

Ants (Hymenoptera: Formicidae) of the South Atlantic islands of Ascension Island, St Helena, and Tristan da Cunha

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Abstract

The isolated Mid-Atlantic Ridge islands of Ascension Island (8° S), St Helena (16° S), and Tristan da Cunha (37° S) are 1700 - 2800 km from Africa, the nearest continent. We compiled published, unpublished, and new records of ants from these islands and evaluated the probable origin of each species.

We examined specimens representing 20 different ant species: ten from Ascension, 16 from St Helena, and one from Tristan da Cunha. These included three new records from Ascension (*Pheidole teneriffana* FOREL, 1893, *Solenopsis* sp. 1, *Strumigenys emmae* (EMERY, 1890)), five new records from St Helena (*Hypoponera* sp. 1, *Linepithema humile* (MAYR, 1868), *Monomorium latinode* MAYR, 1872, *Monomorium cf. sechellense*, *Pheidole teneriffana*), and the first identification of the only ant species known from Tristan da Cunha (*Hypoponera eduardi* (FOREL, 1894)). All confirmed island records, except *Camponotus fabricator* (F. SMITH, 1858) and *Hypoponera punctatissima* (ROGER, 1859) on St Helena, included specimens from 1995 or later. We could not confirm two additional published ant species records from Ascension (*Cataglyphis* sp., *Tapinoma* sp.) and one from St Helena (*Camponotus castaneus* (LATREILLE, 1802)).

Most, if not all, of the 20 ant species we documented on South Atlantic islands, including *C. fabricator*, a putative St Helena endemic, may be exotic species that arrived accompanying humans. However, it is possible that some ants were present before human arrival. One candidate for native status is *Cardiocondyla mauritanica* FOREL, 1890, a widespread tramp species originally from Africa, found on Ascension in many uninhabited areas.

Key words: Atlantic islands, exotic ants, *Linepithema humile*, Mid-Atlantic Ridge.

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Introduction

Ants are an important component of the native community on all continents except, ironically, Antarctica. Some isolated oceanic islands, however, may lack any native ants. For example, WILSON & TAYLOR (1967) hypothesized that all of the ants on Polynesian islands east of Samoa, Tonga, and New Zealand may be exotic. WETTERER (2006), however, proposed that on the isolated island of Niue, to the east of Tonga, 16 species of the 33 known species seem likely to be native, i.e., predating human arrival. Here, we examine the ant fauna of the isolated islands of the Mid-Atlantic Ridge.

The Mid-Atlantic Ridge is the world's longest mountain range, extending > 15,000 km down the middle of the Atlantic Ocean from 87° N to 54° S. Only its highest peaks extend above the ocean's surface, forming isolated volcanic islands, including Iceland and the Azores in the North Atlantic, and Ascension, St Helena, Tristan da Cunha, and

Gough Island in the South Atlantic. Mid-Atlantic Ridge islands are important breeding sites for many oceanic birds, but have a species-poor invertebrate fauna. For example, WOLLASTON (1861 in DUFFEY 1964) wrote that the few beetles found on Ascension "would be totally unworthy of notice if it were not as a voucher for the utter sterility of this miserable spot and to warn naturalists from ever attempting to go there again for the purposes of collecting." Perhaps heeding Wollaston's warning, few people have collected ants on any Mid-Atlantic Ridge island. Recent work, however, contradicts Wollaston's conclusion that Ascension is entomologically uninteresting (ASHMOLE & ASHMOLE 1997, 2000).

In the past, all ants known from Mid-Atlantic Ridge islands were generally thought to be exotics that arrived accompanying humans (VOISIN 1980, ASHMOLE & ASHMOLE 1997). For example, the one ant species known to have a

long-term population on Iceland is certainly exotic: *Hypo-ponera* cf. *punctatissima* (ROGER, 1859), found there only in houses (OLAFSSON & RICHTER 1985) and geothermal areas (E. Olafsson, pers. comm.). WETTERER & al. (2004), however, recently proposed that five of the 14 ant species known from the Azores may be native.

In the present study, we compiled published, unpublished, and new records of ants from the three inhabited islands of the southern Mid-Atlantic Ridge: Ascension Island (8° S; 97 km²), St Helena (16° S; 126 km²), and Tristan da Cunha (37° S; 103 km²). We found no records of ants from uninhabited Gough Island (40° S; 67 km²); BREYTENBACH (1986) stated "Gough Island has no ant fauna." Whereas the Azores are 1500 km from the nearest continent (i.e., Europe), these South Atlantic islands are even more isolated (distance from Africa, the nearest continent: Ascension 1700 km, St Helena 1920 km, Tristan da Cunha and Gough 2800 km).

Published ant records from Ascension, St Helena, and Tristan da Cunha

We found published records of nine ant species from Ascension (DAHL 1892, DUFFEY 1964, BOLTON 1987, ASHMOLE & ASHMOLE 1997), 12 from St Helena (SMITH 1858, MELLISS 1875, FOREL 1879, TAYLOR & WILSON 1961, TAYLOR 1976, BOLTON 1980, ASHMOLE & ASHMOLE 2000), and one from Tristan da Cunha (VOISIN 1980; see Tab. 1).

