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Worldwide spread of the stigma ant, *Pachycondyla stigma* (Hymenoptera: Formicidae)

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Abstract

The stigma ant, *Pachycondyla stigma* (FABRICIUS, 1804), is an inconspicuous forest species that generally nests in and under rotten logs and feeds on termites. This species has an extensive range in both the New World and Old World tropics, but there has been disagreement on where *P. stigma* is native. To evaluate its known distribution and consider hypotheses on its native range, I compiled and mapped records of *P. stigma* from > 600 sites. I documented the earliest known *P. stigma* records for 55 geographic areas (countries, island groups, major West Indian islands, and US states) including several for which I found no previously published records: Antigua, Montserrat, Nevis, St Kitts, St Lucia, and Tonga.

Pachycondyla stigma shows characteristics of a native species throughout its range in both the New World and Old World, with near continuous distributions in intact forest habitats. The earliest records of *P. stigma* come primarily from the Neotropics; before 1900, there were published Neotropical records from Colombia, Costa Rica, Mexico, Bolivia, Venezuela, Guatemala, Panama, St Vincent, and Cuba, but only one published record from the Old World (Aru Island, Indonesia). Although *P. stigma* has relatives in both the Neotropics and Australia, its closest known relative is from Central America. Thus, the weight of evidence indicates that *P. stigma* originated in tropical South and Central America. Genetic analyses are needed to determine whether the native range of *P. stigma* also includes the West Indies and Florida.

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

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Introduction

The stigma ant, *Pachycondyla stigma* (FABRICIUS, 1804) (Subfamily Ponerinae), is an inconspicuous forest ant that generally nests in or under rotten logs and is thought to feed primarily on termites. WILSON & TAYLOR (1967) wrote that *P. stigma* "is one of the most widespread of all ponerine ants. In the New World it ranges from southern Florida through the Antilles and Central America to southern Brazil. In the Old World it is found continuously from southern China to the Caroline Islands, northern Queensland, and throughout Melanesia (except New Caledonia) to Samoa."

There has been disagreement concerning the native range of *Pachycondyla stigma*. For example, SMITH (1979) wrote that *P. stigma* is "apparently a tramp species distributed by commerce outside the New World. Whether or not it is endemic or adventive to Florida is unknown." DEYRUP & al. (2000), however, classified *P. stigma* as an exotic in Florida, noting, "its wide distribution in the Old World tropics suggests that it is native there." To evaluate its known distribution and consider hypotheses on its native range, I compiled and mapped specimen records of *P. stigma* from sites worldwide.

When evaluating the native and exotic ranges of a species, researchers may consider a spectrum of distributional, historical, evolutionary, ecological, and genetic information (CHAPMAN & CARLTON 1991). Evidence considered indicative of a species' native range includes older records largely confined to a single continuous geographic region, occurrence in intact native communities, high genetic diversity, and proximity to the ranges of closely related species. In contrast, evidence indicative of a species' exotic range includes the sudden appearance and spread of the species through an area discontinuous with other known populations, occurrence exclusively in coastal and highly disturbed environments, low genetic diversity due to a founder effect, and geographic isolation from closely related species.

Taxonomy and identification

FABRICIUS (1804) described *Formica stigma* (= *Pachycondyla stigma*) from "America meridionale" (South America). Junior synonyms of *P. stigma* include: *Ponera quadridentata* SMITH, 1859, *Ponera myopa* ROGER, 1860, *Ponera americana* MAYR, 1862, *Ponera stigma attrita* FOREL, 1893, *Euponera stigma rufescens* WHEELER & MANN, 1914, *Euponera nixoni* DONISTHORPE, 1943, *Euponera brunneus* DONISTHORPE, 1948, and *Euponera sexdentatus* DONISTHORPE, 1949 (see MACKAY & MACKAY 2010). Through numerous taxonomic revisions, authors have grouped *P. stigma* with many other species in several different genera including *Euponera*, *Mesoponera*, *Pachycondyla*, *Ponera*, *Pseudoponera*, and *Trachymesopus*. In his recent dissertation work, SCHMIDT (2009) split up the

Figs. 1 - 2: *Pachycondyla stigma*. (1) Head of a worker from Viti Levu, Fiji; (2) lateral view of the same worker (photos by E. Sarnat).

highly polyphyletic genus *Pachycondyla*, raising the subgenus *Pseudoponera* to genus level, though this new designation is not yet official.

BROWN (1963) placed *Pachycondyla stigma* in the "*stigma* species-group" along with species from both the Neotropics and Australia. Using cladistic analyses of both morphological and molecular data, SCHMIDT (2009) placed *P. stigma* as closest to an undescribed Neotropical species (*Pachycondyla* sp. JTL011), known only from Costa Rica. SCHMIDT (2009) placed these two species in the *stigma* group along with four Neotropical species, *Pachycondyla cauta* (MANN, 1922), *Pachycondyla cognata* (EMERY, 1896), *Pachycondyla gilberti* (KEMPF, 1960), and *Pachycondyla succedanea* (ROGER, 1863), plus one Australian species, *Pachycondyla pachynoda* (CLARK, 1930).

