

Worldwide spread of Alluau's little yellow ant, *Plagiolepis alluaudi* (Hymenoptera: Formicidae)

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Abstract

Plagiolepis alluaudi EMERY, 1894 is a tiny Old World ant that has spread to many parts of the world through human commerce. To examine the worldwide distribution of *P. alluaudi*, I compiled and mapped published and unpublished specimen records from > 450 sites. I documented the earliest known *P. alluaudi* records for 46 geographic areas (countries, island groups, and US states), including several areas for which I found no previously published records: Anguilla, Barbados, Comoros Islands, Grenada, Guadeloupe, Îles Eparses, Martinique, Nevis, St. Kitts, St. Lucia, and St. Martin.

Plagiolepis alluaudi is a primarily tropical species, apparently native to Madagascar and neighboring islands. It has become a pest on Pacific islands and in European greenhouses. Before the present study, the only published reports of *P. alluaudi* in the New World were several records from Bermuda and one record from California. Recent surveys in Bermuda and California have produced no additional reports of *P. alluaudi*. My new records of *P. alluaudi* from nine tropical islands in the West Indies indicate a substantial New World invasion. It may be that the tropical climate of the West Indies is more suitable for *P. alluaudi* than the subtropical climates of Bermuda and California, where it may have died out.

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

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Introduction

FOREL (1911) compiled a list of 15 tramp ant species, spread by human commerce, which had achieved or were in the process of achieving cosmopolitan distributions. Several of these have become major ecological, agricultural, and / or household pests, e.g., *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) (WETTERER 2005, 2008, 2009a, b, 2011a, 2012d, WETTERER & al. 2009). Over the past 100 years, several additional ant species not on FOREL's (1911) list have become or are rapidly becoming cosmopolitan, with broad ranges in both the Old World and New World (e.g., see WETTERER & PORTER 2003, WETTERER 2011b, 2012a, b, c, WETTERER & RADCHENKO 2011, WETTERER & al. 2012). Here, I examine the spread of an Old World tramp ant species that has only recently begun to be found at many sites in the New World: *Plagiolepis alluaudi* EMERY, 1894.

The genus *Plagiolepis* is native to the Old World. SMITH (1957) published the first records of *P. alluaudi* in the New World: specimens collected on Catalina Island, California by W.M. Mann and on Bermuda by I.W. Hughes. In addition, SMITH (1957) reported specimens intercepted in quarantine on plants being imported into the US from Bermuda, St. Lucia, and St. Kitts. SMITH (1957) wrote:

"*Plagiolepis alluaudi* is admirably adapted for becoming widely distributed by commerce throughout the tropical and semitropical parts of the world. It would not be surprising to learn of its presence in many more localities than are now known."

SMITH (1957) concluded, "evidence obtained from literature indicates that *alluaudi* is of Ethiopian origin" (i.e., from sub-Saharan Africa). Although SMITH (1957) did not present this evidence, later authors have agreed with the assessment that *Plagiolepis alluaudi* is of African origin (e.g., TAYLOR & WILSON 1961, WILSON & TAYLOR 1967, DLUSSKY 1994, POHL 2006). SMITH (1957) noted that *P. alluaudi* had been "collected from many islands in the Indian and Pacific Oceans, especially those nearest Africa and Madagascar. Its presence on islands in the Pacific Ocean is presumably due to introduction."

Taxonomy

Plagiolepis alluaudi is a tiny (total length ~ 1.5 mm) yellow ant (Figs. 1 - 3). EMERY (1894) described *P. alluaudi* from the Seychelles, naming it after the collector, Charles A. Alluau, who made extensive insect collections in Africa and surrounding islands from 1887 to 1930. Junior synonyms of *P. alluaudi* include: *Plagiolepis mactavishi* WHEELER, 1908, *Plagiolepis foreli* SANTSCHI, 1920, *Plagiolepis foreli ornata* SANTSCHI, 1920, *Plagiolepis foreli* MANN, 1921, and *Plagiolepis augusti* EMERY, 1921, all synonymized by SMITH (1957), who wrote: "The fact that

it is a tramp species also accounts for many of the synonyms." Instead of the Seychelles, the type locale of *P. alluaudi*, MCGLYNN (1999) incorrectly listed India and that this species was native to India. This error has spread to other publications (e.g., STARR & al. 2007).