DAHL (1892) recorded three ant species from Ascension: *Cataglyphis* sp., *Tapinoma* sp. and *Pheidole pusilla* (HEER, 1852) (= *Pheidole megacephala* (FABRICIUS, 1793)). DUFFEY (1964) recorded six ant species from Ascension: *Cardiocondyla emeryi* FOREL, 1881 (confirmed by SEIFERT 2003a), *Monomorium salomonis* (LINNAEUS, 1758) (re-identified as *Monomorium subopacum* (F. SMITH, 1858); BOLTON 1987), *Paratrechina longicornis* (LATREILLE, 1802), *Pheidole* "?*megacephala*", *Plagiolepis* "sp. ?*alluaudi*", and *Solenopsis globularia steinheilli* FOREL, 1881. ASHMOLE & ASHMOLE (1997) recorded five ant species from caves and on lava flows on Ascension: *C. emeryi*, *Cardiocondyla mauritanica* FOREL, 1890, *P. longicornis*, *Ph. megacephala*, and *Solenopsis globularia* (F. SMITH, 1858).

SMITH (1858) published the first ant record from St Helena, describing a new species of carpenter ant, *Formica fabricator* (= *Camponotus fabricator* (F. SMITH, 1858)). MELLISS (1875) recorded *Ph. megacephala* on St Helena and "another species which appears to be confined to the town; it is slightly larger, quite black, and more active [than *Ph. megacephala*] in its movements." FOREL (1879) reported *Formica melleus* (= *Camponotus castaneus* (LATREILLE, 1802)) collected on St Helena. DONISTHORPE (1927) reported *Hypo-ponera punctatissima exacta* (SANTSCHI, 1923) (= *H. punctatissima*). TAYLOR & WILSON (1961) listed five ant species collected on St Helena by A. Loveridge, between 1958 and 1960: *Paratrechina bourbonica* (FOREL, 1886), *Ph. megacephala*, *Plagiolepis alluaudi* EMERY, 1894, *Solenopsis (Diplorhoptrum)* sp., and *Tetramorium simillimum* (F. SMITH, 1851) (re-identified as *Tetramorium caldarium* (ROGER, 1857); BOLTON 1980). TAYLOR (1976) reported nine ant species from St Helena, combining older records with new specimens collected in 1965 - 1967 by two Musée Royal de l'Afrique Centrale expeditions and in 1966 by Loveridge (Tab. 1); three new spe-

cies records were *C. emeryi*, *S. globularia*, and *Tapinoma melanocephalum* (FABRICIUS, 1793). BOLTON (1982) recorded *C. emeryi* collected by Wollaston, who visited St. Helena in 1875. ASHMOLE & ASHMOLE (2000) mentioned two ant species by name from St Helena, *Ph. megacephala* and *P. longicornis*.

HOLDGATE's (1965) summary of previous land fauna surveys of the Tristan da Cunha included no ant records. VOISIN (1980), however, reported an unidentified *Hypo-ponera*: "A few nests of this ant were discovered under stones on the top of the beach, out of reach of the waves, near the Settlement and south of the Hardies. As this genus has not been previously recorded from Tristan da Cunha, this must also be introduced. Its specific identity could not be determined with certainty."

Here, we report additional ant records from Ascension, St Helena, and Tristan da Cunha and evaluate whether any of the ants might be native to these islands.

Methods

Between 1994 and 2005, Philip and Myrtle Ashmole collected ants on Ascension and St Helena, publishing some of these records (ASHMOLE & ASHMOLE 1997, 2000). In October 2002, Chris Cutler and Amma Szal collected ants for one day each on Ascension, St Helena, and Tristan da Cunha. In February - March 2003, Alan Gray collected ants at South Gannet Lava Flow, Ascension. In July - August 2003, Howard Mendel collected ants on Ascension. In March 2004, Judith Endeman collected ants for one day each on Ascension, St Helena, and Tristan da Cunha. Endeman also searched for ants on the Falkland Islands and the South Georgia Islands. In July - August 2005, Alexandra Cripps collected ant specimens on Ascension. In December 2005 - January 2006, Howard Mendel collected ants on St Helena. In December 2005 - March 2006 Philip and Myrtle Ashmole collected ants on St Helena, and in December 2005 and March 2006 they collected ants on Ascension. Xavier Espadaler identified specimens using keys by BOLTON (1980, 1987, 2000), SEIFERT (2003a), TRAGER (1984) and WILSON (2003). For species described by Forel, Xavier Espadaler examined type material in the Forel collection in Geneva. Morphometric measures (average \pm 1 SD), made using a Nikon SMZ-U stereomicroscope, at 75 - 150 \times magnification, followed BOLTON (1987) for head length (HL), head width (HW), scape length (SL) and pronotum width (PW), and SEIFERT (2003b) for cephalic length (CL), cephalic width (CW), and cephalic size (CS).

In August 2003, James Wetterer recorded label data from specimens in the collection of the Natural History Museum in London (BMNH) of several common tramp ant species, including *P. longicornis*, *Ph. megacephala*, and *Linepithema humile* (MAYR, 1868). In November 2005, Kim Goodger searched the BMNH collection for specimens of all other ant species previously reported from Ascension, St Helena, and Tristan da Cunha. Xavier Espadaler examined BMNH specimens of *Camponotus* and *Hypo-ponera* to confirm species identifications.