Workers of *Pachycondyla stigma* are 4 - 5 mm in length and are dark brown with lighter, orange-brown appendages (Figs. 1 - 3). Workers may be distinguished from related species by having mandibles with six teeth, tiny eyes (< 25 ommatidia), and a blunt petiolar node. DEYRUP & al. (2000) called *P. stigma* the "pantropical nimrod ant." I have used a simpler common name, "stigma ant," based on the Latin name.

Fig. 3: *Pachycondyla stigma*, worker at Archbold Biological Station, Florida (photo by A. Wild).

Materials and Methods

Using published and unpublished records, I documented the worldwide range of *Pachycondyla stigma*. I 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), and the Smithsonian Institution (SI, identified by M. Smith). In addition, I used on-line databases with collection information on specimens by Antweb (www.antweb.org) and the Global Biodiversity Information Facility (www.gbif.org). I received an unpublished record from D. Ward (Tonga). Finally, I collected *P. stigma* specimens on islands of the Pacific and the West Indies.

I obtained geo-coordinates for collection sites from published references, specimen labels, maps, or geography web sites (e.g., earth.google.com, 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 *Pachycondyla stigma* 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 *Pachycondyla stigma* specimen records from > 600 sites worldwide (Fig. 4). I documented the earliest known *P. stigma* records for 55 geographic areas (countries, island groups, major Caribbean islands, and US states; Tabs. 1 - 3), including several for which I found no previously published records: Antigua, Montserrat, Nevis, St Kitts, St Lucia, and Tonga.

Tab. 1: Earliest known records for *Pachycondyla stigma* from South and Central America. MCZ = Museum of Comparative Zoology. Unpublished records include collector, museum source, and site.

	Earliest record
South America	≤ 1804 (FABRICIUS 1804)
Colombia	≤ 1862 (MAYR 1862 as *P. americana*)
Costa Rica	1889 (EMERY 1890)
Bolivia	≤ 1894 (EMERY 1894)
Cocos Island	1898 (SOLOMON & MIKHEYEV 2005)
Mexico	≤ 1899 (FOREL 1899)
Venezuela	≤ 1899 (FOREL 1899)
Guatemala	≤ 1899 (FOREL 1899 as *P. stigma attrita*)
Panama	≤ 1899 (FOREL 1899 as *P. stigma attrita*)
Brazil	≤ 1905 (EMERY 1906)
Ecuador	1905 (SANTSCHI 1913)
Belize	1905 - 1906 (WHEELER 1907)
Guyana	1911 (WHEELER 1916)
Honduras	1920 (MANN 1922)
Surinam	1926 (N.A. Weber, MCZ): King Fred William IV Falls
El Salvador	1951 (E.S. Ross, MCZ): La Libertad
Peru	1954 (E.I. Schlinger & E.S. Ross, MCZ): Monsón
Argentina	≤ 1960 (KEMPF 1960)
Nicaragua	≤ 1989 (MAES & MACKAY 1993)
Paraguay	1996 (WILD 2002)
French Guiana	≤ 2001 (ORIVEL & al. 2001)

The northernmost record of *Pachycondyla stigma* came from Tunica Hills Wildlife Management Area in Louisiana (30.9° N; DASH 2004); the southernmost record came from Asuncion Botanical Garden in Paraguay (25.3° S; WILD 2002).

In the Pacific, I collected *Pachycondyla stigma* on three Manu'a Islands of Samoa: Ofu, Olesega, and Ta'u. In the West Indies, I collected *P. stigma* on 15 islands: Antigua, Grenada, Margarita, Montserrat, Nevis, Puerto Rico, St Croix, St John, St Kitts, St Lucia, St Thomas, St Vincent, Tobago, Tortola, and Trinidad. Almost all my records came from intact tropical moist forest. In addition, I made three collections of *P. stigma* in botanical gardens: in Puerto Rico (Rio Piedras) and St Lucia (Mamiku Garden and Diamond Botanical Garden).

MCGLYNN (1999) listed a tentative record of *Pachycondyla stigma* from the Galapagos in the Smithsonian collection, but I was not able to find this specimen and so I did not include this record. NELDER & al. (2006) cited DEYRUP & al. (1989) as including records of *P. stigma* from Alabama, but this citation is in error.

Tab. 2: Earliest known records for *Pachycondyla stigma* from the West Indies and the USA. + = no previously published records. Abbreviations as in Tab. 1.

