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ANTS (HYMENOPTERA: FORMICIDAE) OF BERMUDA

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ABSTRACT

For more than 50 years, two exotic ant species, *Linepithema humile* (Mayr) and *Pheidole megacephala* (F.), have been battling for ecological supremacy in Bermuda. Here we summarize known ant records from Bermuda, provide an update on the conflict between the dominant ant species, and evaluate the possible impact of the dominant species on the other ants in Bermuda. We examined ant specimens from Bermuda representing 20 species: *Brachymyrmex heeri* Forel, *B. obscurior* Forel, *Camponotus pennsylvanicus* (De Geer), *Cardiocondyla emeryi* Forel, *C. obscurior* Wheeler, *Crematogaster* sp., *Hypoponera opaciceps* (Mayr), *H. punctatissima* (Roger), *L. humile*, *Monomorium monomorium* Bolton, *Odontomachus ruginodis* Smith, *Paratrechina longicornis* (Latreille), *P. vividula* (Nylander), *P. megacephala*, *Plagiolepis alluaudi* Forel, *Solenopsis* (*Diplorhoptrum*) sp., *Tetramorium caldarium* Roger, *T. simillimum* (Smith), *Wasmannia auropunctata* (Roger), and an undetermined Dacetini. Records for all but three (*H. punctatissima*, *P. vividula*, *W. auropunctata*) include specimens from 1987 or later. We found no specimens to confirm records of several other ant species, including *Monomorium pharaonis* (L.) and *Tetramorium caespitum* (L.). Currently, *L. humile* dominates most of Bermuda, while *P. megacephala* appear to be at its lowest population levels recorded. Though inconspicuous, *B. obscurior* is common and coexists with both dominant species. *Paratrechina longicornis* has conspicuous populations in two urban areas. Three other ant species are well established, but inconspicuous due to small size (*B. heeri*, *Solenopsis* sp.) or subterranean habits (*H. opaciceps*). All other ant species appear to be rare, including at least one, *O. ruginodis*, which was apparently more common in the past.

Key Words: Atlantic islands, biodiversity, exotic ants, *Pheidole megacephala*, *Linepithema humile*, tramp ants

RESUMEN

Durante más de 50 años, dos especies exóticas de hormiga, *Linepithema humile* (Mayr) y *Pheidole megacephala* (F.), han estado combatiendo la supremacía ecológica en Bermuda. Aquí resumimos los registros conocidos de hormiga de Bermuda, ponemos al día el estado de la cuestion en el conflicto entre la especie dominante de hormiga, y evalúamos el impacto posible de la especie dominante en las otras hormigas en Bermuda. Examinamos especímenes de hormiga de Bermuda que representan 20 especies: *Brachymyrmex heeri* Forel, *B. obscurior* Forel, *Camponotus pennsylvanicus* (De Geer), *Cardiocondyla emeryi* Forel, *C. obscurior* Wheeler, *Crematogaster* sp., *Hypoponera opaciceps* (Mayr), *H. punctatissima* (Roger), *L. humile*, *Monomorium monomorium* Bolton, *Odontomachus ruginodis* Smith, *Paratrechina longicornis* (Latreille), *P. vividula* (Nylander), *P. megacephala*, *Plagiolepis alluaudi* Forel, *Solenopsis* (*Diplorhoptrum*) sp., *Tetramorium caldarium* Roger, *T. simillimum* (Smith), *Wasmannia auropunctata* (Roger), y un Dacetini indeterminado. Los registros para todo excepto tres (*H. punctatissima*, *P. vividula*, *W. auropunctata*) incluyen los especímenes de 1987 o más tarde. No encontramos ningún especímen para confirmar los registros de varias otras especies hormiga, inclusyendo *Monomorium pharaonis* (L.) y *Tetramorium caespitum* (L.). Actualmente, *L. humile* domina la mayor parte de Bermuda, mientras *P. megacephala* parece estar en su nivel de población más baja que se haya registrado. Aunque pasa inadvertido, *B. obscurior* es común y coexiste con ambas especies dominantes. *Paratrechina longicornis* tiene poblaciones visibles en dos áreas urbanas. Otras tres especies de hormiga se han establecido bien, aunque no llanan la atencion debido al tamaño pequeño (*B. heeri*, *Solenopsis* sp.) o hábitos subterráneos (*H. opaciceps*). Todas las otras especies hormigas parecen ser raras, incluyendo por lo menos una, *O. ruginodis*, que era más común en el pasado.

Translation provided by the authors.

A battle for territorial supremacy has been raging on the Atlantic islands of Bermuda for more than 50 years. The combatants are two species of exotic ants, one Old World (the big-headed ant, *Pheidole megacephala* (F.)) and one New World (the Argentine ant, *Linepithema humile* (Mayr)). As documented in studies conducted 1927-1986 (Haskins 1939; Haskins & Haskins 1965, 1988;

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Crowell 1968; Lieberburg et al. 1975), *P. megacephala* was the dominant ant in Bermuda when *L. humile* arrived in the 1940s. This new invader quickly overran much territory, excluding *P. megacephala*. *Pheidole megacephala*, however, persisted, and ever since, these two species have been contesting ever-shifting battlefronts between mutually exclusive territories. Largely ignored in this drama, however, are the other ant species in Bermuda.