We evaluated exotic versus native status of each ant species based on its known worldwide distribution and whether it occurred in disturbed or relatively undisturbed habitats. Species distributed around the world through human commerce and found primarily in heavily disturbed environ-

ments we considered probably exotic to the islands. Ant species not widely distributed beyond Africa and Macaronesia (the Azores, Madeira, the Canary Islands, and Cape Verde), or found only in relatively intact native habitat were considered as possibly native (i.e., predating human arrival).

Results

We examined specimens representing 20 different ant species collected on southern Mid-Atlantic Ridge islands: ten on Ascension, 16 on St Helena, and one on Tristan da Cunha (Tab. 1). All confirmed island records, except *C. fabricator* and *H. punctatissima* on St Helena, included specimens from 1995 or later. Specimens included three new species records for Ascension (*Pheidole teneriffana*

Tab. 1: Ant records from Ascension, St Helena, and Tristan da Cunha (in chronological order).

Published records: a = SMITH (1858), b = MELLISS (1875), c = FOREL (1879), d = DAHL (1892), e = TAYLOR & WILSON (1961), f = DUFFEY (1964), g = Loveridge 1966 in TAYLOR (1976), h = Musée Royal de l'Afrique Centrale 1965-1967 in TAYLOR (1976), i = VOISIN (1980), j = ASHMOLE & ASHMOLE (1997), k = ASHMOLE & ASHMOLE (2000). Unpublished records (see text): 1 = Wollaston < 1877, * = record in DONISTHORPE (1927) probably collected by Wollaston, 2 = Wallace 1959, 3 = Ashmole & Ashmole 1994 - 1995, 4 = Cutler & Szal 2002, 5 = Gray 2003, 6 = Mendel 2003, 7 = Endeman 2004, 8 = Cripps 2005, 9 = Mendel, Ashmole, & Ashmole 2005 - 2006. North Atlantic range: b = Bermuda, z = Azores, m = Madeira, c = Canary Islands, v = Cape Verde. Status: A = African, M = Mediterranean, N = New World, O = Asian, T = known tramp.

Species	Ascension	St Helena	Tristan da Cunha	North Atlantic	Status
<i>Camponotus fabricator</i>		a			?
<i>Cardiocondyla emeryi</i>	fj456	1h49		b mcv	A T
<i>Cardiocondyla mauritanica</i>	j4567			mc	A T
<i>Hypoponera eduardi</i>			i4	zmcv	M
<i>Hypoponera punctatissima</i>		1*h9		zmcv	A T
<i>Hypoponera</i> sp. 1		3		m	?
<i>Linepithema humile</i>		479		bzmc	N T
<i>Monomorium</i> cf. <i>sechellense</i>		3			?
<i>Monomorium latinode</i>		3			O T
<i>Monomorium subopacum</i>	f7			mcv	M
<i>Paratrechina bourbonica</i>		12eh49		b	? T
<i>Paratrechina longicornis</i>	fj4678	k7		bzmcv	O T
<i>Pheidole megacephala</i>	dfj467	b1eh2k479		zmcv	A T
<i>Pheidole teneriffana</i>	4	4		b c	M T
<i>Plagiolepis alluaudi</i>	f46	2eh49		b	A T
<i>Solenopsis globularia</i>	fj56	fh39			N T
<i>Solenopsis</i> sp. 1	68	eg4			?
<i>Strumigenys emmae</i>	6			v	A T
<i>Tapinoma melanocephalum</i>		h39		cv	O T
<i>Tetramorium caldarium</i>		eg4		bzmcv	O T
Unconfirmed records:					
<i>Camponotus castaneus</i>		c			N
<i>Cataglyphis</i> sp.	d			?	?
<i>Tapinoma</i> sp.	d			?	?

FOREL, 1893, *Solenopsis* sp. 1, *Strumigenys emmae* (EMERY, 1890)) and five new species records for St Helena (*Hypoponera* sp. 1, *L. humile*, *Monomorium latinode* MAYR, 1872, *Monomorium* cf. *sechellense*, *Ph. teneriffana*). We identified the *Hypoponera* species from Tristan da Cunha for the first time: *Hypoponera eduardi* (FOREL, 1894). We could not confirm two additional published records from Ascension and two from St Helena (see below).

In the BMNH, we noted specimens of ten ant species from South Mid-Atlantic Ridge islands. These included published records in SMITH (1858), DUFFEY (1964), and TAYLOR & WILSON (1961), and previously unreported specimens from St Helena: *C. emeryi*, *H. punctatissima*, *P. bourbonica*, *Ph. megacephala* collected by T.V. Wollaston (registered in the BMNH collection in 1877) and *P. bourbonica*, *Ph. megacephala*, and *P. alluaudi* collected by C. R. Wallace in 1959.

We could not document any ants on the Falkland Islands or the South Georgia Islands. Six Falklanders (including those at the local museum) and three people working at the museum in South Georgia all said that they had never seen any ants on these islands.