EMERY (1921) placed *Plagiolepis alluaudi* as most closely related to *Plagiolepis exigua* FOREL, 1894 known from Australia, Hawaii, India, Indonesia, Madagascar, Saudi Arabia, Scotland, Taiwan, and Yemen, *Plagiolepis bicolor* FOREL, 1901 known from New Guinea, and *Plagiolepis brunni* MAYR, 1895 known from Sudan, Mozambique, Kenya, Zimbabwe, and South Africa.

Of these, only *Plagiolepis alluaudi* and *P. exigua* are yellow in color, but *P. alluaudi* has a round head with strongly convex posterior margin, whereas *P. exigua* has an oblong head (longer than wide) with a somewhat concave posterior margin.

The only common name widely used for *Plagiolepis alluaudi* is "little yellow ant", though certainly this name could apply to many other ant species as well, notably numerous small yellow *Solenopsis* and *Brachymyrmex* species. In fact, *P. alluaudi* workers closely resemble in size and color workers of *Brachymyrmex* cf. *heeri*, a very common species in the West Indies. These two species, however, can be easily distinguished because, as noted by SANTSCHI (1920), *P. alluaudi* workers have eleven antennal segments whereas *Brachymyrmex* workers have nine.

Materials and Methods

Using published and unpublished records, I documented the worldwide range of *Plagiolepis alluaudi*. I obtained unpublished site records from museum specimens in the collections of the Museum of Comparative Zoology (MCZ, identified by S. Cover) and the Smithsonian Institution (SI, identified by B. Bolton). In addition, I used on-line databases with collection information on specimens by the Essig Museum of Entomology at the University of California, Berkeley (UCB), AntWeb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). I received unpublished *P. alluaudi* records from R. Guillem (England). Finally, I collected *P. alluaudi* specimens on islands of the Pacific and the West Indies. Published records came almost exclusively from publication indexed in the FORMIS Ant Bibliography.

I 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 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. 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.

I did not map records of *Plagiolepis alluaudi* found in newly imported goods or intercepted in transit by quarantine inspectors because the original source of such material is never known. For example, I did not include SMITH'S (1957) records of *P. alluaudi* "from St. Lucia and St. Kitts in the British West Indies intercepted on plants by Plant

Quarantine Inspectors of the U.S. Department of Agriculture". Nor did I include records of *P. alluaudi* listed in KEMPF'S (1972) catalog from St. Lucia and St. Kitts, because these are almost certainly based on SMITH'S (1957) records.

Results

I compiled published and unpublished specimen records from > 450 sites worldwide (Fig. 4). I documented the earliest known *Plagiolepis alluaudi* records for 46 geographic areas (countries, island groups, major Caribbean islands, and US states), including many areas for which I found no previously published records: Anguilla, Barbados, Comoros Islands, Grenada, Guadeloupe, Îles Eparses, Martinique, Nevis, St. Kitts, and St. Lucia (Tab. 1).

I collected *Plagiolepis alluaudi* in a wide variety of natural and disturbed habitats on islands of the Pacific and the West Indies:

Hawaii (one site): Big Island, Panaewa Forest Reserve, *Cecropia* by road (1994).

Tonga (four sites): Vava'u, Disaster Point, forest (1995), Ha'apai, Lifuka; Niu'akalo, beach (1995), Tongatapu, Hofoa, vacant lot (1995), Tongatapu, Keleti, beach (1995).

Fiji (one site): Viti Levu, Waisoi Forest Camp, forest; inside epiphyte (1997).

Anguilla (one site): Meads Bay, hotel grounds (2006).

