

Worldwide spread of the woolly ant, *Tetramorium lanuginosum* (Hymenoptera: Formicidae)

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Abstract

The woolly ant, *Tetramorium lanuginosum* MAYR, 1870 (senior synonym of *Triglyphothrix striatidens* (EMERY, 1889)), has long been recognized as a widespread tramp species dispersed through human commerce. To evaluate the worldwide spread of *T. lanuginosum*, I compiled published and unpublished specimen records from > 400 sites. I documented the earliest known *T. lanuginosum* records for 77 geographic areas (countries, island groups, major Caribbean islands, and US states), including many locales for which I found no previously published records, primarily islands in the West Indies: Antigua, Aruba, Barbuda, Bhutan, Comoro Islands, Curaçao, Dominica, Dominican Republic, Egypt, Îles Eparses, Martinique, Montserrat, Nevis, St Vincent, Tobago, Trinidad, and the Virgin Islands. Based on its distribution and those of its closest known relatives, *T. lanuginosum* appears to be native to tropical and subtropical East Asia and perhaps also northern Australia and western Oceania. *Tetramorium lanuginosum* appears to be particularly common on small islands, possibly due to reduced competition with dominant ants in these habitats. Recent first records of *T. lanuginosum* on many islands of Samoa, the Galapagos, Madagascar (and neighboring island groups), and the West Indies suggest that exotic populations of *T. lanuginosum* are expanding on numerous tropical islands. Nonetheless, it appears unlikely that *T. lanuginosum* will ever become a significant exotic pest species, except perhaps on small tropical islands.

Key words: Biogeography, biological invasion, exotic species, invasive species, island fauna.

Myrmecol. News 13: 81-88 (online 20 January 2010)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 22 September 2009; revision received 27 October 2009; accepted 28 October 2009

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Introduction

FOREL (1911) listed fifteen tramp ant species, spread by human commerce, which had achieved or were in the process of achieving cosmopolitan distributions. Eight of these species have become major ecological, agricultural, and / or household pests: *Anoplolepis gracilipes* (SMITH, 1857), *Linepithema humile* (MAYR, 1868), *Monomorium destructor* (JERDON, 1851), *Monomorium pharaonis* (LINNAEUS, 1758), *Paratrechina longicornis* (LATREILLE, 1802), *Pheidole megacephala* (FABRICIUS, 1793), *Solenopsis geminata* (FABRICIUS, 1804), and *Tapinoma melanocephalum* (FABRICIUS, 1793) (e.g., see WETTERER 2005, 2007, 2008, 2009a, b, WETTERER & al. 2009). Here, I examine the spread of one of FOREL's (1911) cosmopolitan ants that has not, as yet, developed into a major pest: *Tetramorium lanuginosum* MAYR, 1870. DEYRUP & al. (2000) proposed the common name "wooly groove-headed ant" for *T. lanuginosum*, but I have used simply "wooly ant" (*lanuginosum* = wooly in Latin).

Identification and taxonomy

Tetramorium lanuginosum workers are monomorphic (~ 2.5 mm total length), robust ants with a slow and steady gait. A striking character that distinguishes them from most other ants is their thick coat of soft, erect hairs (Figs. 1 - 4). Some hairs have two or three branches, a characteristic

once used to distinguish the now-synonymized polyphyletic genus *Triglyphothrix* (see BOLTON 1985).

Tetramorium lanuginosum was originally described from Java, Indonesia. Junior synonyms of *T. lanuginosum* (all synonymized by BOLTON 1976) include: *Tetramorium obeum striatidens* EMERY, 1889 (described from Burma), *Triglyphothrix striatidens laevidens* FOREL, 1900 (described from Mexican orchids shipped to Germany), *Triglyphothrix striatidens australis* FOREL, 1902 (described from Australia), *Triglyphothrix striatidens orissana* FOREL, 1902 (described from India), *Triglyphothrix ceramensis* STITZ, 1912 (described from Ceram, Indonesia), *Triglyphothrix striatidens felix* FOREL, 1912 (described from the Seychelles), *Triglyphothrix striatidens flavescens* WHEELER, 1929 (described from Singapore), *Triglyphothrix mauricei* DONISTHORPE, 1946 (described from Mauritius), and *Triglyphothrix tricolor* DONISTHORPE, 1948 (described from Irian Jaya, Indonesia). Before BOLTON's (1976) revision, almost all reports of this species used the junior synonym *Triglyphothrix striatidens*.

