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Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae)

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Abstract

The longhorn crazy ant, *Paratrechina longicornis* (LATREILLE, 1802), is a ubiquitous agricultural and household pest throughout much of the tropics and subtropics and a pervasive indoor pest in temperate areas. I compiled specimen records of *P. longicornis* from > 2100 sites worldwide and analyzed historical, ecological, and evolutionary information to evaluate its known distribution, geographic origin, and potential future spread. I documented the earliest known *P. longicornis* records for 181 geographic areas (countries, major islands, island groups, US states, and Canadian provinces), including many for which I found no previously published records, e.g., Anguilla, Argentina, Austral Islands, Bahrain, British Indian Ocean Territory, Cayman Islands, Comoro Islands, Dominica, East Timor, El Salvador, Gambia, Ghana, Gibraltar, Guatemala, Iles Eparses, Kenya, Maldives, Mali, Montserrat, Nepal, Nevis, Pakistan, St. Kitts, St. Lucia, Turks and Caicos Islands, Tuvalu, Maryland, Missouri, and Virginia. *Paratrechina longicornis* is arguably the most broadly dispersed of all ant species, distributed widely across the Old World and New World in both the northern and southern hemispheres. The successful worldwide spread of *P. longicornis* relates to its ability to flourish in highly disturbed and artificial environments, including ships at sea. Whereas *P. longicornis* records are most frequent near major commercial waterways, I expect that with the increasing importance of air transport, *P. longicornis* will spread to more inland areas as well. Many *P. longicornis* records, including most if not all records from temperate latitudes, come from inside or near buildings. Because *P. longicornis* can live indoors anywhere that humans live, there is no limit to the latitude where it could thrive. The worldwide distribution records of *P. longicornis* and two species-specific symbionts provide ambiguous clues to the original native range of *P. longicornis*. However, the distributions of three closely related *Paratrechina* species offer good evidence that *P. longicornis* is native to Southeast Asia and Melanesia.

Key words: Biogeography, biological invasions, worldwide distribution, exotic species, Formicidae, invasive species, tramp ants.

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Introduction

Tramp ants are species that commonly are spread by human commerce and associate with human disturbance. Perhaps the most widespread of all tramp ants is the longhorn crazy ant, *Paratrechina longicornis* (LATREILLE, 1802). *Paratrechina longicornis* is a ubiquitous household and garden pest throughout much of the tropics and subtropics and is a pervasive indoor pest in temperate areas. In addition, *P. longicornis* can be a significant agricultural pest, enhancing populations of phloem-feeding Hemiptera, such as mealybugs, scale insects, and aphids. Hemiptera cause damage by sapping plants of nutrients and increasing the occurrence of diseases, including viral and fungal infections. Although *P. longicornis* is usually rare or absent in intact natural environments, it can be very common in disturbed and semi-natural environments. For example, FORYS & ALLEN (2005) found that *P. longicornis* was by far the most widespread exotic ant in the lower Florida Keys. *Paratrechina longicornis* has long been known as an important greenhouse pest, in both temperate and tropical regions (e.g., France: NYLANDER 1856, Sri Lanka: MOTSCHOULSKY 1863), where it can reach enormously high population levels. *Paratrechina longicornis* has even invaded Biosphere 2, a 1.3-hectare greenhouse structure in the Arizona desert used as a microcosm for studying ecological interactions and global change. WETTERER & al. (1999) found that virtually all ants (> 99.9 %) coming to bait in Biosphere 2 were *P. longicornis*. WETTERER & al. (1999) observed *P. longicornis* foragers feeding almost exclusively on the sugary excretions (honeydew) produced by vast numbers of Hemiptera found on many plants. The only invertebrates thriving in Biosphere 2, besides *P. longicornis* and phloem-feeding Hemiptera, were either species with effective defenses against ants (well-armored isopods and millipedes) or tiny subterranean species that can escape ant predation (mites, thief ants, and springtails). A convergent pattern of biodiversity occurs in disturbed tropical and subtropical ecosystems dominated by tramp ants (e.g., COLE & al. 1992). Here, I document the known distribution of *P. longicornis*, and evaluate where it may have originated and where it may spread in the future.

Determining the native and exotic ranges of pest species can be useful in management strategies, such as searching for appropriate biocontrol agents. When evaluating the native and exotic ranges of a species, researchers may consider a spectrum of distributional, historical, evolutionary, ecological, and genetic information (e.g., see EMERY 1893, WASMANN 1905a, b, CHAPMAN & CARLTON 1991). Evidence considered indicative of a species' native range includes older records largely confined to a single continuous geographic region, occurrence in inland native communities, high genetic diversity, co-occurrence of species-specific symbionts, 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, absence of species-specific symbionts, and geographic isolation from closely related species. In addition, the absence of natural enemies in a species' exotic range may result in population explosions. Finally, some tramp ant species (e.g., *Linepithema humile* (MAYR, 1868) and *Solenopsis invicta* BUREN, 1972) show extensive unicoloniality within their exotic range, where colonies spread over a broad geographic area show no intraspecific aggression, behaving as if they all belonged to a single colony (e.g., see WETTERER & WETTERER 2006).