Both *P. megacephala* and *L. humile* are well-known for killing off native invertebrates, particularly native ants (Erickson 1971; Human & Gordon 1996; Holway 1999; Vanderwoude et al. 2000; Wetterer et al. 2000, 2001; Wetterer 2002). This paper presents combined published, unpublished, and new ant records from Bermuda, provides an update on the conflict between the two dominant ant species, and examines the possible impact of the dominant ants on the other ant species that persist in Bermuda.

Published Ant Records from Bermuda

Many early accounts describe enormous ant plagues in Bermuda in the 17th and 19th centuries (Jones 1859; LeFroy 1882; Hurdis 1897; Kevan 1981), but no specimens of these ants are known and the species involved have never been identified. Wheeler (1906) proposed that the plague ants might have been *Solenopsis geminata* (F.) or *Monomorium destructor* (Jerdon).

In the first identification of an ant species from Bermuda, Kirby (1884) of the British Museum identified one ant species collected by the HMS Challenger expedition in April 1873 as *Formica nigra* L. (= *Lasius niger* (L.)). Kirby (1884) noted that this species was "probably introduced" and that "the specimens do not appear to differ from the ordinary European species."

Dahl (1892) identified two species of ants from Bermuda, collected in 1889 by the Humboldt-Stiftung Expedition, as *Pheidole pusilla* Heer (= *P. megacephala*) and an *Odontomachus* species, "probably" *Odontomachus insularis* Guérin-Méneville.

Verrill (1902) reported that on expeditions to Bermuda in 1898-1901 "ants of several undetermined species were collected by us which have not yet been fully studied by a specialist." Nonetheless, Verrill (1902) recognized specimens of the "small House-ant" *Monomorium minutum* (Buckley) (= *Monomorium monomorium* Bolton) and the "Garden-ant or Pavement-ant" *Tetramorium caespitum* (L.), and wrote: "probably these were early introduced from England." In addition, Verrill (1902) received from V. Hayward specimens of *P. megacephala* collected on St. David's Island, and received from L. Mowbray "a few Hymenoptera, including males, females, and very small workers of one or two species of the genus *Pheidole*, as determined by Mr. Th. Pergande. These are common, as House-ants, and destructive." Verrill (1902) also mentioned "a few ants," found in guts of the endemic Bermuda lizard *Eumeces longirostris* Cope. Finally, Verrill (1902) cited Kirby's (1884) record of the "European Black ant" *L. niger*, and Dahl's (1892) records of *P. megacephala* and *Odontomachus* sp. near *insulans*.

Wheeler (1906) made a comprehensive list of Bermuda ants, based on the three past accounts (Kirby 1884; Dahl 1892; Verrill 1902) and on new specimens supplied by T. Kincaid and J. H. Comstock. Of the 11 taxa on his list, Wheeler (1906) examined specimens of eight: *Hypoponera opaciceps* (Mayr), *Odontomachus haematodes insularis ruginodis* Smith (= *O. ruginodis*), *Cardiocondyla emeryi* Forel, *P. megacephala*, *Brachymyrmex heeri* Forel, *Brachymyrmex heeri obscurior* Forel (= *B. obscurior*), *Prenolepis kincaidi* Wheeler (= *Paratrechina vividula* (Nylander)), and *Prenolepis* sp. The other three records came from previously published reports: *L. niger*, *M. minutum* (= *M. monomorium*), and *T. caespitum*. Wheeler (1906) believed, however, that the last two records were probably misidentifications of *Monomorium pharaonis* (L.) and *Tetramorium guineense* (Bernard) respectively.

Ogilvie (1928) presented a Bermuda ant list that was the same as Wheeler's (1906), except that it included *O. haematodes insularis* (= *O. insularis*) instead of *O. ruginodis*, and omitted *Prenolepis* sp.

Starting in 1927, Haskins repeatedly visited Bermuda, recording the ecological dominance of *P. megacephala* (Haskins 1939). Haskins (1939) noted that *O. insularis* was common in 1927, but became rare in the 1930s, writing: "In the few *Odontomachus* colonies remaining on the Islands great numbers of *Pheidole* workers are to be found killing and carrying off the larvae, fastening themselves in myriads to the bodies of the workers, and forcing their early abandonment of the site. Within another ten years, the Ponerine [*Odontomachus*] species, which inhabited Bermuda as its undisturbed Arthropod mistress for millennia, and has in fact developed a characteristic variety there, will have been exterminated."

The first published record of *L. humile* in Bermuda included it as prey recovered from stomachs of exotic *Anolis* lizards (Simmonds 1958). Simmonds (1958) found 4105 prey in 176 *Anolis grahami* Gray specimens, of which 2176 were ants (21% *L. humile*, 26% *P. megacephala*, 52% *Brachymyrmex* sp., 2% ant species A), and 587 prey in 46 *Anolis leachi* Duméril & Birron specimens of which 153 were ants (97% *L. humile*, 3% *Brachymyrmex* sp.). Bennett & Hughes (1959) reported that *L. humile* "was first recorded in Bermuda in 1948 and has since become numerous." Further, Bennett & Hughes (1959) reported that *L. humile* was gradually replacing *P. megacephala*. Nonetheless, Wingate (1965) found that *P. megacephala* was still common among 319 ant prey of 30 *Anolis roquet* (Lacépède) (12% *L. humile*, 85% *P. megacephala*, 3% *B. obscurior*).