BOLTON (1976) concluded that the two closest known relatives of *T. lanuginosum* are *Tetramorium coonoorense* FOREL, 1902 (known only from India) and *Tetramorium obesum* ANDRÉ, 1887 (known from India and Burma).



Figs. 1 - 4: *Tetramorium lanuginosum*. (1) Head of worker from Suva, Fiji; (2) lateral view of the same worker; (3) dorsal view of the same worker; (4) workers on log in Suva, Fiji (photos by Eli Sarnat).

Methods

Using published and unpublished records, I documented the worldwide range of *T. lanuginosum*. I obtained unpublished site records from museum specimens in the collections of the British Natural History Museum (BMNH), the Museum of Comparative Zoology (MCZ), and the Smithsonian Institution (SI). In addition, I used on-line databases with collection information on specimens by Antweb (www.antweb.org), Asociación Ibérica de Mirmecología (www.hormigas.org), the Chinese Ant Database (sciencer.net/ant/english.html), and the Global Biodiversity Information Facility (www.gbif.org). I also received unpublished records from J. Woinarski (Australia), D. Ward (Fiji), M. Lush (Australia), and M. DaSilva (St Vincent). Finally, I collected *T. lanuginosum* specimens on numerous Pacific and Caribbean 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 *T. lanuginosum* on boats, found in newly imported goods (e.g., FOREL 1900; see above), 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 date based on information on the collector's travel dates or limit the date by the collector's date of death. For example, an undated specimen collected by Harold Swale in Samoa must have been collected before Swale's death in 1919. Stefan Cover confirmed identification for all specimens in the MCZ.

Results

I compiled *T. lanuginosum* specimen records from > 400 sites worldwide (Fig. 5). I documented the earliest known *T. lanuginosum* records for 77 geographic areas (countries, island groups, major Caribbean islands, and US states; Tabs. 1 - 5), including many locales for which I found no previously published records: Antigua, Aruba, Barbuda, Bhutan, Comoro Islands, Curaçao, Dominica, Dominican Republic, Egypt, Îles Eparses, Martinique, Montserrat, Nevis, St Vincent, Tobago, Trinidad, and the Virgin Islands.

Tetramorium lanuginosum is widespread in tropical and subtropical parts of Asia, Australia, and Oceania (Fig. 5; Tabs. 1 - 2). Outside of this region, most *T. lanuginosum*