EMERY (1893) evaluated the geographic origins of several widespread ant species, but was unable to discern an original homeland of *P. longicornis*, because it was already very broadly dispersed in tropical areas around the world. WASMANN (1905b) speculated on the geographic origin of *P. longicornis* and two myrmecophiles that live in *P. longicornis* nests: *Coluocera maderae* WOLLASTON, 1854 (Coleoptera: Lathridiidae) and *Myrmecophilus americanus* SAUSSURE, 1877 (Orthoptera: Myrmecophilidae). WASMANN (1905b) noted that *P. longicornis* and its symbionts were widespread in India and neighboring parts of Southeast Asia, whereas in other parts of the world *P. longicornis* was known only from coastal areas along major trade routes used by Portuguese and Spanish ships and the two symbionts were rarely encountered. From this, WASMANN (1905b) concluded that *P. longicornis* and its symbionts probably originated in the Indian region. WHEELER (1910) wrote that WASMANN (1905b) offered "good reasons for believing that the original home of this ant is India, and that it has been carried to all parts of the tropics in ships." Later, WHEELER (1919) wrote with apparent confidence that *P. longicornis* "is of Indomalaysian origin." WILSON & TAYLOR (1967) wrote that *P. longicornis* "probably originated within the Old World tropics, perhaps specifically in southeastern Asia or Melanesia." BERNARD (1968) and DLUSSKY (1994) also judged *P. longicornis* to be of Asian origin, and in earlier papers I have considered it an Asian species (e.g., WETTERER 2002, WETTERER & VARGO 2003). In contrast, FOWLER & al. (1994) listed *P. longicornis* as originating in tropical Africa and HOLWAY & al. (2002) also called this species African. KENNE & al. (2005) premised their study of the predatory behavior of *P. longicornis* in Cameroon on the assumption that *P. longicornis* was native to West Africa. Thus, whereas there is general agreement that *P. longicornis* originated in the Old World tropics, there is disagreement as to the subregion. I therefore evaluated multiple lines of evidence in an effort to discern the native range of *P. longicornis*.

Common names

By far the most-used common English name for *P. longicornis* is the "crazy ant," due to its rapid, seemingly erratic movements. Unfortunately, this common name is also often used for many other ant species, including all *Paratrechina* species, many of which are also widespread tramp species, e.g., *P. bourbonica* (FOREL, 1886), *P. flavipes* (SMITH, 1874), *P. fulva* (MAYR, 1862), *P. guatemalensis* (FOREL, 1885), *P. jaegerskioeldi* (MAYR, 1904), *P. pubens* (FOREL, 1893), and *P. vividula* (NYLANDER, 1846). Recently, some authors have begun to use the name "black crazy ant" to distinguish *P. longicornis* from another widespread pest species often called the "crazy ant" or the "yellow crazy ant," *Anoplolepis gracilipes* (SMITH, 1857) (e.g., HOFFMANN & O'CONNER 2004). Unfortunately, the common name "black crazy ant," does not refer to a unique character and may better describe other *Paratrechina* species, e.g., *P. bourbonica*, which is darker in color than *P. longicornis*. Additional common names for *P. longicornis* include the long-horned ant (NEUMANN 1993 in HARRIS & BERRY 2005), the hairy ant (CHIN 1998), and the slender crazy ant (DEYRUP & al. 2000). I propose that "longhorn crazy ant" is a more descriptive common name, derived from a primary distinguishing characteristic and its Latin name (*longicornis* = longhorn). This name is unlikely to be confused with the common name of any other ant species.

Methods

I documented the worldwide range of *Paratrechina longicornis* using both published and unpublished records. Unlike many other major pest ant species, *P. longicornis* is very easy to identify correctly, and therefore identifications in the literature are highly reliable. I obtained unpublished site records from museum specimens in the collections of the American Museum of Natural History (AMNH), the Archbold Biological Station (ABS), the British Natural History Museum (BMNH), the Museum of Comparative Zoology (MCZ), the National Museums Liverpool (NML), the Oxford University Natural History Museum (ONHM), the Smithsonian Institute's National Museum of Natural History (SI), Tel Aviv University (TAU), and the University of Guam Museum (UGM). I also examined specimens at the MCZ on loan from Museum Paris (MP). In addition, I used on-line databases with collection data of specimens in the Australian National Insect Collection (ANIC), the Essig Museum at UC Berkeley (UCB), and the California Academy of Sciences (CAS). I received unpublished site records and specimens from many sources: O. Bourquin (Mariana Islands), H. Cagniant (Algeria, Morocco), R. Clouse (Micronesia), M. Deyrup (Florida), G. Dlussky (Samoa), J. Endeman (Antigua, Ascension Island, Barbados, British Indian Ocean Territory, Colombia, East Timor, Grenada, Indonesia, the Maldives, Peru, St Helena), X. Espadaler (Brazil, Canary Islands, India, Malaysia, Nepal, Spain, Thailand), J. Fellowes (China), A. Francoeur (Canada), M. Haji (Pakistan), S. Hedges (Bahamas), G. Heller (Canary Islands, Germany), W. Jaitrong (Thailand), M.A. Kabir (Bangladesh), G. Knight (Cape Verde), J. Lewallen (Vietnam), M. Lush (Gambia), J. MacGown (Florida, Louisiana, Mississippi), P.D Rajan (India), A. San Juan (Mex-

ico), M. Vonshak (Israel), D. Ward (Fiji), and J. Woinarski (Australia). Finally, I collected *P. longicornis* specimens on numerous Pacific, Atlantic, and Caribbean islands (e.g., WETTERER 1997, 1998a, 2002, WETTERER & VARGO 2003, WETTERER & WETTERER 2004, WETTERER & al. 2004, 2006), in Costa Rica (e.g., WETTERER 1998b), and Florida (e.g., WETTERER & O'HARA 2002, WETTERER & MOORE 2005).

I obtained geographic coordinates for sites from published references, from specimen labels, or I looked up the coordinates. For older references and specimens, many site names, particularly in Asia, were no longer in use or are now spelled differently and I searched, not always successfully, to determine current names.

Many authors reported that *P. longicornis* was found in an area, but presented no specific data. For example, BINGHAM (1903) wrote that *P. longicornis* in India, Sri Lanka, and Burma was found "throughout our limits and spread over all tropical countries," but did not provide a single site record. If a 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. If one source had many sites less than 10 - 20 km apart (e.g., HUDDLESTON & FLUKER 1968; my own collections on Pacific and Caribbean islands), I often did not plot every site. I did not map records of *P. longicornis* intercepted in transit by quarantine inspectors.

