

Since arriving in South Florida sometime before 1960, *P. gracilis* populations have expanded to occupy much of the state up to almost 31°N. Recently, *P. gracilis* has spread to southern Louisiana and Mississippi. It seems very likely that *P. gracilis* is now present in adjacent parts of southern Alabama and Georgia.

It is unclear why *P. gracilis* populations have spread only recently along the Gulf coast in Louisiana and Mississippi. It could be that recent habitat and/or climate changes allowed the eastward expansion of native populations out from Texas. Alternatively, populations of *P. gracilis* suited to

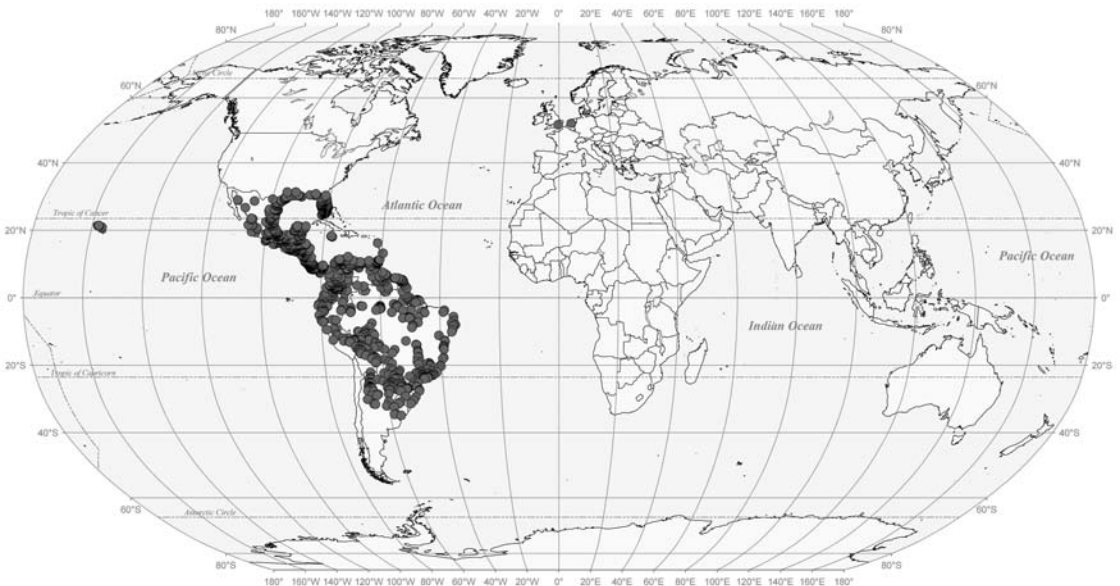


Fig. 1. Worldwide distribution records of *Pseudomyrmex gracilis*.

regional conditions may have been introduced from elsewhere, perhaps Florida. Genetic analyses of *P. gracilis* in Louisiana and Mississippi are needed to determine the origin of these populations.

In Hawaii, *P. gracilis* is now known from 3 islands. Beardsley (1979) first reported *P. gracilis* collected in 1976 on Oahu. Leong & Grace (2008) recently reported 15 complaints to the Department of Health between 1990 and 1999 on Oahu concerning *P. gracilis*. *Pseudomyrmex gracilis* was found on Kaho'olawe in 2003 (Starr et al. 2004) and on Maui in 2008 (N. J. Reimer, pers. comm.). This expansion of *P. gracilis* populations to >20 sites on Oahu and its spread to Kaho'olawe and Maui should be cause of some concern. Neil Reimer (pers. comm.) reported that in Hawaii, *P. gracilis* "is most likely more widely spread and present on all islands but we don't have the records to show it yet. It is common in areas of lower rainfall and people living there know not to irritate it as the stings can be quite painful."

There are a few scattered exotic records of *P. gracilis* from the West Indies: Barbados, Guadeloupe, and Jamaica. It seems likely that *P. gracilis* is now extinct on Barbados, where it has not reported since Smith (1877) first recorded its presence. It may have been incidentally extirpated due to widespread deforestation. Alternatively, these arboreal ants may have been only temporary populations introduced on imported lumber. In Guadeloupe, I found only a single 1977 report of *P. gracilis* (Table 2). In Jamaica, I found only 3 site-records, dating from ≤1911, 1985, and 1989. Thus, there is as yet little indication that exotic populations of *P. gracilis* in the West Indies are expanding.

Remarkably, of the ~200 described species in the subfamily Pseudomyrmecinae, *P. gracilis* is the only one known to establish populations outside its native range. It remains to seen whether or not this wide-ranging species, which has become so well established across Florida, will show comparable success in Hawaii and other regions it has invaded and whether or not *P. gracilis* will invade other parts of the world. It would be valuable to assess whether *P. gracilis* is having a significant impact on native species in Florida, as Deyrup et al. (2000) predicted.