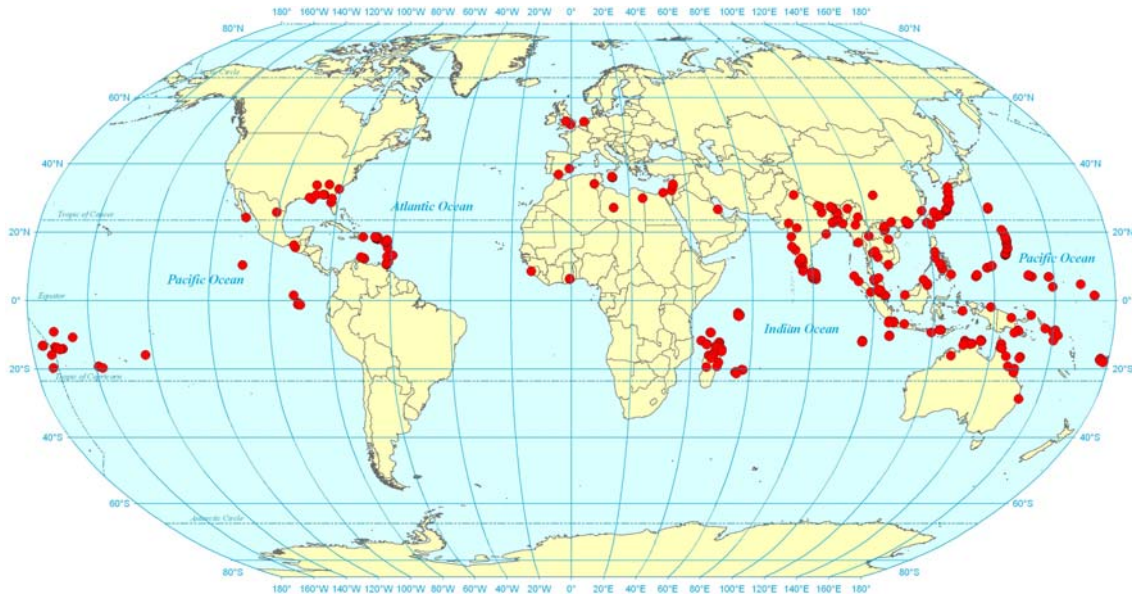


Fig. 5: Worldwide distribution records of *Tetramorium lanuginosum*.

records are concentrated in just three areas, where nearly all records come from the past ten years: Madagascar (and neighboring island groups), the Galapagos, and the Eastern Caribbean (Fig. 5; Tabs. 3 - 4). There have also been scattered reports of *T. lanuginosum* from other areas, including tropical Africa, the Mediterranean, Mexico, and the southeastern US (Fig. 5; Tabs. 3 - 5). In Northern Europe *T. lanuginosum* has been reported from three sites in England (Kew Gardens, the Birmingham Botanical Garden, and the Dudley Zoo) and one site in the Netherlands (an indoor record in Amsterdam; DE JONGE 1985).

In a number of places, *T. lanuginosum* has been intercepted in quarantine, but no established population is known. For example, WHEELER (1934) reported *T. lanuginosum* (as *T. striatidens*) intercepted in Hawaii on cargo from Manila, Philippines, but no populations in Hawaii have been reported. MARLATT (1924) reported *T. lanuginosum* (as *T. striatidens*) intercepted in New York on melons from Italy and on oranges from Brazil, but I found no collection records of this ant from New York, Italy, or Brazil.

Discussion

FOREL (1903) first noted that *Tetramorium lanuginosum* (as *T. striatidens*) was becoming a cosmopolitan species, though at that time this species had very few published records outside Asia: only from Australia, Sierra Leone, and Tunisia (Tabs. 2 - 3). Since then, however, records have accumulated from many other parts of the world, and this species can truly be considered cosmopolitan, with a worldwide distribution (Fig. 5).

Native range

WHEELER (1916) reviewed all known records of *T. lanuginosum* (as *T. striatidens*), and, based on its known distribution, concluded that this species was of Indian origin. Since then, there has been a general consensus that *T. lanuginosum* is native to tropical Asia (e.g., FOREL 1928, TAYLOR & WILSON 1961). CREIGHTON (1950) stated that the original home of *T. lanuginosum* (as *T. striatidens*) was southern India. BOLTON (1976) concurred that *T. lanuginosum* was probably native to tropical Asia because its two clos-

est relatives are known only from India and Burma. In Asia, *T. lanuginosum* commonly inhabits not only disturbed environments, but also natural areas far from human disturbance, a trait usually indicative of a native species. For example, WHEELER (1924) reported *T. lanuginosum* (as *T. striatidens*) from a cave in India "nesting in complete darkness, 400 feet from the entrance of the cave, under stones in ground heavily manured with bat-guano." SENTHONG (2003) found *T. lanuginosum* at all eight sites surveyed in urban Bangkok, Thailand. THIENHAWORN (2004) collected *T. lanuginosum* at 13 of 19 sites in more rural areas of Ratchaburi, Thailand.