I documented the range of two symbionts that inhabit *P. longicornis* nests and three closely related *Paratrechina* species (*Paratrechina pallida* DONISTHORPE, 1947, *Paratrechina otome* TERAYAMA, 1999, and *Paratrechina yambaru* TERAYAMA, 1999) using published and unpublished records. In addition, in May - July 2007, while surveying ants on seven West Indian islands (Antigua, Aruba, Barbuda, Montserrat, Nevis, St. Kitts, and St. Martin), I looked for symbionts in every large *P. longicornis* nest I encountered.

Results

I plotted records of *P. longicornis* from > 2100 sites around the world, based on information in > 400 published articles, from thousands of museum specimens, and specimens I collected from hundreds of sites (Fig. 1). In total, I found *P. longicornis* records for 181 geographic areas (i.e., countries, island groups, US states, and Canadian provinces), including many from geographic areas for which I found no previously published records, e.g., Anguilla, Argentina, Austral Islands, Bahrain, British Indian Ocean Territory (BIOT), Cayman Islands, Comoro Islands, Dominica, East Timor, El Salvador, Gambia, Ghana, Gibraltar, Guatemala, Iles Eparses, Kenya, Maldives, Mali, Montserrat, Nepal, Nevis, Pakistan, St. Kitts, St. Lucia, Turks and Caicos Islands, Tuvalu, Maryland, Missouri, and Virginia (Tabs. 1 - 7). *Paratrechina longicornis* has not yet been recorded from only a limited number of tropical maritime countries (Africa: Angola, Benin, Djibouti, Gabon, Gambia, Guinea-Bissau, Ivory Coast, Liberia, Mauritania, Mozambique, Namibia, Togo, and Western Sahara; Asia: Brunei and Cambodia; Oceania: Nauru; Neotropics: none). By 1900, *P. longicornis* was already known from a diversity of locales worldwide (Tabs. 1 - 7).

In all parts of its range, *P. longicornis* occurs primarily in highly disturbed coastal and urban environments. For

Tab. 1: Earliest known records for *Paratrechina longicornis* from Asia, the Middle East, and neighboring islands. Unpublished records include collector, museum source, and site. BIOT = British Indian Ocean Territory. BMNH = Natural History Museum, London. SI = Smithsonian Institute. MCZ = Museum of Comparative Zoology. + = no known published records.

	Earliest record
India	≤ 1851 (JERDON 1851)
Sri Lanka	1858 (MAYR 1862)
Indonesia	≤ 1866 (MAYR 1867)
Palestine/Israel	≤ 1880 (ANDRÉ 1881)
Syria	≤ 1880 (ANDRÉ 1881)
Yemen	≤ 1880 (EMERY 1881)
Burma/Myanmar	≤ 1887 (EMERY 1889)
Papua New Guinea	≤ 1901 (FOREL 1901b)
Taiwan	≤ 1909 (WHEELER 1909)
Philippines	1913 (STITZ 1925)
Malaysia	≤ 1914 (VIEHMEYER 1915)
Iraq	1917 (DONISTHORPE 1918)
Vietnam	≤ 1920 (SANTSCHI 1920a)
China	≤ 1921 (WHEELER 1921)
Japan	≤ 1924 (TERANISHI 1924 in ONOYAMA 1980)
Thailand	1928 (T.D. Cockerell, SI): Nan
Singapore	1931 (collector unknown, BMNH): site unknown
Christmas Island	1933 (DONISTHORPE 1935)
+ Bahrain	1951 (N.A. Weber, MCZ): site unknown
+ Nepal	1956 (E.I. Coher, MCZ): Amlekhganj
Lebanon	≤ 1970 (CAGNIANT 1970)
+ BIOT	1971 (Hutson, BMNH): Diego Garcia Island
Saudi Arabia	1979 (COLLINGWOOD 1985)
Oman	≤ 1985 (COLLINGWOOD 1985)
United Arab Emirates	1995 (COLLINGWOOD & al. 1997)
Iran	≤ 2000 (ALIPANAH 2000 in PAKNIA & KAMI 2007)
+ Maldives	2004 (J. Endeman, MCZ): Hulhule Island
Bangladesh	2005 (HANNAN 2007)
+ East Timor	2005 (J. Endeman, MCZ): Dili
+ Pakistan	2007 (S. & Z. Valliani, MCZ): Karachi

Tab. 2: Earliest known records for *Paratrechina longicornis* from Africa and neighboring islands. Abbreviations as in Tab. 1, and MP = Museum Paris. NML = National Museums Liverpool.

	Earliest record
Senegal	≤ 1802 (LATREILLE 1802)
Madeira	≤ 1859 (ROGER 1859)
Guinea	≤ 1876 (MAYR 1876)
Rodrigues Island	≤ 1879 (SMITH 1879)
Egypt	≤ 1880 (ANDRÉ 1881, EMERY 1881)
Madagascar	≤ 1891 (FOREL 1891)
Canary Islands	≤ 1893 (FOREL 1893a)
Réunion	≤ 1895 (FOREL 1895)
Seychelles	≤ 1897 (FOREL 1897a)
Congo (Zaire)	≤ 1901 (FOREL 1901a)
Eritrea	1906 (FOREL 1910)
Sudan	≤ 1911 (KARAVAIEV 1911)
Central African Rep.	1911 (STITZ 1916)
Tanzania	1912 (SANTSCHI 1914b)
Somalia	1913 (MENOZZI 1926)
Nigeria	≤ 1914 (SANTSCHI 1914a)
Cameroon	1916 (G. Schwab, MCZ): Batanga
Sao Tome & Principe	≤ 1920 (SANTSCHI 1920b)
South Africa	≤ 1922 (ARNOLD 1922)
Morocco	≤ 1929 (SANTSCHI 1929)
Ethiopia	≤ 1933 (SANTSCHI 1935)
Mauritius	1942 (R. Mamet, BMNH): Beau Bassin
Equatorial Guinea	≤ 1940 (MENOZZI 1942)
Cape Verde	1953 (O. Wellenius, NML): Ribeira Juliao
Algeria	1962 (H. Cagniant, pers comm.): Algiers
+ Iles Eparses	1964 (R. Legendre, MP): Europa Island
+ Ghana	1968 (C. Collingwood, BMNH): Accra
Malawi	< 1970 (SWEENEY 1970 in MORRIS 2004)
+ Mali	1970 (P. Room, BMNH): Gao
Sierra Leone	1976 (GRIFFITHS 1980)
+ Comoro Islands	1994 (Roger, MCZ): Mutasamudu
+ Kenya	< 2004 (collector unknown, BMNH): Nairobi
+ Gambia	2007 (M. Lush, pers. comm.): Kololi