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Haskins & Haskins (1965) documented interactions in Bermuda between *P. megacephala* and *L. humile*, with some mention of other ant species, e.g., noting that "in 1933, no *O. insularis* could be found," and that areas not occupied by either of the dominant species, "were extensively occupied by colonies of *B. heeri*, and required considerably more careful examination. Occasional colonies of *Ponera opaciceps* [= *H. opaciceps*] were also found in such areas."

Crowell (1968) further studied *P. megacephala* and *L. humile* in Bermuda and noted four other ant species: *B. obscurior*, *O. insularis*, *Wasmannia auropunctata* (Roger), and *Paratrechina* sp. Crowell (1968) wrote: "the presence of *Wasmannia auropunctata* has been recognized by the Bermuda Department of Agriculture and Fisheries since 1950." Lieberburg et al. (1975), in another study of *L. humile* and *P. megacephala* in Bermuda, noted six other ant species: *B. heeri*, *H. opaciceps*, *Odontomachus brunneus* (Patten), *W. auropunctata*, *Cardiocondyla* sp., and *Paratrechina* sp. Crowell (1968) added a personal communication from C. Haskins who found one *O. insularis* colony in 1965.

Kempf (1972), in his catalog of Neotropical ants, listed ten taxa known from Bermuda: *B. heeri*, *Brachymyrmex heeri aphidicola* Forel (= *B. obscurior*), *B. obscurior*, *C. emeryi*, *H. opaciceps*, *O. insularis*, *O. ruginodis*, *P. megacephala*, *Plagiolepis alluaudi* Forel, and *T. caespitum*. Brandão (1991), in his addendum to Kempf's (1972) catalog, listed *B. obscurior*, *O. brunneus*, *O. insularis*, and *P. vividula* from Bermuda.

Haskins & Haskins (1988) revisited Bermuda for a "final survey" of *P. megacephala* and *L. humile*. Haskins & Haskins (1988) wrote that "the genus *Odontomachus* (*insularis* and *brunnei*) . . . is now a rare form. Other long-term survivors include the genus *Brachymyrmex* (still relatively abundant in niches unoccupied by either tramp ant) and the genera *Paratrechina*, *Cardiocondyla*, *Hypoponera*, and *Wasmannia*."

Hilburn et al. (1990) listed 14 ant taxa reported from Bermuda, eight apparently based on specimens (*B. heeri*, *Brachymyrmex* sp., *C. emeryi*, *L. humile*, *Monomorium* sp., *Paratrechina* sp., *P. megacephala*, and *W. auropunctata*) and six apparently from published reports (*H. opaciceps*, *L. niger*, *M. pharaonis*, *O. brunneus*, *P. vividula*, and *T. caespitum*). Hilburn et al. (1990) also listed three additional ant species that had been intercepted on goods being imported into Bermuda, but had not become established (*Camponotus noveboracensis* (Fitch), *Crematogaster* sp., and *Paratrechina longicornis* (Latreille)).

Materials and Methods

We looked for Bermuda ant specimens in the collections of the American Museum of Natural History, New York (AMNH), the Academy of Natural Sciences, Philadelphia (ANS), the Bermuda Aquarium, Museum and Zoo (BAMZ), the Bermuda Dept. of Agriculture (BDOA), British Natural History Museum in London (BNHM), Harvard's Museum of Comparative Zoology (MCZ), the Smithsonian Institute (SI), and Yale's Peabody Museum (YPM).

From 27 February to 5 March 2002, we surveyed ants using visual search in a wide range of habitats. Our sites included both highly disturbed environments (e.g., port areas in Hamilton, St. George, and Ireland Island North) and lesser-disturbed reserve areas (e.g., Spittal Pond and Paget Marsh). We also surveyed ants on two small, isolated islands, Nonsuch and Horn. These two islands are nesting areas for the endemic cahow (*Pterodroma cahow* Nichols & Mowbray). In addition, we resurveyed ten sites that Haskins & Haskins (1988) had repeatedly surveyed to evaluate changes over time in which ant species dominated an area. In June-August 2002, A. Lines, W. Sterrer, and Z. Amaral of the BAMZ collected additional ant specimens.

Stefan Cover examined most specimens. Mark Deyrup examined all specimens with uncertain identifications. Further evaluations were made by Xavier Espadaler (*Monomorium*, *Plagiolepis*), Bernhardt Seifert (*Cardiocondyla*), and James Trager (*Paratrechina*, *Crematogaster*). We will deposit vouchers at the BAMZ, MCZ, and Archbold Biological Station.