ANDERSEN (1992) found *T. lanuginosum* at 14 of 16 rainforest sites surveyed in Northern Kimberley, Western Australia (also see ANDERSEN & MAJER 1991, ANDERSEN & REICHEL 1996, REICHEL & ANDERSEN 1996). Alan Andersen (pers. comm.) wrote that *T. lanuginosum* "occurs throughout higher rainfall areas of North Queensland, the Top End and the Kimberley, where it is one of the most abundant ants in rainforest patches and riparian zones, including those remote from any human settlement (e.g. including those that you need a helicopter to get to)." ANDERSEN (2000) reported that *T. lanuginosum* was one of the most common ants in Australian monsoon rainforests, and based on this ubiquity, ANDERSEN (2000) concluded that *T. lanuginosum* was "almost certainly native to Australia."

In fact, *T. lanuginosum* occurs over a seemingly continuous range from India, through tropical and subtropical East Asia, to northern Australia (Fig. 5), and thus is probably native to much of this region, and perhaps even to parts of western Oceania, e.g., the Solomon Islands, Palau, and the Mariana Islands. Because native populations usually have much greater genetic diversity than introduced populations due to the founder effect, future molecular analyses should allow delineation of the native range of *T. lanuginosum*.

Exotic range

Outside of Asia, Australia, and western Oceania, *T. lanuginosum* is apparently exotic, introduced through human com-

Tab. 1: Earliest known records for *Tetramorium lanuginosum* from East Asia and neighboring islands. Unpublished records include collector, museum source, and site. BMNH = Natural History Museum in London, MCZ = Museum of Comparative Zoology, SI = Smithsonian Institution. + = no known published record.

	Earliest record
Indonesia	≤ 1870 (MAYR 1870, type locality)
Burma/Myanmar	1886 (EMERY 1889 as <i>T. striatidens</i>)
India	1890 (R.C. Wroughton, SI): Poona
Sri Lanka	1892 (EMERY 1893 as <i>T. striatidens</i>)
Papua New Guinea	≤ 1901 (FOREL 1901 as <i>T. striatidens</i>)
Taiwan	≤ 1909 (WHEELER 1909 as <i>T. striatidens</i>)
Singapore	1913 (VIEHMEYER 1916 as <i>T. striatidens</i>)
Christmas Island	1914 (CRAWLEY 1915 as <i>T. striatidens</i>)
Malaysia	≤ 1916 (WHEELER 1916 as <i>T. striatidens</i>)
Vietnam	1925 (WHEELER 1927 as <i>T. striatidens</i>)
Macao	≤ 1928 (WHEELER 1928 as <i>T. striatidens</i>)
China	≤ 1929 (WHEELER 1929 as <i>T. striatidens</i>)
Hong Kong	≤ 1929 (WHEELER 1929 as <i>T. striatidens</i>)
Japan	1945 (F.N. Young, SI): Okinawa
Philippines	1945 (E.S. Ross, BMNH): San José, Mindoro Occidental
Nepal	1956 (E.I. Coher, MCZ): Amlekhganj
Bangladesh	1961 (E.S. Ross & D.O. Cavagnaro, BMNH): Chittagong
+ Bhutan	1972 (Basel Bhutan Expedition, BMNH): Phutsholing
Thailand	2002 (WAANTHOGCHAI & HASIN 2002)
Cocos (Keeling) Island	2005 (NEVILLE & al. 2008)

merce. On the central Pacific islands of Wallis and Futuna, WILSON & HUNT (1967) found that *T. lanuginosum* (as *T. striatidens*) "proved unexpectedly abundant on the islets" that surround the main island of Uvéa, indicating that they "are especially adapted to the islet environment or else thrive there in the lack of competition from ecological vicars limited to the larger islands." On Nukunonu Atoll, Tokelau Islands, LESTER & TAVITE (2004) found that *T. lanuginosum* was the most common ant in pitfall traps at forest sites where the dominant *Anoplolepis gracilipes* was absent, but *T. lanuginosum* numbers were greatly reduced in forest and urban areas with *A. gracilipes* present. WILSON & TAYLOR (1967) reported only one record of *T. lanuginosum* from Samoa, writing "the Samoan record is based on a sin-

Tab. 2: Earliest known records for *Tetramorium lanuginosum* from Australia and Oceania. Abbreviations as in Tab. 1.