Tab. 3: Earliest known records for *Paratrechina longicornis* from Australia and Pacific Ocean islands. Abbreviations as in Tab. 1, and ONHM = Oxford University Natural History Museum. UCB = Essig Museum at UC Berkeley.

	Earliest record
Samoa	≤ 1870 (MAYR 1870)
Australia	≤ 1886 (EMERY 1886)
Hawaii	≤ 1887 (BLACKBURN & CAMERON 1887)
Galapagos	1906 (WHEELER 1919)
Society Islands	1907 (WHEELER 1908b)
Mariana Islands	1911 (WHEELER 1912)
New Caledonia	≤ 1914 (EMERY 1914)
Banaba	1914 ("DWP", ONHM): Ocean Island
Solomon Islands	1916 (MANN 1919)
Fiji	1920 (MANN 1921)
Tonga	1923 (WILSON & TAYLOR 1967)
Tokelau Islands	1924 (WILSON & TAYLOR 1967)
Cook Islands	1925 (WILSON & TAYLOR 1967)
Marquesas Isl.	1925 CHEESMAN & CRAWLEY 1928)
New Zealand	≤ 1926 (GRIMMETT 1926)
Vanuatu	1930 (L.E. Cheesman, BMNH): Malekula
Pitcairn Islands	1934 (WHEELER 1936)
Line Islands	1935 (WILSON & TAYLOR 1967)
FS Micronesia	1935 (CLOUSE 2007)
Marshall Islands	1937 (CLOUSE 2007)
Phoenix Islands	1940-41 (VAN ZWALUWENBURG 1943)
Palau	1952 (CLOUSE 2007)
Wake Island	1957 (NLH Krauss, SI): site unknown
Gilbert Islands	1957 (NLH Krauss, MCZ): Butaritari
Wallis & Futuna	1965 (WILSON & HUNT 1967)
Niue	≤ 1967 (TAYLOR 1967)
Easter Island	1971 (WILSON 1973)
+ Tuvalu	1976 (P. Maddison, BMNH): Vaitupu
Tuamotu Islands	1996 (MORRISON 1997)
+ Austral Islands	2006 (P.D. Krushelnycky; UCB): Rimatara

example, on islands in the Pacific, the Atlantic, the Caribbean, and in Costa Rica and Florida, I usually found *P. longicornis* in weedy areas and in trees at most waterfront and urban sites. A few records of *P. longicornis*, however, came from inland natural areas, including national parks and wildlife sanctuaries. For example, in Thailand, *P. longicornis* has been documented at diverse sites throughout all provinces in the country, including more than 30 national parks and wildlife sanctuaries (JAITRONG & NAB-

Tab. 4: Earliest known records for *Paratrechina longicornis* from South and Central America. Abbreviations as in Tab. 1.

	Earliest record
Mexico	≤ 1859 (ROGER 1859)
Chile	1859 (MAYR 1862)
French Guiana	1868 (RADOSZKOWSKY 1884)
Brazil	≤ 1876 (MAYR 1876)
Colombia	≤ 1876 (MAYR 1876)
Nicaragua	1897 (Baker, SI): Chinandega
Costa Rica	≤ 1899 (FOREL 1899)
Panama	≤ 1899 (FOREL 1899)
Belize	1906 (WHEELER 1907)
+ Guatemala	1911 (W.M. Wheeler, MCZ): Zacapa
Guyana	1911 (WHEELER 1916)
+ Argentina	1915 (collector unknown, SI): La Plata
Honduras	1916 (F.J. Dyer, SI): La Ceiba
Surinam	≤ 1932 (BÜNZLI 1935)
Venezuela	1935 (N.A. Weber, MCZ): Orinoco Delta
Peru	1939 (W. Weyrauch, MCZ): Lima
+ El Salvador	1958 (L.J. Bottimer, SI): Volcan de Conchagua
Ecuador	≤ 1969 (GUTIERREZ 1969 in WOJCIK & PORTER 2005)
Paraguay	1997 (A. Wild, pers. comm.): Asunción

Tab. 5: Earliest known records for *Paratrechina longicornis* from the West Indies. Abbreviations as in Tab. 1.

	Earliest record
Cuba	≤ 1876 (MAYR 1876)
Virgin Islands	1878 (FOREL 1881)
Saint Vincent	≤ 1892 (FOREL 1893b)
Trinidad & Tobago	1895 (WASMANN 1905b)
Grenada	≤ 1897 (FOREL 1897b)
Bahamas	1904 (WHEELER 1905)
Puerto Rico	1906 (WHEELER 1906a)
Jamaica	1906 (WHEELER 1911)
Haiti	≤ 1907 (FOREL 1907)
Martinique	≤ 1913 (WHEELER 1913b)
Dominican Republic	1915 (collector unknown, MCZ): Sanchez
Antigua & Barbuda	1918 (WHEELER 1923)
Barbados	1918 (WHEELER 1923)
+ Montserrat	1934 (N.A. Weber, MCZ): site unknown
+ Saint Kitts	1934 (N.A. Weber, MCZ): site unknown
+ Nevis	1934 (N.A. Weber, MCZ): site unknown
+ Dominica	no date (N.A. Weber, MCZ): site unknown
+ Saint Lucia	1935 (N.E. Box, MCZ): site unknown
Dutch Leeward Is.	1936 (WEBER 1948)
+ Turks & Caicos	1953 (E.B. Haydenin, AMNH): South Caicos
Guadeloupe	≤ 1990 (JAFFE & al. 1990)
Aruba	≤ 1994 (JAFFE & LATTKE 1994)
Saint Martin	≤ 1994 (JAFFE & LATTKE 1994)
+ Anguilla	2006 (J.K. Wetterer, MCZ): Meads Bay
+ Cayman Islands	2008 (J.K. Wetterer, MCZ): Grand Cayman; Websters