West Indies	**Earliest record**
St Vincent	≤ 1893 (FOREL 1893)
Cuba	≤ 1896 (WHEELER 1913)
Bahamas	1904 (WHEELER 1905)
Haiti	≤ 1907 (FOREL 1907)
Grenada	1910 (WHEELER 1911)
Dominica	1911 (WHEELER 1913)
Jamaica	≤ 1913 (WHEELER 1913)
Trinidad	≤ 1916 (WHEELER 1916)
US Virgin Islands	1920 (W.M. Wheeler, MCZ): St Thomas
Dominican Republic	1928 (MENOZZI & RUSSO 1930)
Puerto Rico	1936 (SMITH 1936)
Guadeloupe	1987 (JAFFE & al. 1991)
Martinique	1987 (JAFFE & al. 1991)
+ Montserrat	1991 (J.P.E.C. Darlington, MCZ): Paradise Yard
British Virgin Islands	1992 (SNELLING 1993)
+ St Lucia	2006 (J.K. Wetterer, MCZ): Union Nature Trail
+ Antigua	2007 (J.K. Wetterer, MCZ): Boggy Peak
+ St Kitts	2007 (J.K. Wetterer, MCZ): Belmont
+ Nevis	2007 (J.K. Wetterer, MCZ): Prison Farm
USA	
Florida	1887 (DEYRUP & al. 2000)
Louisiana	1999 (DASH 2004)

Discussion

In both the New World and Old World, *Pachycondyla stigma* appears to have a largely continuous distribution (Fig. 4). The main continental distribution in the New World is almost entirely tropical, but extends into the subtropics in Paraguay (to 25.3° S), northern Argentina (to 23.9° S), and southern Brazil (to 23.5° S) in the south to but just to the edge of the tropics of central Mexico in the north (to 23.0° N; Fig. 4). *Pachycondyla stigma* is also widespread throughout the West Indies. In addition, there are some

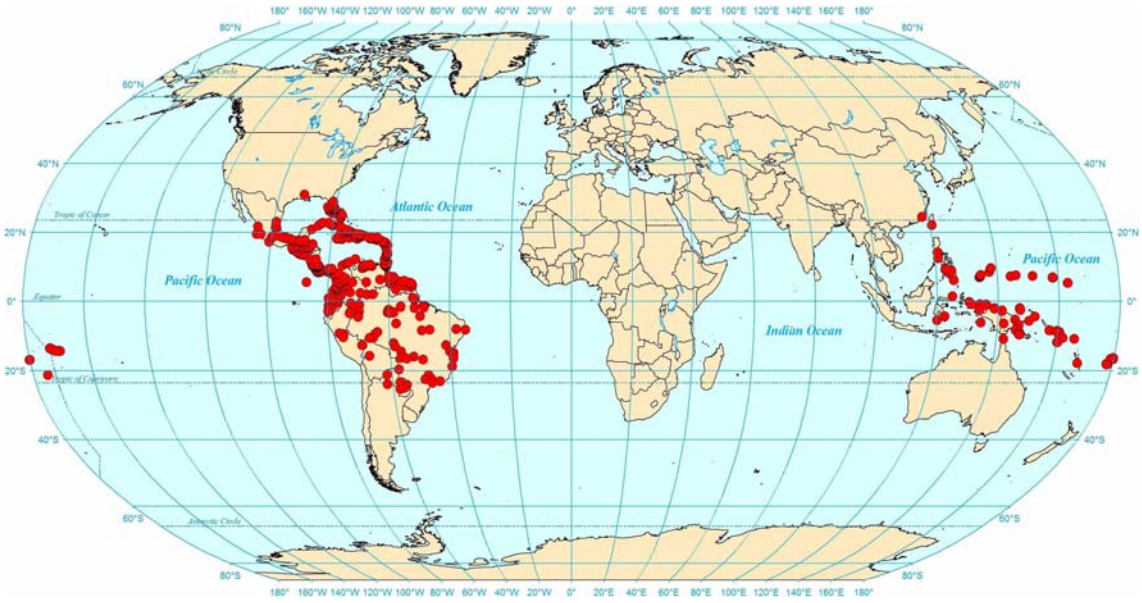

Fig. 4: Worldwide distribution records of *Pachycondyla stigma*.

Tab. 3: Earliest known records for *Pachycondyla stigma* from Asia, Australia, and Oceania. NZAC = New Zealand Arthropod Collection. Other abbreviations as in Tabs. 1 - 2.