Barbados (nine sites): Edghill, weeds by grass field (2003), King George V Park, trees and mowed grass (2003), Black Rock, plantings around apartment (2003), The Valley, sugar field (2003), Black Rock, compost by hotel (2006), Hackleton Cliff, forest below cliff (2006), Hackleton Cliff, grass at top edge of cliff (2006), Marine Gardens, plantings by apartments (2006), Bennett's, trees by Route 2A (2006), Cave Hill, UWI campus (2006), Rockless, gully forest (2006).

Grenada (one site): Grand Etang Lake, south shore forest (2003).

Guadeloupe (two sites): Chabert, forest (2011), Ballif, waterfront park (2011).

Martinique (one site): Dostaly, suburb (2011).

St. Kitts (three sites): Bayford's, forest near radio tower (2007), Jack-in-the-Box, forest near cane field (2007), Romney's, Caribelle Batik garden (2007).

Nevis (one site): Rawlins, Butt-Butt Road (2007).

St. Lucia (three sites): Cap Estate, by golf course (2006), South of Pigeon Point, trees and grass (2003), Barre Le L'Isle, forest 1.4 km West of trail (2003).

St. Martin (one site): Pic Paradis, South side, forest (2006).

AntWeb (accessed on 28 May 2013) reported that *Plagiolepis alluaudi* records (primarily from Madagascar) most commonly came from the following habitats: tropical dry forest (171 sites), rainforest (146 sites), montane rainforest (85 sites), gallery forest (47 sites), littoral rainforest (29 sites), urban / garden (20 sites), spiny forest / thicket (33 sites), park / garden (18 sites), montane forest (11 sites).

Problematic records

SAUNDERS (1896) reported: "*Plagiolepis flavidula*, Rog. - An exotic species introduced into some of the hot houses at Kew and Cambridge. The worker is exceeding small and yellow, and may be known by its eleven-jointed antennae, and its bright shining surface." DONISTHORPE (1908) found

Tab. 1: Earliest known records for *Plagiolepis alluaudi*. Unpublished records include collector, museum source, and site. MCZ = Museum of Comparative Zoology. SI = Smithsonian Institution. * = possible misidentification (see text). + = no previously published records.

Africa	Earliest record
Seychelles	1892 (EMERY 1894)
Réunion	≤ 1895 (FOREL 1895)
Tanzania	≤ 1907 (FOREL 1907)
Kenya	≤ 1920 (SANTSCHI 1920 as <i>P. foreli ornata</i>)
Madagascar	≤ 1921 (EMERY 1921)
Ascension Island	1958 (WETTERER & al. 2007)
Saint Helena	1958 (TAYLOR & WILSON 1961)
Nigeria	≤ 1978 (TAYLOR 1978 as " <i>Plagiolepis</i> species T ¹ ")
Cameroon	2000 (B.L. Fisher, AntWeb): Bimbia Forest
Gabon	2006 (YANOVIK & al. 2007)
+ Rodrigues Island	2007 (A. Meunier, AntWeb): Canyon Tyeul
+ Îles Eparses	2007 (B.L. Fisher & al., AntWeb): Mayotte
+ Comoros Islands	2008 (B.L. Fisher & al., AntWeb): many sites
Asia, Australia, Oceania	
Society Islands	1906 - 1907 (WHEELER 1908 as <i>P. mactavishi</i>)
Taiwan	≤ 1909 (WHEELER 1909 as <i>P. mactavishi</i>)
Hawaii	1913 (GULICK 1913 in KRUSHELNYCKY & al. 2005)
Fiji	1914 (MANN 1921 as <i>P. foreli</i>)
New Caledonia	≤ 1920 (SANTSCHI 1920 as <i>P. foreli ornata</i>)
India	≤ 1921 (EMERY 1921)
Easter Island	≤ 1922 (WHEELER 1922 as <i>P. mactavishi</i>)
Marquesas Islands	1925 (CHEESMAN & CRAWLEY 1928 as <i>P. mactavishi</i>)
Austral Islands	1934 (WHEELER 1936 as <i>P. mactavishi</i>)
Gambier Islands	1934 (WHEELER 1936 as <i>P. mactavishi</i>)
Indonesia	1944 (DONISTHORPE 1948)
China*	1945 (WILSON & TAYLOR 1967)
New Zealand	1966 (TAYLOR 1971)
Niue	≤ 1967 (TAYLOR 1967)
Cook Islands	≤ 1967 (TAYLOR 1967)
Japan	≤ 1979 (SHINDO 1979 in OGATA 2003)
Christmas Island	≤ 1980 (COLLINGWOOD & HEDLUND 1980 in FRAMENAU & THOMAS 2008)
Tonga	1980 (DLUSSKY 1994)