HITABHATA 2005; W. Jaitrong, pers. comm.). *Paratrechina longicornis* has also been reported from national parks in Australia (HOFFMANN & O'CONNER 2004; ANIC database), Florida (FERSTER & PRUSAK 1994; ABS database), Hawaii (WETTERER 1998a), India (P.D. Rajan; pers. comm.), and Vietnam (YAMANE & al. 2002, EGUCHI & al. 2004).

Many records of *P. longicornis* come from inside or near buildings, particularly greenhouses, including most, if not all records from more temperate parts of Europe and North America. The highest latitude record comes from inside the Orchid House of the Dorpat Botanical Gardens in what is now Tartu, Estonia (latitude = 58.4° N, MÜHLEN 1887). At the Smithsonian, there were *P. longicornis* specimens from Göteborg, Sweden (57.7° N, Tab. 6) labeled "Växthus" (= greenhouse). DONISTHORPE (1927) listed records from 16 sites around England (50.7 - 55.9° N), primarily from indoors. The British Museum has a number of unpublished records of *P. longicornis* collected in England, including specimens from a kitchen in Cheltenham (51.9° N, 1945, H. Donisthorpe), a bakery in Chatham (51.4° N, 1949, collector unknown), and from Redhill (51.4° N, 1906, G.E. Frisby). Other high latitude records come from greenhouses in Hamburg, Germany (53.6° N, JACOBSON 1939), the Vancouver Aquarium in British Columbia (49.3° N, NAUMANN 1994), Paris Botanical Garden greenhouses (48.9° N, NYLANDER 1856), a Zurich, Switzerland airport building (47.5° N, FREITAG & al. 2000), the basement of a convent in Sillery, Quebec (46.8° N, A. Francoeur, pers. comm.), and the Toronto Zoo in Ontario (43.7° N, CUTTEN & al. 1979). The northernmost records in the US come from Buffalo, New York (42.9° N, 1926, collector unknown, CZ), buildings in Boston (42.4° N, MARLATT 1928), and buildings in New York City (40.7° N, WHEELER 1906b). The highest latitude *P. longicornis* records in the southern hemisphere come from New Zealand, primarily from port areas (36.9 - 41.3° S, PASCOE 2002, HARRIS & BERRY 2005, HEMBRY 2005). GRIMMETT (1926) wrote, concerning Hymenoptera in the forest of Days Bay, New Zealand (41.3° S), that *P. longicornis* "is the species most commonly

Tab. 6: Earliest known records for *Paratrechina longicornis* from Europe, the Mediterranean, and Atlantic Islands. Abbreviations as in Tab. 1.

	Earliest record
France	≤ 1856 (NYLANDER 1856)
England	≤ 1859 (ROGER 1859)
Estonia	≤ 1887 (MÜHLEN 1887)
Netherlands	1909 (B. Vierbergen, pers. comm.): site unknown
Azores	1929 (DONISTHORPE 1936)
Czech Republic	1937 (NOVÁK 1947)
Germany	≤ 1939 (JACOBSON 1939)
+ Gibraltar	1956 (N.L.H. Krauss, SI): site unknown
Sweden	1957 (B. Hanson, SI): Göteborg
Ascension Isl.	1958 (DUFFEY 1964)
Malta	1975 (SCHEMBRI & COLLINGWOOD 1981)
Italy	≤ 1981 (SCHEMBRI & COLLINGWOOD 1981)
Greece	≤ 1988 (KUGLER 1988)
Bermuda	1990 (WETTERER & WETTERER 2004)
Saint Helena	1994 (ASHMOLE & ASHMOLE 2000)
Denmark	1996 (JENSEN & BILLE 1997 in WOJCIK & PORTER 2005)
Spain	1998 (TINAUT & AÑO 2000)
Switzerland	1999 (FREITAG & al. 2000)
Balearic Islands	2004 (GÓMEZ & ESPADALER 2006)

found, and in some samples constituted an overwhelming majority of the fauna," though this may have been a transient population.

Nest symbionts

The two myrmecophilic insect species known to live almost exclusively in *P. longicornis* nests have site records from around the world: *Coluocera maderae* and *Myrmecophilus americanus*. WOLLASTON (1854) described the beetle *Coluocera maderae* collected from the nest of an unidentified ant on the Atlantic island of Madeira. *Coluocera maderae* has been subsequently reported from *P. longicornis* nests in Brazil, Burma, Cuba, Galapagos, Haiti, Hawaii, India, Taiwan, and Trinidad (WASMANN 1905b, ASSMUTH 1907, MANN 1915, 1918, ILLINGWORTH 1931, KRAUSS 1944, KISTNER 1982, PECK 1993, TARI 2007). In India, *C. maderae* has also been reported from the nests of *Paratrechina indica* (FOREL, 1894) and an unidentified *Pheidole* species (WASMANN 1905b).