Confirmed records: specimens examined and species accounts

Collectors: A = Ashmole & Ashmole; C = Cripps; C&S = Cutler & Szal, E = Endeman. G = Gray, M = Mendel. + = new island record. BMNH = British Museum, Natural History. When available and relevant, specimen records include collection date, collector, and museum repository.

1. *Camponotus fabricator* (F. SMITH, 1858)

St Helena: no site data (collector and date unknown; BMNH; SMITH 1858).

SMITH (1858) described the carpenter ant *Camponotus fabricator* from St Helena. MAYR (1886) reclassified *C. fabricator* as a variety of *Camponotus sylvaticus* (OLIVIER, 1792). DALLA TORRE (1893) revived its status to full species. EMERY (1896) considered it a subspecies of *Camponotus maculatus* (FABRICIUS, 1782). FOREL (1914) revived *C. fabricator* to full species status.

XE examined one major type specimen and determined that it is not *C. sylvaticus*, *C. maculatus*, or any known European species. Nor did it fit any North American species in CREIGHTON's (1950) key or published digital images available on the web. Disturbingly, the specimen also did not fit SMITH's (1858) original description of *C. fabricator* as a "smooth and shining" species. The type specimen is a major worker that is dull with a fine reticulate sculpture on head and alitrunk; gaster transversely finely striate. This difference in sculpture of worker is very apparent. The head, gaster, and upper half of mesosoma are dark brown, the legs are brownish red, and the funiculus is brownish yellow. Some *Camponotus* from Africa (e.g., *C. acvapimensis* MAYR, 1862) and India (e.g., *C. festinus* (F. SMITH, 1857) have similar coloration. The combination of a dull, dark, bicolored worker with very short and sparse pubescence and poorly developed pilosity (four pronotal hairs, three propodeal hairs, total of five hairs on the central part of tergites 1 - 3 of gaster), tibiae with erect bristles, and a relatively small size (HW 3.4, HL 3.3, SL 2.8, total length ~11 mm) is not known in any other *Camponotus* spe-

cies. Pending further revision, we regard this species as valid.

This species is the sole ant species known only from a Mid-Atlantic Ridge island. Still, it is likely that this is an exotic Old World species brought into St Helena on imported goods. DONISTHORPE (1927) recorded several species of exotic *Camponotus* on imported wood, flowers, and food products in England (also see WETTERER & WETTERER 2004, WETTERER & al. 2006, in press). *Camponotus fabricator* may be extinct on St Helena.

2. *Cardiocondyla emeryi* FOREL, 1881

Ascension: no site data (1958; EAG Duffey; BMNH). South Gannet Lava Flow (1990; A). Two Boats Village, Two Boats Club (2002; C&S). South Gannet (2003; G & M). Devil's Ashpit (2003; M). Grazing Valley (2003; M). US Airbase (2003; M).

St Helena: no site data (< 1877; TV Wollaston; BMNH; BOLTON 1982). Joan Hill (1995; A). Jamestown, downtown park (2002; C&S). Cuckhold's Point, pitfall trap (2005 / 2006; M). Peak's Cabbage, Tree Rd. swept (2005 / 2006; M). Lower House Plain, pitfall traps (2005 / 2006; M). Turks Cap (2006; A). Flagstaff ridge (2006; A). Joan Hill (2006; A). Prosperous Bay Plain (2006; A).

Cardiocondyla emeryi, an African native, is a well-known tramp species distributed worldwide by human commerce (SEIFERT 2003a), and is probably exotic to Ascension and St Helena.

3. *Cardiocondyla mauritanica* FOREL, 1890

Ascension: Command Hill, lava surface (1990; A). South Gannet Lava Flow (1990; A). Letterbox Lava (1990; A). Sisters Cinders (1990; A). Green Mountain, Eliot's Pass trail (2002; C&S). South Gannet (2003; G & M). Grazing Valley (2003; M). Letterbox (2003; M). Command Hill (2003; M). Wideawake colony, in eggshell on lava bed (2004; E).

Cardiocondyla mauritanica is an African native that SEIFERT (2003a) considered a cosmopolitan tramp species. WETTERER & al. (2006, in press) found this species only at urban sites in Madeira and considered it exotic there. ESPADALER & BERNAL (2003), however, considered this species native to the Canary Islands. Given its distribution in isolated, uninhabited parts of Ascension, it seems possible that it is native to Ascension.

4. *Hypoponera eduardi* (FOREL, 1894)

Tristan da Cunha: Beneath stones at three locations beneath Edinburgh and the town dump (2002; C&S).

This is almost certainly the same *Hypoponera* reported under stones by VOISIN (1980). *Hypoponera eduardi* occurs throughout the Mediterranean area, as well as on all four archipelagos of Macaronesia (the Azores, Madeira, the Canary Islands, and Cape Verde), where it appears to be native. Its populations on Tristan da Cunha, however, are far from the rest of its known range, and it therefore seems likely to be exotic.

5. *Hypoponera punctatissima* (ROGER, 1859)

St Helena: no site data (< 1877; TV Wollaston; BMNH). Prosperous Bay Plain (A; 2006).

Wollaston's specimen had the following measurements (in mm): maximum cephalic length 0.669; maximum ceph-

alic width 0.559; cephalic size 0.614; scape length 0.481; scape length / cephalic size 0.783. The biometry fits within the limits of *H. punctatissima* given by SEIFERT (2003b).