Results

We examined ant specimens from Bermuda representing 20 ant species, including nine new records (Table 1; for details species accounts). At the BNHM, we did not find the specimens Kirby (1884) identified as *Lasius niger*. At the YPM, Raymond Pupedis (pers. comm.) found catalog numbers for Hymenoptera specimens in alcohol collected in Bermuda: 4916-4928 (April 1901, AE Verrill & WJ Van Name) and 5003-5008 (Dec 1901, TG Goslin). We did not, however, find any of Verrill's ant specimens in the pinned collection. Chris Cutler searched through all available old vials and bottles in the Yale collection with no success.

In 2002, we found *L. humile* in large numbers at all ten sites studied by Haskins & Haskins (1988; see Table 2). At four of the sites, we also found *P. megacephala* (Table 2). At the intersection of Knapton Hill Road and Harrington Hundreds, we found *L. humile* to the north of Knapton Hill Road and *P. megacephala* south of the road. At Spittal Pond Reserve, we found *L. humile* throughout, except for *P. megacephala* at the eastern entrance and parking area. At Newstead Hotel complex, we found *L. humile* throughout, except for *P. megacephala* at the westernmost end. Finally, on Ireland Island North, we found *L. humile* in all areas we searched, except for

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TABLE 1. ANTS OF BERMUDA.

	2000-2002 records	Record dates	Range	Status
Linepithema humile	27	1948-2002	T–F–XAME	NX
Brachymyrmex obscurior	19	1905-2002	TWFBX–––	N?
Pheidole megacephala	17	1889-2002	TWFBXAME	OX
+*Paratrechina longicornis*	7	1990-2002	TWFBXAME	OX
Brachymyrmex heeri	6	1905-2002	TWFBX––E	N?
Hypoponera opaciceps	4	1905-2002	TWFBX–––	N?
+*Solenopsis* sp.	4	1934-2002	X	??
+*Tetramorium simillimum*	2	1922-2002	TWFBX––E	OX
+*Camponotus pennsylvanicus*	2	2001-2002	––F–X–––	NX
Odontomachus ruginodis	1	1889-2002	TWFBX–––	N?
Monomorium monomorium	1	1900-2002	–W––X––E	OX
Cardiocondyla emeryi	1	1905-2002	TWFBX–M–	OX
+*Tetramorium caldarium*	1	2002	TWFBXAME	OX
Plagiolepis alluaudi		1945-1987	–W––X–––	OX
+*Cardiocondyla obscurior*		1987	–WF–X–––	OX
+*Crematogaster* sp. male		1987	X	??
+Dacetine male		1987	X	??
Wasmannia auropunctata		1925-1966	TWFBX––E	NX
Paratrechina vividula		1905-1925	TWFBX––E	OX
+*Hypoponera punctatissima*		1910	TWFBXAME	OX
Unconfirmed records				
Paratrechina sp.		1966-1973	?	??
Prenolepis sp.		1905	?	??
Tetramorium caespitum		1900	T–––?A–E	O?
Lasius niger		1873	––––?––E	O?
Monomorium pharaonis		?	TWFB?–ME	OX

Species ranked according to number of collection sites in 2000-2002 or date last recorded. + = new record for Bermuda. Range: T = Tropical South and Central America, W = West Indies, F = Florida, B = Bahamas, X = Bermuda, A = Azores, M = Madeira, E = Europe. Status: N = New World native, O = Old World native, X = exotic, ? = possible native.

P. megacephala on the northeast corner, east of the entrance to the Maritime Museum and out the entire length of the North Breakwater, which serves as a cruise ship terminal.

Species Accounts

+ = new record for Bermuda. Collectors: H = DJ Hilburn et al., W = JK Wetterer & AL Wetterer in 2002, Collections: BDOA = Bermuda Department of Agriculture, BAMZ = Bermuda Museum, Aquarium and Zoo, BNHM = British Natural History Museum, London, MCZ = Museum of Comparative Zoology, Harvard University, YPM = Yale Peabody Museum.

1. *Brachymyrmex heeri* Forel

Specimens examined: No site data (1905, T Kincaid, MCZ). Near Hamilton (1910, EG Vanatta, ANS). Padet (sic.) Marsh (1922, HH Whelzel, MCZ). Paget (1925, L Ogilvie, MCZ). No site data (1925, L Ogilvie, AMNH). Hamilton (1934, NA Weber, MCZ). Many sites (1987-1988, H, BAMZ). Admiralty House (1987, H, BAMZ - male labeled "prob. Dolichoderine male det DR Smith"). BAMZ Ops (2001, L. Hinton, BAMZ). Bermuda Biological Station for Research (BBSR), under boards in wooded area (W). Blue Hole Park, forested area (W). Hamilton, waterfront, in a flower planter (W). Wreck Road (W). Jenning's Road (2002, A Lines).

Wheeler (1906), Haskins (1939), Haskins & Haskins (1965), Kempf (1972), Lieberburg et al. (1975), and Hilburn et al. (1990) all recorded this species in Bermuda and it was the most common ant in the collections of Kincaid (in 1905) and Ogilvie (in 1925) in the MCZ. It was also common in Hilburn et al.'s collection of 1987-88. We collected this species in both natural and highly disturbed areas. This very small, orange, New World species is widespread and probably fairly common in Bermuda, but often overlooked because of its very small size.