	Earliest record
Australia	≤ 1902 (FOREL 1902 as <i>T. striatidens australis</i> [sic])
Mariana Islands	1911 (WHEELER 1916 as <i>T. striatidens</i>)
Solomon Islands	1915 - 1916 (W.M. Mann, MCZ): Auki
Samoa	≤ 1919 (H. Swale, AMNH): Apia
Line Islands	1920 (WILSON & TAYLOR 1967 as <i>T. striatidens</i>)
Cook Islands	1924 (WILSON & TAYLOR 1967 as <i>T. striatidens</i>)
FS Micronesia	1940 (CLOUSE 2007)
Palau	1947 (CLOUSE 2007)
Marshall Islands	1953 (CLOUSE 2007)
Gilbert Islands	1957 (CLOUSE 2007)
Wallis & Futuna	1965 (WILSON & HUNT 1967 as <i>T. striatidens</i>)
Tonga	1971 (WETTERER 2002)
Tuamotu Islands	1996 (MORRISON 1997 as <i>T. striatidens</i>)
Tokelau Islands	2002 (LESTER & TAVITE 2004)
Fiji	2004 (WARD & WETTERER 2006)

gle worn specimen taken many years ago; the species has not been recorded from the islands since, despite intensive collecting." WETTERER & VARGO (2003), however, collected *T. lanuginosum* at 12 sites on ten different Samoan islands, including the three main island (Savai'i, Upolu, and Tutuila) as well as seven smaller islands (Albatross Island, Anu'u, Namu'a, Nu'usetoga, Nu'utele, Ofu, and Tauga Rock). WETTERER & VARGO (2003) concluded "this suggests that *T. lanuginosum* has been in Samoa for many years, but perhaps recently expanded its populations."

In the eastern Pacific, a faunal survey in 1958 of Clipperton Island, an isolated 9 km² island more than 1000 km southwest of Mexico, yielded just three ant species, including seven series of *T. lanuginosum* (TAYLOR & WILSON 1961). Based on this, WILSON & HUNT (1967) considered *T. lanuginosum* a dominant species on Clipperton. *Tetramorium lanuginosum* potentially could have an important impact on Clipperton because this island has no native ants and some native species may lack defenses against ants. It is notable that the earliest known record of *T. lanuginosum* on Clipperton came from inside a boobie's nest (Tab. 4). *Tetramorium lanuginosum* was first recorded in the Galapagos Islands in 1997 on Floreana Island (PEZZATTI & al. 1998), but between 2005 and 2007, *T. lanuginosum* was recorded for the first time on five additional islands (Baltra, Española, Gardner, Santa Cruz, and Wolf; antweb.org database).

Tab. 3: Earliest known records for *Tetramorium lanuginosum* from the western Old World. Abbreviations as in Tab. 1, and CAS = California Academy of Sciences.

Tropical Africa	Earliest record
Sierra Leone	≤ 1890 (EMERY 1891 as <i>T. striatidens</i>)
Seychelles	1905 (FOREL 1912a as <i>T. striatidens felix</i>)
Mascarene Islands	1942 (DONISTHORPE 1946 as <i>T. mauricei</i>)
Madagascar	1988 (G.D. Alpert, MCZ): Tamatave
Ghana	2006 (DAVIS & ALONSO 2007)
+ Îles Eparses	2007 (B.L. Fisher, CAS): Mayotte
+ Comoro Is.	2008 (B.L. Fisher, CAS): Mouandzaza
Mediterranean	
Tunisia	≤ 1890 (EMERY 1891 as <i>T. striatidens</i>)
Israel	1922 - 1928 (MENOZZI 1933 as <i>T. striatidens</i>)
Libya	≤ 1932 (MENOZZI 1932 as <i>T. striatidens</i>)
Lebanon	1952 (K. Christiansen, MCZ): Antilias Stream
Malta	1976 (SCHEMBRI & COLLINGWOOD 1981)
+ Egypt	2003 (M. Sharaf, TAYLOR 2007): Damietta
Spain	2004 (REYES & ESPADALER 2005)
Other Old World	
England	1905 (WHEELER 1916 as <i>T. striatidens</i>)
Saudi Arabia	1983 (COLLINGWOOD 1985)
Netherlands	1984 (JONGE 1985)
Yemen	1999 (COLLINGWOOD & al. 2004)