Australia	1981 (DEBAAR 1983)
Malaysia	2004 - 2005 (PFEIFFER & al. 2008 as <i>P. cf. alluaudi</i>)
Samoa	2006 (SAVAGE & al. 2009)
Norfolk Island	≤ 2011 (ANONYMOUS 2011)
Europe	
England	≤ 1896 (SAUNDERS 1896 as <i>P. flavidula</i>)
Switzerland	1904 (SANTSCHI 1920 as <i>P. foreli</i>)
Ireland (Eire)	≤ 1908 (DONISTHORPE 1908)
Scotland	≤ 1908 (DONISTHORPE 1908)
Northern Ireland	≤ 1915 (DONISTHORPE 1915)
Germany	≤ 1920 (SANTSCHI 1920 as <i>P. foreli ornata</i>)
Netherlands	1921 (BOER & VIERBERGEN 2008)
France	≤ 2004 (RADCHENKO 2004)
New World	
California	1928 (W.M. Mann, SI): Catalina Island
Bermuda	≤ 1952 (SMITH 1957)
+ Barbados	1998 (E.O. Wilson & S.P. Cover, MCZ): Barbados Wildlife Reserve
+ St. Lucia	2003 (J.K. Wetterer, MCZ): Pigeon Point
+ Grenada	2003 (J.K. Wetterer, MCZ): South shore of Grand Etang Lake
+ Anguilla	2006 (J.K. Wetterer, MCZ): Meads Bay
+ St. Martin	2006 (J.K. Wetterer, MCZ): Pic Paradis
+ St. Kitts	2007 (J.K. Wetterer, MCZ): Bayford's
+ Nevis	2007 (J.K. Wetterer, MCZ): Rawlins
+ Guadeloupe	2011 (J.K. Wetterer, MCZ): Ballif
+ Martinique	2011 (J.K. Wetterer, MCZ): Dostaly

P. alluaudi at Kew, and DONISTHORPE (1915) designated *P. flavidula* ROGER, 1863, to be a junior synonym of *P. alluaudi*. SMITH (1955), however, asked H. Bischoff to examine Roger's *P. flavidula* type, which he found "to be a *Brachymyrmex*, but he was not able to determine the species". SMITH (1955) therefore transferred *P. flavidula* to *Brachymyrmex*. *Brachymyrmex* species, however, have 9-segment antennae, not 11-segment antennae as in *P. alluaudi*, therefore, although the type specimen of *P. flavidula* may be a *Brachymyrmex*, SAUNDERS' (1896) two *P. flavidula* records appear to be misidentified *P. alluaudi* and so I include these records.

There are specimens of *Plagiolepis alluaudi* in the MCZ labeled as collected by K. Bäckström on the Juan Fernandez Islands, but this is almost certainly a labeling error. WHEELER (1922) reported this species (as *P. mactavishi*) collected by Bäckström on Easter Island, but not from the Juan Fernandez Islands. Similarly, the type specimens of *Nylanderia bourbonica skottsbergi* in the MCZ are labeled as coming from Juan Fernandez Islands, but INGRAM & al. (2006) concluded this was a labeling error and that the specimens are actually from Easter Island.



Figs. 1 - 3: *Plagiolepis alluaudi*. Worker from Forêt d'Orangea, Madagascar (CAS-ENT0429209), (1) head, (2) lateral view, (3) dorsal view (photos by AntWeb).