2. *Brachymyrmex obscurior* Forel

Specimens examined: No site data (1905, T Kincaid, MCZ). Paget (1925, L Ogilvie, MCZ). Hamilton (1934, NA Weber, MCZ). Hamilton (1966, KM, BAMZ, male and queen). Paget (1971,

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TABLE 2. SITES SURVEYED BY HASKINS & HASKINS (IN 1963-1986) AND THE PRESENT STUDY (IN 2002).

	Year				
Site	1963	1966	1973	1986	2002
Great Head Park	—	—	both	L	L
Mullet Bay Rd. & Ferry Road	P	both	both	L	L
Leamington Caves	L	—	P	L	L
Knapton Hill Intersection	L	—	both	L	L
Knapton Hill/Harrington 100s	L	—	P	L	both
Christchurch/Brighton Hill	both	—	P	L	L
Spittal Pond	P	—	P	P	both
Newstead Hotel	L	—	L	both	both
Wreck Road	both	—	both	P	L
Ireland Island	—	P	—	P	both
P. megacephala/*L. humile* sites	0.7	2.0	1.6	0.6	0.4

P = *Pheidole megacephala*, L = *Linepithema humile*, both = both species, — = not sampled.

N Krauss, SI). Many sites (1987-1988, H, BAMZ). Paget Parish (1987, H, BAMZ, labeled "*Paratrechina* sp. det DR Smith"). St. George's (1987, R Gordon, BAMZ, queen, labeled "*Paratrechina* sp. det. D.R. Smith"). 19 sites (W).

Wheeler (1906), Simmonds (1958), Wingate (1965), Crowell (1968), Kempf (1972), Haskins & Haskins (1988), and Brandão (1991) all recorded the presence of *B. obscurior* in Bermuda. As noted in the specimens listed above, we found *B. obscurior* specimens in the BAMZ collection misidentified as "*Paratrechina* sp." Many others were labeled "*Brachymyrmex* sp.". Records listed as *Brachymyrmex* sp. and *Paratrechina* sp. by Hilburn et al. (1990) were probably all *B. obscurior.*

We collected *B. obscurior* at 19 locales across Bermuda, often in areas with dense populations of *P. megacephala* or *L. humile*. In some localities, where neither *P. megacephala* or *L. humile* were present (e.g., forest areas near Blue Hole), we found only this species and/or *B. heeri*. It appears to be the second most common ant species in Bermuda, after *L. humile*. We expect that a close inspection would find these ants at virtually every site in Bermuda. This New World species is extremely variable in size and color, making identification much more difficult.

+3. *Camponotus pennsylvanicus* (De Geer)

Specimens examined: Rockville Close, inside house (2002, E Beek, BDOA). Same site (W). Rockville Close, Bermuda Lumber Company (W).

A resident in Rockville Close reported to the BDOA that ants first she exterminated in her house in August 2001 had returned in January 2002. We collected specimens at the same house. At a lumberyard a few blocks away, employees told us that they often saw large ants. We searched an area where they had killed the ants earlier that day under Virginia cedar lumber from Florida, and found one live and several dead *C. pennsylvanicus* workers. It is unclear whether this North American carpenter ant is actually established in Bermuda. This species has a broad range in the US, from Pennsylvania to Florida, so it seems likely that climate would not limit its establishment in Bermuda. The BDOA had a number of samples of this species intercepted by quarantine in the past few years, often on imported Christmas trees and lumber (see below).

4. *Cardiocondyla emeryi* Forel

Specimens examined: No site data (1905, T Kincaid, AMNH). Ireland Island North, in grassy area outside clayworks (W).

Wheeler (1906), Kempf (1972), Lieberburg et al. (1975), Haskins & Haskins (1988), and Hilburn et al. (1990) also noted the presence of *C. emeryi*. This African native, though apparently not very common, certainly appears to be established in Bermuda. Due to its very small size, it is probably often overlooked.

+5. *Cardiocondyla obscurior* Wheeler

Specimen examined: Paget Parish (1987, H, BAMZ). Identified by S. Cover & B. Seifert.

This Old World tramp species is often misidentified as another tramp, *C. wroughtonii*, but may be distinguished from this species based on coloration and discriminate function analysis (Seifert 2003). Due to its small size, the species often may be overlooked.

+6. *Crematogaster* sp. male

Specimen examined: Berry Hill Road, light trap (1987, H, BAMZ, one male). James Trager identified this specimen as *Crematogaster* sp., Mark Deyrup concurred.

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This species, collected only once, appears to be rare in Bermuda.

7. *Hypoponera opaciceps* (Mayr)

Specimens examined: Spittal Pond, black light (1987, H, BAMZ, one queen). Spittal Pond, under rock (W). Spittal Pond, near Spanish Rock (W). Ireland Island North, under board by dock (W, one queen), Jenning's Road (2002, A Lines).

Wheeler (1906), Haskins & Haskins (1965, 1988), Kempf (1972), and Lieberburg et al. (1975) reported this species. Hilburn et al. (1990) questioned this record as "probably misidentified or no longer established," but the BAMZ actually had a specimen collected by Hilburn. We found a small area near Spanish Rock where *H. opaciceps* was the only species present. This New World native is largely subterranean, and often overlooked.