In Madagascar and neighboring island groups in the western Indian Ocean, there are many, primarily recent records of *T. lanuginosum*. For example, only one of the 22 known site records from Madagascar dates to before 2001 (B.L. Fisher and associates; antweb.org database). All three sites records from Mayotte, Îles Eparses are from 2007 and all nine site records from the Comoro Islands are from 2008 and 2009 (B.L. Fisher and associates; antweb.org database).

TORRES & SNELLING (1997) surveyed Puerto Rican Bank islands and *T. lanuginosum* was one of just five ant species they found on small islands, but not on the main island of Puerto Rico. In my recent surveys of ants of the Eastern Caribbean, I found *T. lanuginosum* on many islands, though it was common only occasionally. For example, on the Puerto Rican island of Vieques, I collected *T. lanuginosum* at 12 locales, including urban, beach, and forest areas. I found *T. lanuginosum* was abundant on the University of the West Indies campus on Barbados.

Tab. 4: Earliest known records for *Tetramorium lanuginosum* from the Neotropics. Abbreviations as in Tab. 1.

West Indies	Earliest record
Barbados	≤ 1912 (FOREL 1912b as <i>T. striatidens</i>)
Puerto Rico	1981 - 1982 (TORRES & SNELLING 1997)
+ Dominican Rep.	2003 (M. Deyrup, MCZ): Santo Domingo
+ Trinidad	2003 (J.K. Wetterer, MCZ): Arima
+ Tobago	2003 (J.K. Wetterer, MCZ): Bon Accord
+ Dominica	2004 (J.K. Wetterer, MCZ): Roseau
+ Curaçao	2004 (J.K. Wetterer, MCZ): Piscadera
+ Virgin Islands	2005 (J.K. Wetterer, MCZ): William, St Croix
+ Antigua	2007 (J.K. Wetterer, MCZ): Elliots
+ Barbuda	2007 (J.K. Wetterer, MCZ): Landing River
+ Aruba	2007 (J.K. Wetterer, MCZ): Bubali
+ Nevis	2007 (J.K. Wetterer, MCZ): White Bay
+ Montserrat	2007 (J.K. Wetterer, MCZ): Marguerita Bay
+ St Vincent	2008 (M. DaSilva, pers. comm.): Canouan
+ Martinique	2008 (J.K. Wetterer, MCZ): Fort-de-France
Other Neotropical	
Clipperton Island	1938 (W.L. Schmitt, SI): boobie's nest
Mexico	1980 (J.A. Rodriguez, SI): Monterrey
Galapagos	1997 (PEZZATTI & al. 1998)

Tab. 5: Earliest known records for *Tetramorium lanuginosum* from the United States. Abbreviations as in Tab. 1.

	Earliest record
Louisiana	1913 (WHEELER 1916 as <i>T. striatidens</i>)
Mississippi	1930 (E.E. Byrd, SI): West Point
South Carolina	1932 (D.E. Read, SI): Beaufort
Alabama	≤ 1933 (SMITH 1933 as <i>T. striatidens</i>)
Florida	≤ 1933 (SMITH 1933 as <i>T. striatidens</i>)
Georgia	≤ 1951 (SMITH 1951 as <i>T. striatidens</i>)

Interestingly, *T. lanuginosum* is not yet known from continental South America, despite records from the nearby islands of Aruba, Curaçao, Trinidad, and Tobago (Fig. 5; Tab. 4). It is also notable that *T. lanuginosum* has not been recorded in southern Florida, where so many other species of exotic ants have flourished. DEYRUP & al. (2000) wrote:

"We have never found this species in Florida; it is evidently rare or local. It is also known from several other southeastern states, so it is unlikely to have been eliminated by cold weather in the southern part of its range." I found few recent records of *T. lanuginosum* from any part of the continental US. Perhaps the many dominant native and exotic ant species in South and North America have prevented widespread establishment of *T. lanuginosum*.