DONISTHORPE (1927) reported *H. punctatissima* from St Helena, presumably based on Wollaston's specimens in the BMNH. TAYLOR (1976) also reported *H. punctatissima* from St Helena. This African native is a well-known tramp species widely distributed throughout the tropics and subtropics, and is probably exotic to St Helena.

6. *Hypoponera* sp. 1

+ **St Helena:** Near Lot, pipe trap (1994 - 1995; A). Potato Bay, traps (1995; A). Flagstaff, male (1995; A).

We are uncertain of the species identity of this yellow-orange species. It is very similar to *Hypoconerops bondroiti* (FOREL, 1911), an apparently New World species described from Belgium, which has also been introduced to Japan (e.g., YAMAUCHI & al. 1996, but see SEIFERT 2003b). Like *H. bondroiti* (YAMAUCHI & al. 1996), this species has ergatoid males. Workers of this species may be distinguished from *Hypoconerops punctatissima* as follows:

- Frontal line absent. Petiole with medium long hairs. Mesopleurae not smooth and shiny. Ommatidium whitish, larger (0.026 ± 0.0005 mm; $n = 3$). *Hypoconerops* sp. 1
- Frontal line present. Petiole with long hairs. Mesopleurae smooth and shiny. Ommatidium smaller (0.013 ± 0.0005 mm; $n = 3$).
. *Hypoconerops punctatissima*

WETTERER & al. (2006, in press) found this same species on Madeira, where it was common in dry habitats of eastern Madeira and Porto Santo, and less common in urban parks. WETTERER & al. (2006, in press) considered this species to be most likely exotic to Madeira, and the same is probably true for St Helena.

7. *Linepithema humile* (MAYR, 1868)

+ **St Helena:** Longwood, Longwood House gardens (2002; C&S). Jamestown, downtown park (2002; C&S). Jamestown, wharf (2004; E). Jamestown, garden wall (2004; E). St Paul's, near Plantation House entrance (2004; E). Longwood, Piccolo Hill (2006; A).

This is the first record of *L. humile*, the infamous Argentine ant, from St Helena. *Linepithema humile* is native to South America but has been spread to many temperate and subtropical locales around the world through human commerce. Most other published tropical records of *L. humile* are from high elevations in Hawaii. Additional tropical records for *L. humile* come from Bolivia, Brazil, Cameroon, Colombia, Costa Rica, Guyana, Indonesia, Mexico, Namibia, Peru, and Surinam.

This species is already known from the Atlantic islands of Bermuda, the Azores, Madeira, and the Canary Islands (WETTERER & WETTERER 2004, WETTERER & al. 2004, 2006, in press, ESPADALER in press). Populations of *L. humile* on the Azores, Madeira, and the Canary Islands show no aggression towards *L. humile* workers from other parts of these archipelagos, nor towards *L. humile* workers from southwestern Europe (WETTERER & WETTERER 2006, ESPADALER in press). WETTERER & WETTERER (2006) concluded that this behavior, combined with his-

torical and genetic evidence, suggests that the first *L. humile* population in the region was established in Madeira and that propagules from Madeira gave rise to population in other parts of the region. Behavioral and genetic analyses would be useful in evaluating whether the *L. humile* population on St Helena shares a common origin with those on the Azores, Madeira, and the Canary Islands.

8. *Monomorium latinode* MAYR, 1872

+ **St Helena:** Ebony Plain (1994 - 1995; A). Heart Shape Waterfall (1994 - 1995; A).

This Asian native is also known from Africa, Christmas Island in the Indian Ocean (BOLTON 1987), and Hawaii (WILSON & TAYLOR 1967). It is certainly exotic to St Helena.

9. *Monomorium* cf. *sechellense* EMERY, 1894

+ **St Helena:** Prince Andrew School, subterranean traps (1994 - 1995; A).

The single specimen we studied has the following measurements: HL 0.42, HW 0.34, SL 0.33, PW 0.22. Color is uniform yellow and the entire mesopleuron is sculptured with ten longitudinal ridges, which in the lower half become a reticle. The propodeum has three longitudinal ridges below the propodeal spiracle. The specimen clearly belongs in the *M. fossulatum* group as defined in BOLTON (1987). An alternative name might be *Monomorium cryptobium* (SANTSCHI 1921), a widely distributed ant in litter of Central and West African forests, but in this species the mesopleuron is completely smooth (BOLTON 1987).

Monomorium sechellense is an Asian native that has been spread around the world, particularly the Pacific (e.g., Samoa, Tonga, Cook Islands, Hawaii, Mariana Islands, and Micronesia), through human commerce.

10. *Monomorium subopacum* (F. SMITH, 1858)

Ascension: no site data (1958; EAG Duffey; BMNH). Georgetown, garden above museum (2004; E).

This species is widely distributed in North Africa and drier parts of the Mediterranean region. It appears to be native to Madeira, the Canary Islands, and Cape Verde. Although not considered a tramp species, it has been introduced to Sri Lanka (BOLTON 1987). It is possible that this species is native to Ascension, though the sole urban locality where we collected it suggests it is an exotic.