+8. *Hypoponera punctatissima* (Roger)

Specimen examined: Hamilton (1910, EG Vanatta, ANS, one queen).

We have seen only one specimen of *H. punctatissima* from Bermuda. It is a well-known tramp species distributed throughout the tropics and subtropics and almost certainly an exotic in Bermuda. Due to its subterranean habits, *H. punctatissima* is probably often overlooked.

9. *Linepithema humile* (Mayr)

Specimens examined: No site data (1953, FD Bennett, BNHM). Many sites (1987-1988, H, BAMZ). 25 sites in Bermuda (W). Walsingham Jungle (2002, A. Lines). Spittal Pond (2002, A. Lines).

Starting with Bennett & Hughes (1959), every paper on Bermuda ants recorded this species. This South American native is currently the most common ant in Bermuda in both terms of the number of sites we found this species and in terms of its extremely high densities at these sites. We found this ant almost everywhere we collected in Bermuda, though we did not find it on three small islands we surveyed: Nonsuch Island, Horn Island, and Ordinance Island.

10. *Monomorium monomorium* Bolton

Specimens examined: Spittal Pond (1987, H, BAMZ, male labeled "*Monomorium* sp. male det DR Smith"). Ordinance Island, flowerbeds (W). Identified by X. Espadaler.

Verrill (1902) identified *Monomorium minutum* (= *M. monomorium*) and specimens of *M. monomorium* collected in 1987 and 2002 support this identification. Hilburn et al. (1990) list the above 1987 specimen as *Monomorium* sp. We collected this species at only one site, Ordinance Island, a small island where ships dock, connected to the town of St. George's by a bridge. *Monomorium monomorium* is common in the Mediterranean. In the West Indies it has been recorded in Barbados (Kempf 1972).

11. *Odontomachus ruginodis* Smith

Specimens examined: No site data (1905, T Kincaid, AMNH). Near Sharks Hole (1910, EG Vanatta, ANS, labeled *O. haematodes insularis* det Gregg 1956). Nonsuch Island (1931, no collector data, AMNH, labeled *O. haematodes insularis*). Walsingham Jungle (2002, A Lines & W Sterrer, BAMZ). Identified by M. Deyrup.

Dahl (1892) identified Bermuda specimens as "probably" *Odontomachus insularis*. Wheeler (1906) recorded a closely related variety, now considered a separate species: *O. ruginodis*. Later authors list one or two *Odontomachus* species from Bermuda: *O. insularis* and/or *O. brunneus*. Based on worker morphology, Brown (1976) regarded *O. ruginodis* as synonymous with *O. brunneus*. Brown (in Deyrup et al. 1985), however, changed his mind, and again separated them into two distinct species. Because all specimens that we examined were *O. ruginodis*, we will assume that all other published records were this species as well.

Jeremy Madeiros (Bermuda Department of Conservation Services, pers. comm.) reported seeing this large trap-jaw ant twice at night in 2001, on Long Rock and near Spanish Rock. We searched the area around Spanish Rock for more than an hour without finding this ant. After we left Bermuda, Alex Lines & Wolfgang Sterrer of the BAMZ, collected two specimens in Walsingham. This species used to be common in Bermuda but now appears to be quite rare (see Introduction). It is considered to be native to the West Indies and the Bahamas (Deyrup et al. 1998), but may be exotic in Florida (Deyrup 1991).

+12. *Paratrechina longicornis* (Latreille)

Specimens examined: Brighton Nursery, on *Poinsettia* from California (1990, no collector data, BDOA). Hamilton, three sites (W). Ireland Island North, four sites (W).

Hilburn et al. (1990) recorded this species as intercepted on imported plants in 1971 and on imported *Dahlia* bulbs in 1987, but considered it not established in Bermuda. We found *P. longicornis* well established over broad stretches of the Hamilton waterfront as well as on a large portion of Ireland Island North. This conspicuous Old World tramp has never before been recorded out of quarantine in Bermuda.

13. *Paratrechina vividula* (Nylander)

Specimens examined: No site data (1905, T Kincaid, MCZ, types for *Prenolepis kincaidi*). Paget (1925, L Ogilvie, MCZ).

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Paratrechina vividula has not been collected since 1925 and may be extinct in Bermuda. This Old World tramp species has been widely distributed through human commerce.

14. *Pheidole megacephala* (F.)

Specimens examined: No site data (no date, Pergande collection, SI, "480" - probably collected ~1890). No site data (1905, T Kincaid, MCZ & AMNH), Five sites (1910, EG Vanatta, ANS). Padet Marsh (1922, HH Whelzel, MCZ). Cooper's Island (1922, HC Hoyt, ANS). Hamilton (1934, NA Weber, MCZ). Paget (NLH Krauss, 1971, SI). Many sites (1987-1988, H, BAMZ). 15 sites (W). Brimstone Hill (2002, Z. Amaral). Lambda Island (2002, A. Lines).