SAUSSURE (1877) described the ant cricket *Myrmecophilus americanus* from an unspecified locale in Colombia, with no indication of the host ant species. Published site records of *M. americanus* come from around the world, including India, the western Indian Ocean (Madagascar, Seychelles, Réunion), Oceania (Hawaii), and the Neotropics (Brazil, Colombia, Cuba, Haiti). Additional records of *M. americanus* come from Sudan, Libya, Egypt, and Israel, though some or all of these may be *Myrmecophilus cottami* CHOPARD, 1922, if this species proves to be valid (see WETTERER & HUGEL in press). In all recorded cases except one, the ant host of *M. americanus* was the longhorn crazy ant, *Paratrechina longicornis*. Finally, WETTERER & HUGEL (in press) collected *M. americanus* specimens from *P. longicornis* nests at 13 sites on six West Indian islands: Antigua, Aruba, Montserrat, Nevis, St. Kitts, and St. Martin.

Tab. 7: Earliest known records for *Paratrechina longicornis* from the United States and Canada. Abbreviations as in Tab. 1.

	Earliest record
New York	1886 (C.V. Riley, SI): site unknown
Washington DC	1886 (C.V. Riley, SI): site unknown
+ Missouri	1901 (collector unknown, MCZ): Shaw Botanic Garden
Texas	1905 (F.C. Pratt, SI): Dallas
Florida	≤ 1906 (WHEELER 1906b)
Pennsylvania	1906 (collector unknown, MCZ): Philadelphia
Alabama	1910 (W.D. Pierce, SI): Mobile
Georgia	≤ 1913 (WHEELER 1913a)
+ Maryland	1913 (R.L. Ball, SI): Baltimore
+ Virginia	1915 (D.E. Finck, SI): Norfolk Navy Yard
Indiana	≤ 1921 (DIETZ 1921)
Mississippi	1922 (J. MacGown, pers. comm.): Oktibbeha
Massachusetts	≤ 1928 (MARLATT 1928)
South Carolina	≤ 1934 (SMITH 1934)
Oklahoma	≤ 1935 (SMITH 1935)
North Carolina	≤ 1937 (POWELL 1937 in WOJCIK & PORTER 2005)
Louisiana	1943 (W. Buren, SI): Alexandria
Quebec	1963 (A. Francoeur, pers. comm.): Sillery
California	1967 (F. Yaruss, SI): San Diego
Ontario	1978 (CUTTEN & al. 1979)
Illinois	≤ 1988 (DUBOIS & LABERGE 1988)
Arizona	1993 (WETTERER & al. 1999)
British Columbia	1994 (NAUMANN 1994)
Ohio	≤ 1998 (HEDGES 1998)
New Mexico	≤ 2000 (HEDGES 2000)

Related *Paratrechina* species

WILSON & TAYLOR (1967) proposed that *P. longicornis* is most closely related to *Paratrechina pallida*, a species known only from the lowlands of New Guinea, primarily

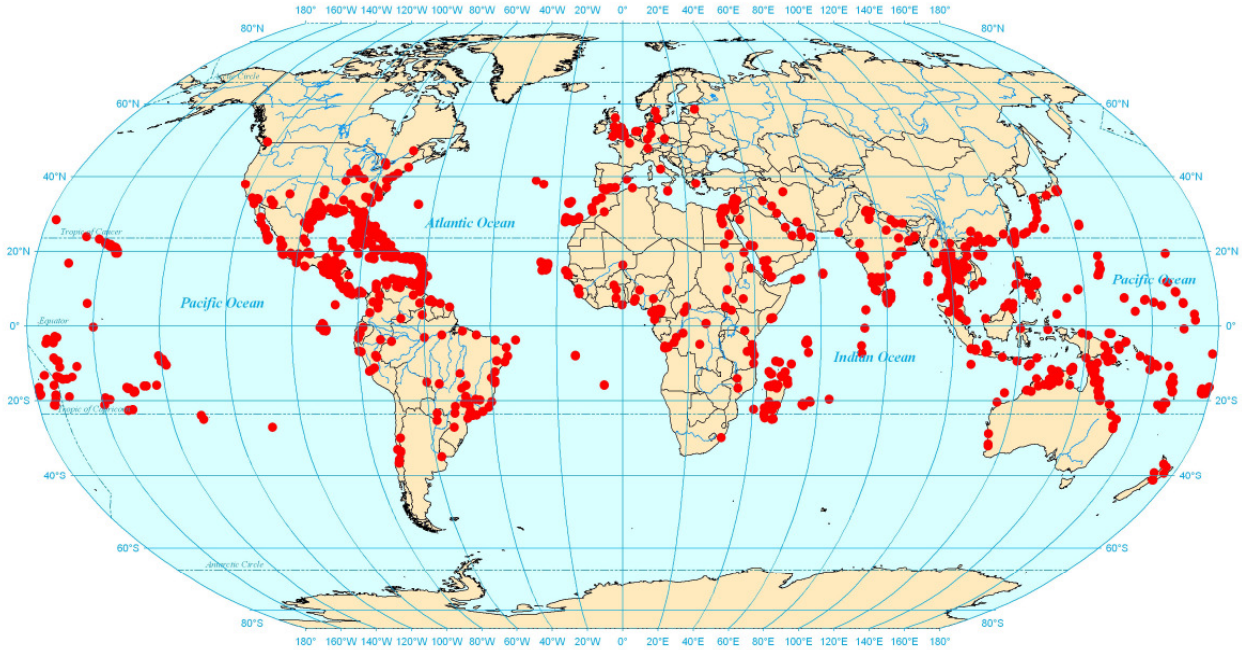

Fig. 1: Worldwide records of *Paratrechina longicornis*.

from intact rainforest (DONISTHORPE 1947, WILSON 1959, ROOM 1975, SNELLING 2000, unpublished records in the MCZ). TRAGER (1984) similarly concluded that: "*longicornis* and *pallida* appear to form a real species-group."

Recently, TERAYAMA (1999) described two *Paratrechina* species from grasslands and forest margins in the far south of Japan that closely resemble *P. longicornis*: *Paratrechina otome* from two of the Yaeyama Islands and *Paratrechina yambaru* from northern Okinawa Island.