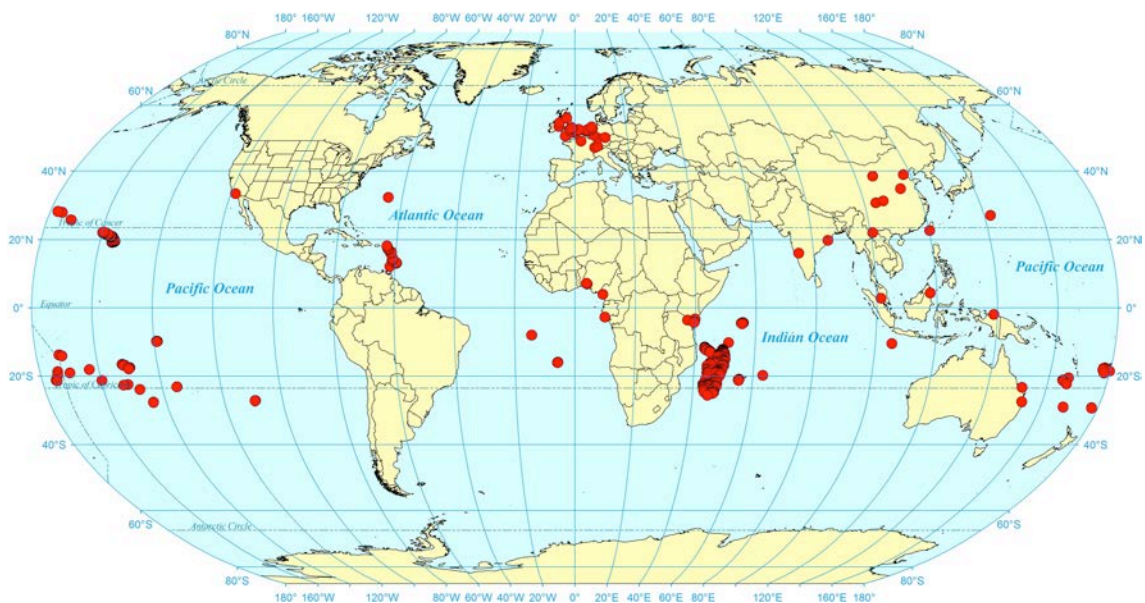


Fig. 4: Worldwide distribution records of *Plagiolepis alluaudi*. Records from central China are probably based on mis-identifications (see text).

PFEIFFER & al. (2008) reported uncertain *Plagiolepis* cf. *alluaudi* from Malaysia, but I included these records because PFEIFFER & al. (2011) later cited them as *P. alluaudi*.

Discussion

The majority of *Plagiolepis alluaudi* records come from islands in the Indian and Pacific Oceans (Fig. 4). *Plagiolepis alluaudi* is a primarily tropical species; almost all subtropical records come from southernmost Madagascar (Fig. 4). *Plagiolepis alluaudi* is particularly widespread in the forests of Madagascar and neighboring islands, suggesting that it is native to this region. Although *P. alluaudi* is widespread and common in some parts of Melanesia and Polynesia, there is an enormous distributional gap where this species is virtually unknown between the western Indian Ocean and the Pacific islands, supporting SMITH's (1957) supposition that *P. alluaudi* is exotic to the Pacific.

The 25 records from the West Indies reported here (one by E.O. Wilson and S.P. Cover in Tab. 1; 24 by J.K. Wetterer in Results) are the only New World specimen records of *Plagiolepis alluaudi* not intercepted on imported goods, except for a few records from Bermuda (SMITH 1957, WETTERER & WETTERER 2004) and one record from Catalina Island, California (collected by William M. Mann; SMITH 1957). WETTERER & WETTERER (2004) surveyed ants in Bermuda in 2002 and did not find any *P. alluaudi*, suggesting that this species is rare or extinct on Bermuda. Many researchers have made extensive ant collections in California, but have never produced another record of *P. alluaudi*, suggesting that either the California population has been extirpated or the one record was based on a labeling error. In fact, this one record of *P. alluaudi* is very suspect: I have been unable to find any other records of ants collected by William M. Mann on Catalina Island.