Every paper on Bermuda ants beginning with Dahl (1892) has recorded *P. megacephala*. Of 122 specimens collected by Vanatta in 1910, 117 were *P. megacephala*, suggesting that this species was dominant in Bermuda at this time. At the ten sites repeatedly surveyed since 1963, the latest survey found *P. megacephala* at four sites and *L. humile* at all ten, the lowest ratio of *P. megacephala* to *L. humile* yet recorded. Still, we found *P. megacephala* in numerous other sites in Bermuda, including three islands where *L. humile* was absent: Nonsuch Island, Horn Island, and Ordinance Island.

15. *Plagiolepis alluaudi* Forel

Specimens examined: No site data (1945, Stern & Pruit, SI, "NY-95303 46-1072 Surinam Cherry lvs"). No site data (1950, no collector data, SI, "NY110550 50-3046 on *Zebrina pendula* cut"). No site data (1950, no collector data, SI, "52-3330"), Warwick Parish (1987, J Hendrickson, BAMZ, "Brightside on *Cassia*").

Kempf (1972) listed this species in the New World from Bermuda, St. Kitts, and St. Lucia. This small orange ant is an African tramp species that has been spread around the world, particularly in the Pacific, through human commerce (Wilson & Taylor 1967).

+16. *Solenopsis* (*Diplorhoptrum*) sp.

Specimens examined: Hamilton (1934, NA Weber, MCZ). Brimstone Hill (2000, no collector data, BDOA), BBSR, under boards and under concrete (W). Hamilton, waterfront, in planters (W). Hamilton, around Ambouy Point (W).

We suspect that this small orange thief ant is probably common throughout Bermuda, but generally overlooked due to its size and primarily subterranean habits. Thief ants commonly persist at high densities in areas invaded by dominant exotic ants such as *P. megacephala* and *L. humile* (Wetterer et al. 2001). The taxonomy of thief ants is in disarray and more than one species of thief ant may have been collected in Bermuda.

+17. *Tetramorium caldarium* Roger

Specimen examined: Newstead Hotel complex, west end (W).

We collected a single *T. caldarium* worker found battling with a *P. megacephala* worker on a bare dirt bank. It is the only species that we found for the first time in 2002. This Old World tramp species appears to be rare in Bermuda.

+18. *Tetramorium simillimum* (Smith)

Specimens examined: Padet Marsh (1922, HH Whelzel, MCZ). Ferry Point Park entrance, side of the road (W). Devonshire, Happy Talk Road (2002, A. Lines).

This Old World tramp species seems to have a long history in Bermuda but remains rare.

19. *Wasmannia auropunctata* (Roger)

Specimens examined: Paget (1925, L Ogilvie, MCZ).

We examined one *W. auropunctata* specimen collected by Ogilvie, though this species was not on Ogilvie's (1928) list. Crowell (1968) recorded *W. auropunctata* and mentioned a 1950 record. Lieberburg et al. (1975), Haskins & Haskins (1988), and Hilburn et al. (1990) also reported *W. auropunctata*. Hilburn et al. (1990) wrote that this species is "now fairly common." However, because we did not collect this ant and did not find any specimens collected by Hilburn, we believe that Hilburn and others may have mistaken other small orange ants in Bermuda (e.g., *B. heeri*, *P. alluaudi*, or *Solenopsis* sp.), as being *W. auropunctata*. Populations of *W. auropunctata* may have declined or become extinct in Bermuda. This ant was first recorded in Florida in 1924 and soon became a major pest. However, densities of *W. auropunctata* appear to have declined in many parts of Florida (Deyrup et al. 2000). Bermuda is the northernmost outdoor locale recorded for *W. auropunctata* (Wetterer & Porter 2003).

+20. Dacetine male

Specimen examined: Paget Parish, Malaise trap (1987, H, BAMZ, one male, labeled "Myrmacinae male, det DR Smith").

No dacetines have been previously reported from Bermuda. Unfortunately, no one could identify this specimen to genus. Barry Bolton (BNHM, personal communication) wrote: "there is so little male-associated material that defining the genera on this sex just can't be achieved yet. As far as I can tell, *Strumigenys* and *Pyramica* cannot be separated on males." Xavier Espadaler determined that it was not a European species.

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Unconfirmed Status (No Specimens Examined)

Lasius niger (L.)

Although Kirby (1884) listed *L. niger* from Bermuda, *Lasius* specimens from Madeira and the Azores, originally identified as *L. niger*, have been recently reclassified as *L. grandis* (Seifert, 1992), so the same may be true for the *Lasius* of Bermuda. It is also possible that the ants were not *Lasius* at all. Clark (1930) re-examined other ant specimens evaluated by Kirby and considered his identifications and descriptions to be "worthless." We did not find these specimens in the BNHM where Kirby worked.

Monomorium pharaonis (L.)

Wheeler (1906) speculated without examination that Verrill's (1902) *M. monomorium* specimens were actually *M. pharaonis*, a conclusion accepted by Ogilvie (1928) and Hilburn et al. (1990). Ogilvie (1928) wrote that *M. pharaonis* is a common house species, and Hilburn et al. (1990) wrote that it was "not an important household pest in Bermuda in recent years," but it is unclear whether either actually examined any *M. pharaonis* specimens from Bermuda.

Paratrechina sp.