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REFERENCES CITED

- BEARDSLEY, J. W. 1979. Notes and exhibitions: *Pseudomyrmex gracilis mexicanus* (Roger). Proc. Hawaiian Entomol. Soc. 13: 23.
- BELT, T. 1874. The Naturalist in Nicaragua. E. Bumpus, London. 306 pp.
- BOER, P. D., AND VIERBERGEN, B. 2008. Exotic ants in the Netherlands (Hymenoptera: Formicidae). Entomol. Bericht. 68: 121-129.
- DASH, S. T. 2004. Species Diversity and Biogeography of Ants (Hymenoptera: Formicidae) in Louisiana, with Notes on their Ecology. M.S. thesis, Louisiana State Univ. 290 pp.
- DEYRUP, M., DAVIS, L., AND COVER, S. 2000. Exotic ants in Florida. Trans. American Entomol. Soc. 126: 293-326.
- DONISTHORPE, H. ST. J. K. 1915. British ants, their life-history and classification. Brendon & Son Ltd. Plymouth. 379 pp.
- EMERY, C. 1889. Estudios sobre las hormigas de Costa Rica. Anal. Mus. Nac. Costa Rica 1889: 45-67.
- EMERY, C. 1890a. Studi sulle formiche della fauna neotropica. Boll. Soc. Entomol. Italiana 22: 38-80.
- EMERY, C. 1890b. Voyage de M. E. Simon au Venezuela (Décembre 1887 - Avril 1888). 7e Mémoire. Formicides. Ann. Soc. Entomol. France (6)10: 55-76.
- FABRICIUS, J. C. 1804. Systema Piezatorum. Carolum Reichard, Brunsviga. 439 pp.
- FERSTER, B., DEYRUP, M., AND SCHEFFRAHN, R. H. 2000. The pest ants of Florida: elongate twig ant *Pseudomyrmex gracilis*. <http://frec.ifas.ufl.edu/entomo/ants/Pest%20Ants%20of%20FL/Elongate%20Twig%20ant.htm>
- FOREL, A. 1899. Biologia Centrali-Americana; or, Contributions to the Knowledge of the Fauna and Flora of Mexico and Central America. Insecta. Hymenoptera. Vol. III. (Formicidae). London. 169 pp.
- FOREL, A. 1907. Formiciden aus dem Naturhistorischen Museum in Hamburg. Mit. Naturhist. Mus. Hamburg 24: 1-20.
- GUÉRIN-MÉNEVILLE, F. E. 1844. Iconographie de règne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables, et souvent non encore figurées, de chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Tome III. J. B. Baillièrre, Paris. 276 pp.
- KUSNEZOV, N. 1978. Hormigas Argentinas. Clave para su identificación. Fundación Miguel Lillo, Tucumán. 148 pp.
- LEONG, M. K. H., AND GRACE, J. K. 2008. Occurrence and distribution of ants (Hymenoptera: Formicidae), cockroaches (Blattodea), centipedes (Chilopoda), and wasps (Hymenoptera: Vespidae) of public health importance on the island of Oahu. Proc. Hawaiian Entomol. Soc. 40: 33-49.
- O'KEEFE, S. T., COOK, J. L., DUDEK, T., WUNNEBURGER, D. F., GUZMAN, M. D., COULSON, R. N., AND VINSON, S. B. 2000. The distribution of Texas ants. Southwest. Entomol. Suppl. 22: 1-93.

- ROGER, J. 1863. Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses, nebst Ergänzung einiger früher gegeben Beschreibungen. Berliner Entomol. Z. 7: 131-214.
- ROTHNEY, G. A. J. 1889. Notes on Indian ants. Trans. Entomol. Soc. London 1889: 347-374.
- ROTHNEY, G. A. J. 1903. The aculeate Hymenoptera of Barrackpore, Bengal. Trans. Entomol. Soc. London 1903: 93-116.
- SMITH, F. 1855. Descriptions of some species of Brazilian ants belonging to the genera *Pseudomyrma*, *Eciton* and *Myrmica* (with observations on their economy by Mr. H. W. Bates). Trans. Entomol. Soc. London (2)3: 156-169.
- SMITH, F. 1862. Descriptions of new species of aculeate Hymenoptera, collected at Panama by R. W. Stretch, Esq, with a list of described species, and the various localities where they have previously occurred. Trans. Entomol. Soc. London (3)1: 29-44.
- SMITH, F. 1877. Descriptions of new species of the genera *Pseudomyrma* and *Tetraponera*, belonging to the family Myrmicidae. Trans. Entomol. Soc. London (4)10: 57-72.
- STARR, F., STARR, K., AND LOOPE, L.L. 2004. New arthropod records from Kaho'olawe. Bishop Mus. Occas. Pap. 79: 50-54.
- WARD, P. S. 1989. Systematic studies on pseudomyrmecine ants: revision of the *Pseudomyrmex oculatus* and *P. subtilissimus* species groups, with taxonomic comments on other species. Quaest. Entomol. 25: 393-468.
- WARD, P. S. 1992. Ants of the genus *Pseudomyrmex* (Hymenoptera: Formicidae) from Dominican amber, with a synopsis of the extant Antillean species. Psyche 99: 55-85.
- WARD, P. S. 1993. Systematic studies on *Pseudomyrmex* acacia-ants (Hymenoptera: Formicidae: Pseudomyrmecinae). J. Hymenopt. Res. 2: 117-168.
- WETTERER, J. K., AND WETTERER, A. L. 2003. Ants (Hymenoptera: Formicidae) on non-native Neotropical ant-acacias (Fabales: Fabaceae) in Florida. Florida Entomol. 86: 460-463.
- WHEELER, W. M. 1911. Additions to the ant fauna of Jamaica. Bull. Amer. Mus. Natur. Hist. 30: 21-29.
- WHEELER, W. M. 1916. Ants collected in British Guiana by the expedition of the American Museum of Natural History during 1911. Bull. Amer. Mus. Natur. Hist. 35: 1-14.
- WHEELER, W. M. 1922. The ants of Trinidad. American Mus. Novit. 45: 1-16.
- WHEELER, W. M. 1942. Studies of Neotropical ant-plants and their ants. Bull. Mus. Comp. Zool. 90: 1-262.
- WHITCOMB, W. H., DENMARK, H. A., BUREN, W. F., AND CARROLL, J. F. 1972. Habits and present distribution in Florida of the exotic ant, *Pseudomyrmex mexicanus* (Hymenoptera: Formicidae). Florida Entomol. 55: 31-33.