11. *Paratrechina bourbonica* (FOREL, 1886)

St Helena: no site data (< 1877; TV Wollaston; BMNH). Sandy Bay (1959; CR Wallace; BMNH). Birddown (1994 - 1995; A). Ruperts (1995; A). Potato Bay (1995; A). Broad Gut (1995; A). Gregory's Battery (1995; A). Prosperous Bay Plain (1995, 2006; A). Longwood, Longwood House gardens (2002; C&S). Peak's Cabbage, Tree Rd. swept (2005 / 2006; M). Diana's Peak, swept (2005 / 2006; M). Actaeon Mt., pitfall trap (2005 / 2006; M). Diana's Peak (2006; A). Casons, George Benjamin Reserve (2006; A). Teutonic Hall (2006; A). Man and Horse (2006; A). Joan Hill (2006; A). Peaked Island (2006; A).

It seems likely that the active black ant mentioned by MELLISS (1875) was this species. *Paratrechina bourbonica* is a tramp species spread throughout the Old World tropics, Oceania (WILSON & TAYLOR 1967), and a few New World sites (e.g., see TRAGER 1984, DEYRUP & al. 1988,

1998, 2000, WETTERER & al. 1999) by human commerce. DLUSSKY (1994) considered it native to Asia, but TAYLOR (1976) believed it is native to Africa. It is probably exotic to St Helena.

12. *Paratrechina longicornis* (LATREILLE, 1802)

Ascension: no site data (1958; EAG Duffey; BMNH). Command Hill, deep cave zone and lava surface (1990; A). Green Mountain, on rock wall by old barracks (2002; C&S). Two Boat Village, Two Boats Club (2002; C&S). Grazing Valley (2003; M). Red Lion (2003; M). Green mountain, above barracks (2003; M). near Spoon Crater (2003; M). Airport (2003; M). Chapel (2003; M). Green Mountain (2004; E). Georgetown, garden wall (2005; C). Green Mountain, Bells Cottage, wall (2005; C). Green Mountain Road, near Bells Cottage, wall (2005; C). Green Mountain Garden, wall (2005; C).

St Helena: Birddown (1994; A). Jamestown, garden wall (2004; E).

Paratrechina longicornis is one of the two most commonly reported ant species from Ascension. It is a tramp species spread throughout the tropics and subtropics by human commerce. DLUSSKY (1994) considered it native to Asia. It is certainly exotic to Ascension and St Helena.

13. *Pheidole megacephala* (FABRICIUS, 1793)

Ascension: no site data (1958; EAG Duffey; BMNH). Command Hill, lava surface (1990; A). Two Boat Village, Two Boats Club (2002; C&S). Mt. Red Hill (2003; M). Devil's Ashpit (2003; M). Grazing Valley (2003; M). Devil's Cauldron (2003; M). Jamestown, Castle Gardens (2004; E).

St. Helena: no site data (< 1875; JC Melliss; BMNH). no site data (< 1877; TV Wollaston; BMNH). Varneys (1959; CR Wallace; BMNH). Lot (1994 - 1995; A). Potato Bay (1995; A). Heart Shape Waterfall (1994 - 1995; A). Prince Andrew School (1994 - 1995; A). Foxes Folly (1995; A). Turks Cap Ridge (1995, 2006; A). High Knoll (1995; A). Coles Rock Scree (1995; A). Prosperous Bay Plain (1995, 2006; A). Joan Hill (1995, 2006; A). Flagstaff (1995, 2006; A). Powell's Valley (1995; A). Ruperts Hill (1995; A). Longwood House, garden (2002; C&S). St Paul's, near Plantation House entrance (2004; E). Lower House Plain, pitfall traps and under stones and logs (2005 / 2006; M). Peak Dale (2005 / 2006; M). Peak Dale (2005; A). Diana's Peak, swept (2005 / 2006; M). High Peak, Malaise trap (2005 / 2006; M). Hooper's Ridge (2006; A). Lot, summit (2006; A). Deep Valley (2006; A). Horse Point (2006; A).

Pheidole megacephala, the infamous big-headed ant, is one of the two most commonly reported ant species from Ascension (along with *P. longicornis*) and by far the most common ant collected on St Helena. Apparently, this species has been the most common ant on St Helena for at least 130 years. MELLISS (1875) reported *Ph. megacephala* (as *Ph. pusilla*) from St Helena, writing, "Without exception it is the most abundant insect at St. Helena, where it exists in swarms on both high and low land. Most houses are plagued with it, more especially in wet weather, when it is driven indoors. It attacks everything and even finds its way into beds, hats, brushes, and clothing. Out of doors it exists in colonies under stones on barren land, where it is difficult to discover what it feeds upon."

Pheidole megacephala, an African native, is an important pest ant spread throughout the tropics and subtrop-

ics by human commerce. Although it could be native to Ascension and St Helena, this seems unlikely.

14. *Pheidole teneriffana* FOREL, 1893

+ **Ascension:** Georgetown, in grocery store (2002; C&S).
+ **St Helena:** Jamestown, downtown park (2002; C&S).