Discussion

Paratrechina longicornis is arguably the most broadly dispersed of any ant species, with records widely distributed across the Old World and New World in both the northern and southern hemispheres (Fig. 1). DELABIE & BLARD (2002) proposed that the ant *Hypoponera punctatissima* (ROGER, 1859) "has the widest distribution within Formicidae, being present on many oceanic and continental islands and all continental regions except Antarctica and the Orient." However, in compiling worldwide site records for > 40 major tramp ants, my analyses indicate that several ant species have broader distributions than *H. punctatissima.* Although *H. punctatissima* is widespread in Europe and on Pacific Islands, it has a very limited distribution in other parts of the world, particularly in South America (two records), Asia (one record), and Australia (no continental records). In addition, ant specimens that have been identified as *H. punctatissima* represent more than one species (S. Cover, pers. comm.; SEIFERT 2003).

I found that the only ant species that might be considered as widely distributed as *P. longicornis* is the Pharaoh ant, *Monomorium pharaonis* (LINNAEUS, 1758), a species thought to be from Africa or Asia that has long been known as an important house pest in Europe and North America. WEBER (1939) wrote that *P. longicornis* and *Monomorium pharaonis* "are probably the most common ship ants and may be expected on any vessels visiting ports in warmer regions." In much of its range, however, *M. pharaonis* has been collected only inside buildings.

Paratrechina longicornis has become so widespread, in part, because it can thrive in even the most artificial environments, including ships at sea. For example, the British Museum collection included a *P. longicornis* specimen that E.S. Brown collected on a boat traveling from Mombasa, Kenya to the Seychelles Islands, and J. Endeman sent me *P. longicornis* specimens she collected on a tour boat visiting Komodo Island, Indonesia (for additional records from ships, see WHEELER 1908a, 1916, MYERS 1934, WEBER 1939, 1940, MILLER 1994). Its habit of hitchhiking in cargo has allowed *P. longicornis* to spread quickly around the world. HEDGES (1998) reported *P. longicornis* from a car driven from Florida to Indiana, and noted "this species' propensity for nesting in the soil of potted tropical plants enables it to be shipped literally anywhere in the United States." Internationally, *P. longicornis* is one of the most common ant species intercepted in cargo by quarantine officials (e.g., see LESTER 2005).

There are only a few tropical maritime nations from which *P. longicornis* has not yet been recorded. All these countries, however, have been poorly sampled for ants. For example, I found no published records for any ants at all from Nauru, the only tropical Pacific nation without *P. longicornis* records. It seems likely that even a cursory ant survey in Nauru or any tropical port city would find *P. longicornis* already present. In fact, TRAGER (1984) speculated that *P. longicornis* was so ubiquitous that: "perhaps no large city in the tropics is without this ant."

Currently, *P. longicornis* records are uncommon in many inland tropical areas, except along major waterways, such as the Nile, Congo, and Amazon Rivers (Fig. 1). With the increasing prevalence of air commerce, I expect that in the future *P. longicornis* will spread to other inland areas as well. Because *P. longicornis* can live indoors anywhere that humans live, there is no limit to the latitude where this spe-

cies could thrive, joining humans and German cockroaches (*Blattella germanica* LINNAEUS, 1767) (Blattodea: Blattellidae), as one of the most widespread and populous animal species on Earth.

Native and exotic range

The worldwide distribution of all known *P. longicornis* site records (Fig. 1) offers ambiguous clues to where the species is native. The greatest saturation of *P. longicornis* site records comes from around the Caribbean, but this pattern is almost certainly a result of higher sampling intensity in this region, including my own collecting. In the Old World, the greatest saturation of *P. longicornis* site records is in Southeast Asia and to a lesser extent the north coast of Australia, but again, this may be an artifact of sampling intensity.

In 1900, when most of the world's ant fauna was still very poorly documented, *P. longicornis* was already known from a diversity of locales scattered across Asia, Africa, the Middle East, the Indian Ocean, Central America, South America, the West Indies, and Atlantic islands, as well as a few records in Europe and the US (Tabs 1 - 7). Although WASMANN (1905b) wrote that *P. longicornis* was more widespread in India and neighboring areas than in other parts of the world, he provided scant evidence to support this claim in terms of site records. In many parts of the world, the earliest collection date for *P. longicornis* does not appear to indicate the earliest arrival of the ant, but often corresponds to the date of the first thorough ant surveys. Thus, reconstructing the spread of *P. longicornis* out from its original native range is not possible using a chronology of historical specimen records.

The occurrence of *P. longicornis* in inland natural areas appears to offer some useful evidence about the native range of the species. The greatest number of records of *P. longicornis* in national parks and wildlife refuges come from Southeast Asia. For example, YAMANE & al. (2002) and EGUCHI & al. (2004) reported *P. longicornis* from two inland national parks in Vietnam. In Thailand, *P. longicornis* was found even in extremely remote forest reserves (JAITRONG & NABHITABHATA 2005, W. Jaitrong, pers. comm.), suggesting that it is native to the area. In contrast, in natural areas elsewhere in the world, *P. longicornis* may invade only human-impacted areas. For example, I found *P. longicornis* only once in Hawaii Volcanoes National Park, in the cooking shelter at a campground (WETTERER 1998a), a site not indicative of a native species (and, in fact, no ants are thought to be native to Hawaii). FERSTER & PRUSAK (1994) and HOFFMANN & O'CONNER (2004) considered *P. longicornis* to be exotic to Everglades National Park, USA and Kakadu National Park, Australia, respectively.

In some ant species, intraspecific aggression is common in native populations, but largely absent in exotic populations (e.g., see WETTERER & WETTERER 2006). LIM & al. (2003), in the only published study of intraspecific aggression in *P. longicornis*, found that colonies from five sites on Panang Island, Malaysia all showed fierce intercolonial aggression. But this intercolonial aggression does not appear to provide strong evidence that *P. longicornis* is native to this region: a preliminary study of intraspecific aggression among *P. longicornis* colonies in Florida, where *P. longicornis* is certainly exotic, also found no evidence of unicoloniality (A. Corsaro & J. Wetterer, unpubl.). It is unclear how widespread unicoloniality is among invasive ant species.