Crowell (1968), Lieberburg et al. (1975), Haskins & Haskins (1988), and Hilburn et al. (1990) reported an unidentified *Paratrechina*. Hilburn et al. (1990) wrote that this species was "now common and widespread." However, all of the specimens from Hilburn et al. (1990) at the BAMZ labeled "*Paratrechina* sp." were actually *B. obscurior*. The same may be true of the other records.

Prenolepis sp.

Wheeler (1906) wrote that the *Prenolepis* sp. sample collected by Kincaid included "seven workers, apparently all from the same colony, but varying much in size (from 2-3 mm). They are very pilose and pubescent, with subopaque surface and finely punctate mesonotum." Wheeler (1906) felt that males were needed for definitive identification. We did not find these specimens at the MCZ, where Wheeler worked. It is possible that this species is a *Paratrechina* or perhaps a *Plagiolepis*.

Tetramorium caespitum (L.)

Verrill (1902) recorded *T. caespitum*, the European "pavement ant," in Bermuda. Wheeler (1906) speculated, without examining the specimens, that they were *T. guineense*. *Tetramorium caespitum* is common in Europe and Asia, as well as in the Azores. *Tetramorium guineense* is native to Africa, though Wheeler (1906) was no doubt actually referring to *Tetramorium bicarinatum* (Nylander), a common tramp ant once considered a synonym of *T. guineense*. Unfortunately, we did not find any of Verrill's specimens in the YPM, where he worked.

Ants Intercepted by Bermuda Department of Agriculture

Several species of ants in the BDOA collection were intercepted on incoming products, including: *Camponotus floridanus*, *C. novoboracensis*, *C. pennsylvanicus*, *Camponotus* sp. near *pennsylvanicus*, *Camponotus zonatus*, *Crematogaster steinheili*, and *Pheidole moerens*.

Discussion

Our study confirms the conclusions of earlier research (Haskins & Haskins 1965, 1988; Crowell 1968; Lieberburg et al. 1975) that Bermuda is largely partitioned between two dominant ant species, *Pheidole megacephala* and *Linepithema humile*. Although *P. megacephala* appeared to show a resurgence in the late 1960s and early 1970s (Table 2, Haskins & Haskins 1988), *L. humile* now has the upper-hand, dominating most parts of the main islands of Bermuda. The recent populations of *P. megacephala* in Bermuda appear to be the lowest recorded. Still, this species persists in pockets on the main islands and on small islands not connected to the main islands. We found that *P. megacephala* dominated and *L. humile* was absent on two small islands, Nonesuch and Horn, with breeding population of cahow (*Pterodroma cahow*), an endangered endemic bird. The absence of *L. humile* is relatively good news for the cahow because *L. humile* seems to pose a greater threat to ground-nesting birds than does *P. megacephala*. For example, Newell & Barber (1913) observed *L. humile* attacking young birds, swarming over and devouring nestlings.

In additional to the two dominant species, we examined specimens of 18 other ant species from Bermuda. *Brachymyrmex obscurior*, though small and inconspicuous, is very common in Bermuda and coexists with both *L. humile* and *P. megacephala*. *Paratrechina longicornis*, which was not previously reported from Bermuda, has substantial populations in two urban areas. Three other ant species appear to be well established, but very inconspicuous due to their very small size (*Brachymyrmex heeri* and *Solenopsis* sp.) or subterranean habits (*Hypoponera opaciceps*). The rest of the recorded ant species appear to be rare. Only three ant species with confirmed records from Bermuda have not been collected recently (1987 or later): *Hypoponera punctatissima*, *Paratrechina vivid-*

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ula, and *Wasmannia auropunctata*. All three are common tramp species and almost certainly exotic to Bermuda.

It is an open question as to whether Bermuda ever had any native ants. It is feasible that Bermuda, like Hawaii, had no ants before people arrived. In fact, 13 of the 17 confirmed ant taxa in Bermuda identified to species are almost certainly exotic. Candidate for native status include *Brachymyrmex heeri*, *Brachymyrmex obscurior*, *Hypoponera opaciceps*, and *Odontomachus ruginodis*, all native to the West Indies and the Bahamas. Some species may have had native populations augmented by subsequent human-assisted immigration.

DNA analyses should be useful in evaluating native versus exotic status of ants in Bermuda, e.g., to determine whether or not populations of *B. heeri*, *B. obscurior*, *H. opaciceps*, and *O. ruginodis* show the genetic uniformity consistent with exotic introductions. DNA analyses may also allow evaluation of the geographic origins of populations of exotic species. DNA analyses of 35 of our *L. humile* specimens (five each from seven populations) showed that all individuals had the same haplotype for two mitochondrial markers (cytb and COI). These haplotypes have been found in one native Argentine population and in one introduced Chilean population, and but in no other introduced populations analyzed (V. Vogel et al., unpublished data; see Giraud et al. 2002).

More thorough ant surveys of Bermuda would be valuable. Of the 20 ant species with confirmed records from Bermuda, five have been collected only once. From this, we expect that there are several additional undocumented ant species established in Bermuda. The impact of ants on the native fauna and flora of Bermuda also deserves careful study.

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