In contrast, the new *Plagiolepis alluaudi* records presented here are broadly distributed in the West Indies, coming from nine different islands. Although all *P. alluaudi* records from the West Indies are recent, it is likely that this species has been in the region for many years, based on the two early quarantine records from St. Lucia, and St. Kitts (SMITH 1957; see Introduction). This species may have been overlooked in part because of its close resemblance to the very common native *Brachymyrmex* cf. *heeri*. It appears that the tropical climate of the West Indies is more suitable for *P. alluaudi* than the subtropical climates of Bermuda (32.2° N) and Catalina Island (33.4° N). If this is true, then this suggests that outdoor records of *P. alluaudi* from subtropical and temperate parts of central China (up to 38.9° N; CHANG & al. 1999, WANG & LI 2009, WANG & al. 2009) are probably based on misidentifications of a similar species, perhaps *Plagiolepis cardiocarenis* CHANG & HE, 2002, which was described from this region (CHANG & HE 2002a). CHANG & HE (2002b), however, list both *P. alluaudi* and *P. cardiocarenis* as present in Central China.

Plagiolepis alluaudi has been reported from a wide range of habitats. AntWeb specimen records came mainly from natural forest areas. In contrast, I found *P. alluaudi* primarily in disturbed habitats, but this difference is likely due to differences in sampling: I primarily collect in disturbed habitats.

Plagiolepis alluaudi has become a minor house and agricultural pest in some areas. For example, EHRHORN (1931) reported *P. alluaudi* as a house pest in Hawaii. KRAUSS

(1957) reported "an unusual abundance of this ant in Manoa Valley, Honolulu. They feed on sweets and are a general nuisance." JONES & al. (2001) reported that *P. alluaudi* made up 51.2% of specimens collected by sticky traps in a macadamia orchard in Pahala, Hawaii. Many studies have noted *P. alluaudi* tending plant-feeding Hemiptera (e.g., on Laysan Island: BUTLER & USINGER 1963). WANG & al. (2009) observed *P. alluaudi* preying on the larvae of the emerald ash borer, *Agilus planipennis* FAIRMAIRE, 1888, a pest species highly destructive to ash trees.

Plagiolepis alluaudi also has been reported from numerous greenhouses in Europe. For example, DONISTHORPE (1908) wrote that *P. alluaudi* was "abundant in the Palm House" at Kew Gardens, England and that it "occurs in the Botanic Gardens in Edinburgh and Dublin". DONISTHORPE (1915) listed additional records of *P. alluaudi* from botanical gardens and greenhouses in six locations in England (Cambridge, Oxford, Edgbaston, Bramcote, Notts, and Beccles) and one in Northern Ireland (Belfast). SANTSCHI (1920) reported *P. alluaudi* (as *P. foreli*) from the Zurich Botanical Garden in Switzerland. BOER & VIERBERGEN (2008) listed *P. alluaudi* from zoos and botanical gardens in five cities in Holland (Groningen, Emmen, Leiden, Delft, and Arnhem). POHL (2006) reported *P. alluaudi* tending a variety of plant-feeding Hemiptera in the botanical garden at Universität Bayreuth in Germany. In 2011, D. Stradling collected *P. alluaudi* in the Tropical House of the Paignton Zoo, South Devon, England (R. Guillem, pers. comm.).

Part of the success of *Plagiolepis alluaudi* in exotic locales may be due to its ability of co-exist with dominant invasive ants. SMITH (1957) noted that in Bermuda, *P. alluaudi* "apparently live on good terms with other ants, especially with *Pheidole megacephala*". LE BRETON (2003) found that *P. alluaudi* was common in areas of New Caledonia dominated by *Pheidole megacephala* and *Wasmania auropunctata*, and it was the ant species most successful at defending bait against the aggressive *W. auropunctata*, succeeding in 85% of encounters. BURWELL & al. (2012) found that *P. alluaudi* was the only exotic ant of Great Barrier Reef islands that showed no decreases in the presence of *Pheidole megacephala*.

SMITH (1957) appears to have been correct in his expectation that *Plagiolepis alluaudi* was well suited to spread around the world via human commerce. With the modern global economy, one may expect this species to turn up in many more places in the future.

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