The two myrmecophilic insects (*C. maderae* and *M. americanus*) found almost exclusively in *P. longicornis* nests have been recorded from locales scattered around the world. Thus, the simple presence of these species-specific symbionts is not indicative of the ants' native range. WASMANN (1905b) concluded that the widespread occurrence of these nest associates in India and Southeast Asia indicated that *P. longicornis* originated in this region. In contrast, in other parts of the world, the myrmecophiles seem to be common at only a few scattered locales. For example, MANN (1915) found *P. longicornis* at many sites in Haiti, but collected *C. maderae* and *M. americanus* at only a single site. Similarly, I found *M. americanus* only sporadically in *P. longicornis* colonies in the Caribbean.

The distributions of three *Paratrechina* species believed to be closely related to *P. longicornis* provide the most unambiguous evidence that *P. longicornis* is native to Papuasia (Southeast Asia and Melanesia) as proposed by WILSON & TAYLOR (1967): *P. pallida* known only from New Guinea, and *P. otome* and *P. yambaru* known only from southern Japanese islands. The limits of the native range of *P. longicornis* within Asia and Melanesia, however, remain ambiguous.

Outside of Asia, there are many *P. longicornis* populations that are almost certainly exotic. For example, populations in the New World and on mid-Atlantic islands are all very distant from the range of any closely related *Paratrechina* species. In North America and Europe, *P. longicornis* populations suddenly appeared in isolated urban areas with very extensive earliest sampling for ants, with most records coming from inside buildings. On most or all isolated islands of the eastern Pacific, *P. longicornis* is also probably exotic. In fact, WILSON & TAYLOR (1967) concluded that: "few if any ant species are native to the islands east of Rotuma, Samoa, Tonga, and New Zealand."

I found scant evidence suggesting that *P. longicornis* originated in or is native to Africa. I found relatively few records of *P. longicornis* and few (possibly no) records of its species-specific nest symbionts from continental Africa, a region distant from the range of closely related *Paratrechina* species in East Asia and New Guinea. No African *Paratrechina* species even remotely resemble *P. longicornis* (S. Cover, pers. comm.). KENNE & al. (2005) apparently considered *P. longicornis* native to West Africa simply because DEJEAN & al. (1996) found a *P. longicornis* colony in a Cameroon rainforest, though I do not find this single record from an abandoned termite nest to be compelling evidence. FOWLER & al. (1994) and HOLWAY & al. (2002) may have reported *P. longicornis* as native to Africa simply because LATREILLE (1802) first described the species from Senegal in the far western tip of Africa.

Future research on the phylogeny of the genera *Paratrechina*, *Coluocera*, and *Myrmecophilus*, and on the genetic diversity of *P. longicornis* populations in different parts of the world should help elucidate further the native and exotic ranges of *P. longicornis*.

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Zusammenfassung

Die Ameisenart *Paratrechina longicornis* (LATREILLE, 1802), auch "longhorn crazy ant" genannt, ist ein ubiquitärer Landwirtschafts- und Haushaltslästling in großen Teilen der Tropen und Subtropen und eine Plage in Gebäuden temperater Gebiete. Ich habe Nachweise von *P. longicornis* von > 2100 Fundorten weltweit zusammengetragen und anhand historischer, ökologischer und evolutionsbiologischer Befunde die bekannte Verbreitung, den geographischen Ursprung und die potentielle zukünftige Ausbreitung evaluiert. Ich habe die frühesten bekannten Nachweise für 181 geographische Gebiete (Länder, große Inseln, Inselgruppen, US-Bundesstaaten und Kanadische Provinzen) dokumentiert, einschließlich vieler, für die meines Wissens bisher keine Nachweise veröffentlicht worden sind, beispielsweise Anguilla, Argentinien, Austral-Inseln, Bahrain, British Indian Ocean Territory, Cayman Inseln, Comoro Inseln, Dominica, El Salvador, Gambia, Ghana, Gibraltar, Guatemala, Iles Eparses, Kenya, Malediven, Mali, Montserrat, Nepal, Nevis, Ost Timor, Pakistan, St. Kitts, St. Lucia, Turks und Caicos Inseln, Tuvalu, Maryland, Missouri und Virginia. *Paratrechina longicornis* ist somit die nachweislich am weitesten verbreitete aller Ameisenarten, mit Vorkommen in der Alten und Neuen Welt, sowohl auf der Nord- als auch der Südhalbkugel. Die erfolgreiche weltweite Ausbreitung von *P. longicornis* fußt auf der Fähigkeit, vitale Populationen in hochgradig gestörten und künstlichen Lebensräumen aufzubauen, sogar in Schiffen auf See. Nachweise von *P. longicornis* stammen meist aus der Nähe großer kommerzieller Wasserwege, aber ich erwarte, dass die Art mit der zunehmenden Bedeutung des Lufttransports auch Gebiete im Landesinneren verstärkt besiedeln wird. Viele Nachweise, insbesondere die meisten, wenn nicht sogar alle, aus temperaten Breiten, stammen von innerhalb oder aus der Nähe von Gebäuden. Weil *P. longicornis* in Gebäuden überall dort leben kann, wo Menschen leben, ist der Ausbreitung in hohe Breitengrade keine Grenze gesetzt. Die weltweiten Nachweise von *P. longicornis* und von zwei artspezifischen Symbionten geben wenig eindeutige Hinweise auf den geographischen Ursprung von *P. longicornis*. Die Areale von drei nahe verwandten *Paratrechina*-Arten jedoch machen Südostasien und Melanesien als natives Verbreitungsgebiet von *P. longicornis* glaubhaft.

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