	Earliest record
Indonesia	≤ 1858 (SMITH 1859 type *P. quadridentata*)
Papua New Guinea	≤ 1901 (FOREL 1901 as *P. stigma quadridentata*)
Philippines	1911 (C.F. Clagg, MCZ): Calian
Fiji	1915 - 1916 (MANN 1920)
Solomon Islands	1916 (MANN 1919)
Samoa	≤ 1918 (SANTSCHI 1919 as *P. stigma quadridentata*)
China	≤ 1927 (S.F. Light, MCZ): Backliang
FS Micronesia	1938 (CLOUSE 2007)
Palau	1945 (CLOUSE 2007)
Australia	1958 (Darlingtons, MCZ): Lockerie
Vanuatu	≤ 1959 (WILSON 1959)
+ Tonga	1975 (P.A. Maddison & M.V. Light, NZAC): near Tupou College
Taiwan	2001 - 2002 (HWANG 2006)

highly populations of *P. stigma* that extend well into the subtropics in the Bahamas (to 25.1° N), Florida (to 28.9° N), and Louisiana (to 30.9° N). In the Old World, *P. stigma* has a seemingly continuous, entirely tropical distribution from Philippines and Indonesia in the west through Melanesia and Micronesia to Samoa and Tonga in the east (Fig. 4). In addition, there are single records each from tropical China, Taiwan, and northernmost Australia. Distributional gaps may be due to common difficulties in finding this inconspicuous species.

In both the New World and Old World, *Pachycondyla stigma* is typically found in intact forest, nesting in or under rotten logs. For example, Deyrup (pers. comm.) wrote: "In Florida *P. stigma* usually occurs in open pine stands, including wet or seasonally flooded flatwoods. It is usually found in habitats that are relatively undisturbed, except by natural disturbances such as floods or fires. It often lives around dead pines whose bark is intact."

Because *Pachycondyla stigma* workers rarely forage above ground and do not generally come to bait, most collectors may fail to detect the presence of this species unless they break open rotten logs. For example, WILSON & TAYLOR (1967) wrote of *P. stigma*: "Although widely distributed on Samoa, it is evidently scarce there, being known chiefly from occasional collections of winged queens and males," and "may indeed be extinct on Samoa since it has not been collected since 1940, in spite of the efforts of Woodward, the Taylors, and Ettershank." In 1995, however, I sampled extensively from in and under logs and found *P. stigma* at eight sites in Samoa. In Chiapas, Mexico, DE LA MORA & PHILPOTT (2010) found *P. stigma* was the most common ant species encountered in rotten logs.

Pachycondyla stigma shows characteristics of a native species in both the New World and Old World, with near continuous distributions in forest habitats. Although distributional data do not provide definitive evidence for the native range of *P. stigma*, the earliest records of *P. stigma* come primarily from South America. Before 1900, there are many published records of *P. stigma* from the Neotropics (Colombia, Costa Rica, Mexico, Bolivia, Venezuela, Guatemala, Panama, St Vincent, and Cuba), but only one published record from the Old World (Aru Island, Indonesia; Tabs. 1 - 3). In addition, although *P. stigma* has close relatives in both the Neotropics and Australia, the closest known relationship is with a Neotropical species. Thus, the weight of evidence suggests a New World origin for *P. stigma*. Genetic analyses are needed to determine more definitively what constitutes the native range of this

species, e.g., whether its native range includes the West Indies and Florida.

Pachycondyla stigma does not fit the usual profile of a tramp ant, i.e., a species commonly spread by human commerce and associated with human disturbance. It is curious to speculate on how *P. stigma* came to have two extensive, apparently continuous ranges that are widely separated from each other, and yet few isolated populations elsewhere. This pattern suggests extensive short-range dispersal allowing it to saturate discrete areas, but rare long-range dispersal to new distant locations. *Pachycondyla stigma* has winged queens that can achieve short-range dispersal. Recent long-range dispersal seems most likely inside rotten logs transported by humans. Such transport may be rare compared with the dispersal of tramp ant species that commonly nest inside commercial products or hitch ride on air, sea, and land vehicles. It is possible that geographic barriers alone have kept *P. stigma* from expanding its Old World range to neighboring regions with hospitable climates, such as western Indonesia, Southeast Asia, and south India. But it is unclear what has prevented the overland spread of this ant through tropical Australia, which seems to lack geographic barriers.

Despite its extensive worldwide range, *P. stigma* has remained quite inconspicuous. In contrast, two other ponerine species (Ponerinae) have recently become recognized as important pests in human-disturbed environments. The Asian needle ant, *Pachycondyla chinensis* (EMERY, 1895), is an East Asian species now spreading through temperate North America, where severe allergic reactions to its painful stings have been reported (NELDER & al. 2006). The closely related samsum or sword ant, *Pachycondyla sennaarensis* (MAYR, 1862), is a widespread pest in tropical Africa and the Middle East, well known and feared for its powerful sting that can lead to anaphylactic shock and even death (AL-SHAHWAN & al. 2006). Although *P. stigma* can sting, this species rarely comes in contact with humans, except those breaking open rotten logs. It seems unlikely that *P. stigma* will ever achieve pest status.

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