This species was described from the Canary Islands, but ESPADALER & BERNAL (2003) considered this species as exotic there. It is also known from Sicily, Egypt, the Arabian Peninsula, Israel, Turkey, Malta, Greece, the Iberian Peninsula, California, and Cuba. WILSON (2003) proposed that this species may be native to the Mediterranean. It may be a very recent arrival on both Ascension and St Helena.

15. *Plagiolepis alluaudi* EMERY, 1894

Ascension: no site data (1958; EAG Duffey; BMNH). Two Boat Village, Two Boats Club (2002; C&S). Mt. Red Hill (2003; M). Devil's Cauldron (2003; M); Devil's Ashpit (2003; M). Grazing Valley (2003; M).

St Helena: Varneys (1958; A Loveridge; BMNH). no site data (1959; CR Wallace; BMNH). Lot (1994-95; A). Gregory's Battery (1995; A). Ruperts Hill (1995; A). Longwood, Longwood House gardens (2002; C&S). Peak Dale (2005 / 2006; M). Horse Point Plain, under stones (2005 / 2006; M). Prosperous Bay Plain (2006; A). Blue Point (2006; A). Deep Valley (2006; A). Turks Cap ridge (2006; A). Man and Horse (2006; A).

DUFFEY (1964) tentatively recorded *Plagiolepis* "*alluaudi*" on Ascension. This small orange ant is a tramp species that has been spread around the world, particularly in the Pacific, through human commerce (WILSON & TAYLOR 1967). In the Atlantic, it also occurs on Bermuda. It is probably exotic to Ascension and St Helena.

16. *Solenopsis globularia* (F. SMITH, 1858)

Ascension: no site data (1958; EAG Duffey; BMNH). Command Hill, lava surface (1990; A). Comfortless Crevices, cave threshold zone (1990; A). South Gannet Lava Flow (1990; A). Wideawake colonies (1990; A). Boatswainbird Island: (1990; A). South Gannet (2003; G & M). Turtle Shell/Pan-Am, Grubbing, beach (2003; M). Command Hill (2003; M).

St Helena: Birddown (1994 - 1995; A). Egg Island (1995, 2006; A). Gill Point (1995; A). Gregory's Battery (1995; A). Broad Gut (1995; A). Breakneck Valley (1995; A). Prosperous Bay Plain (2006; A). Ruperts Cave (2006; A).

DUFFEY (1964) recorded this ant on Ascension as the subspecies *Solenopsis globularia steinheilli* (still valid; BOLTON 1995). *Solenopsis globularia* is a New World native that is almost certainly exotic on Ascension and St Helena.

17. *Solenopsis (Diplorhoptrum) sp. 1*

+ **Ascension:** Devil's Ashpit (2003; M). Red Lion (2003; M). Green mountain, above barracks (2003; M). Green Mountain Road, near Bells Cottage, on wall and in leaf litter (2005; C).

St Helena: Napoleon's Tomb Quarry subterranean trap (1994 - 1995; A). Heart Shape Waterfall traps (1995; A). Prince Andrew School, subterranean traps (1994 - 1995; A). Wash House Gut subterranean trap (1995; A). Rock

Rose subterranean trap (1995; A). Longwood House gardens (2002; C&S).

This thief ant is probably the same species reported earlier (TAYLOR & WILSON 1961, TAYLOR 1976). This uniformly olive-brown species is clearly different from the yellow *Solenopsis* species known from Madeira, Azores, and the Canary Islands (WETTERER & al. 2005, 2006, in press, ESPADALER in press). Two specimens were measured, the smallest and largest workers available: HL = 0.38 - 0.40 mm; HW = 0.30 - 0.32; SL = 0.26 - 0.27; cephalic index (CI = (HW * 100) / HL) = 79 - 80; scape index (SI = (SL * 100) / HL) = 67 - 68.

Thief ants are often overlooked due to their small size and primarily subterranean habits. The taxonomy of thief ants is in disarray. This species is probably exotic to Ascension and St Helena.

18. *Strumigenys emmae* (EMERY, 1890)

+ **Ascension:** Grazing Valley (2003; M).

A single *Strumigenys emmae* queen was collected in a pitfall trap. This species is probably often overlooked due to its small size and primarily subterranean habits. This Dacetine species is a common Old World tramp, is found in tropical regions worldwide and is probably exotic to Ascension.

19. *Tapinoma melanocephalum* (FABRICIUS, 1793)

St Helena: Prosperous Bay Plain (1995, 2006; A).

TAYLOR (1976) previously reported this species from St Helena. *Tapinoma melanocephalum*, the ghost ant, is an Old World species that has become a common pest in disturbed areas of the tropics worldwide and is probably exotic to St Helena.

20. *Tetramorium caldarium* (ROGER, 1857)

St Helena: Varneys (1958; A Loveridge; BMNH). Longwood, Longwood House gardens (2002; C&S).

BOLTON (1980) identified Loveridge's *Tetramorium* samples from St Helena as *Tetramorium caldarium*. This species is a common Old World tramp that is probably exotic to St Helena.

Unconfirmed records (no specimens examined)

FOREL (1879) reported *Camponotus castaneus* (LATREILLE, 1802), a North American species, collected by M. Schaufuss on St Helena. It is possible that this ant is conspecific with *C. fabricator*.