The many recent first records for *T. lanuginosum* in Samoa, the Galapagos, Madagascar (and neighboring island groups), and the West Indies suggest an on-going expansion of this species on numerous tropical islands outside its native range. Alternatively, *T. lanuginosum* may be much more widespread than generally recognized, occurring in native forest areas and on small islands throughout the tropics and subtropics, but not identified to species in published surveys. In any event, although *T. lanuginosum* has become established in many sites around the world, it appears unlikely that *T. lanuginosum* will ever become a significant pest species, except perhaps on small and / or isolated tropical islands.

Acknowledgements

I thank A. Wetterer, M. Wetterer, and A. Andersen for comments on this manuscript; S. Cover for help, encouragement, and ant identification; B. Bolton (BMNH), S. Cover (MCZ), M. Deyrup (ABS), J. Hogan (ONHM), and T. Schultz (SI) for help with their respective ant collections; J. Woinarski, D. Ward, M. Lush, and M. DaSilva for providing unpublished specimens records; O'Brien for GIS help; E. Sarnat for use of his excellent photos; D.P. Wojcik and S.D. Porter for compiling the FORMIS bibliography; C. Scheid and R. Pasos of the FAU library for processing so many interlibrary loans; Florida Atlantic University, the National Science Foundation (Award #0515648), and the National Geographic Society (Award #7241-02) for financial support.

Zusammenfassung

Von der Ameisenart *Tetramorium lanuginosum* MAYR, 1870 (älteres Synonym von *Triglyphothrix striatidens* (EMERY, 1889)), auch "wooly ant" genannt, ist seit langem bekannt, dass sie durch menschliche Handelsaktivitäten weit verbreitet wird. Um die weltweite Verbreitung von *T. lanuginosum* abzuschätzen, habe ich veröffentlichte und unveröffentlichte Nachweise von > 400 Fundorten zusammengetragen. Ich dokumentiere die frühesten bekannten Nachweise der Art für 77 geographische Gebiete (Länder, Inselgruppen, große karibische Inseln und US-Bundesstaaten), einschließlich vieler, für die ich keine bisher veröffentlichten Nachweise gefunden habe, darunter insbesondere einige der Westindischen Inseln: Ägypten, Antigua, Aruba, Barbuda, Bhutan, Curaçao, Dominica, Dominikanische Republik, Îles Eparses, Jungferninseln, Komoren, Martinique, Montserrat, Nevis, St. Vincent, Tobago und Trinidad. Anhand seiner Verbreitung und jener seiner nächsten Verwandten beurteilt, scheint *T. lanuginosum* im tropischen und subtropischen Ostasien und möglicherweise auch im nördlichen Australien und westlichen Ozeanien heimisch zu sein. *Tetramorium lanuginosum* dürfte auf kleinen Inseln besonders häufig sein, möglicherweise wegen der in diesen Lebensräumen verminderten Konkurrenz mit dominanten Ameisen. Erstnachweise von *T. lanuginosum* aus der jüngsten Zeit von vielen Inseln von Samoa, den Galapagosinseln, Madagaskar (und

benachbarten Inselgruppen) sowie den Westindischen Inseln legen nahe, dass sich exotische Populationen der Art auf zahlreiche tropische Inseln ausdehnen. Insgesamt erscheint es aber unwahrscheinlich, dass *T. lanuginosum* – außer vielleicht auf kleinen tropischen Inseln – jemals zu einem bedeutenden Lästling werden wird.

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