DAHL (1892) recorded *Cataglyphis* sp. and *Tapinoma* sp. from Ascension. There are many species of *Cataglyphis* in the Old World, though only one is known from Atlantic islands, *C. albicans* (ROGER 1859) on Fuerteventura, Canary Islands (BARQUÍN 1981). Three species of *Tapinoma* are known from Atlantic islands: *Tapinoma madeirense* FOREL, 1895 from Madeira, *Tapinoma erraticum* (LATREILLE, 1798) from the Canary Islands, and *T. melanocephalum* from the Canary Islands, Cape Verde, and St Helena.

Discussion

Fourteen of the 20 ant species we documented on the south Mid-Atlantic islands are well-known tramp species, distributed worldwide through human commerce (Tab. 1). Two of these, the big-headed ant (*Ph. megacephala*) and the

Argentine ant (*L. humile*) are invasive species well known for their great impacts on native invertebrates.

Pheidole megacephala appears to be the most common ant on both Ascension and St Helena. ASHMOLE & ASHMOLE (2000) wrote that "it seems likely that the arrival of ants – and in particular *Pheidole megacephala* – on both islands may have led to the extinction of many invertebrates that lived on them in their pristine state." On the Atlantic islands of Cape Verde, *Ph. megacephala* is the dominant ant over large areas, and where it occurs at high densities often no native ant species persist (JKW, unpubl.). In the present study, we report the first record from St Helena of the notorious *L. humile*. It appears that *L. humile* is a recent arrival on St Helena and its populations may still be expanding.

Although *Ph. megacephala* is primarily tropical and *L. humile* is primarily subtropical, some areas have been invaded by both species, notably the tropical Pacific archipelago of Hawaii and the subtropical Atlantic archipelagos of Bermuda and Madeira (see WETTERER & WETTERER 2004, WETTERER & al. 2006, in press). These two invaders appear to have had great long-term impacts on the local biota over extensive areas in Hawaii and Bermuda, but not in Madeira. *Pheidole megacephala* invaded Hawaii in the 19th century, and by 1880 it was dominant through much of the lowlands. *Linepithema humile* was first collected in Hawaii in 1940. Currently, *Pheidole megacephala* is the dominant ant below 1000 m elevation in Hawaii, whereas *L. humile* is largely absent from the Hawaiian lowlands, but dominates areas above 1000 m elevation. *Pheidole megacephala* was first recorded in Bermuda in 1889, and was by far the most dominant ant species there in the early 20th century. When *L. humile* arrived in Bermuda in the 1940s, this new invader quickly overran much of Bermuda, driving back *Ph. megacephala*. *Pheidole megacephala*, however, persisted, and ever since, these two species have been contesting ever-shifting battlefronts between mutually exclusive territories that together occupy most of the land area of Bermuda (WETTERER & WETTERER 2004). On Madeira, *Ph. megacephala* and *L. humile* underwent population explosions in the 1850s and 1890s, respectively. Both species, however, are now uncommon on Madeira (WETTERER & al. 2006, in press). Whether *L. humile* becomes a serious pest on St Helena and displaces *Ph. megacephala* on this island deserves further attention.

Six ant species we documented on the south Mid-Atlantic islands are not known as tramps (Tab. 1). Still, it is possible these and all other ants found on Ascension, St Helena, and Tristan da Cunha are exotic to these islands, including *Camponotus fabricator*, a species known only from St Helena. All ants that occurred on these islands before human arrival may now be extinct. Alternatively, it is possible that some of the ant species we found on Ascension and St Helena predate human arrival. One candidate for native status is *Cardiocondyla mauritanica*, a widespread tramp originally from Africa, found in many uninhabited parts of Ascension. Another candidate is *Monomorium subopacum* on Ascension. *Monomorium subopacum* is an African native that appears to be native also to the Atlantic islands of Madeira, the Canary Islands, and Cape Verde. In Madeira (including Porto Santo) and Cape Verde, it is the most common ant in relatively undisturbed dry habitats (WETTERER & al. 2006, in press; JKW, un-

publ.). In Hawaii, which probably lacks any native ants, WETTERER (1998) found ants were common at most disturbed sites, but absent at 52 of 55 (95 %) relatively undisturbed sites in Hawaii Volcanoes National Park, despite the apparent lack of native competitors.

Because our limited amount of new collecting resulted in several new island records, we believe that more thorough sampling efforts with appropriate techniques should reveal additional undocumented ant species on Ascension and St Helena (see ESPADALER & LÓPEZ-SORIA 1991).

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Zusammenfassung

Die isolierten Inseln Ascension (8° S), St. Helena (16° S) und Tristan da Cunha (37° S) sind Teil des Mittelatlantischen Rückens. Sie sind von Afrika, dem nächstgelegenen Kontinent, 1700 bis 2800 km entfernt. Wir haben veröffentlichte und bisher unveröffentlichte sowie neue Daten zu den Ameisen dieser Inseln zusammengetragen und stellen Überlegungen zum jeweiligen wahrscheinlichen geographischen Ursprung der Arten an.

Wir haben Individuen zu 20 verschiedenen Ameisenarten bestimmt: zehn von Ascension, 16 von St. Helena und eine von Tristan da Cunha. Es waren darunter drei Neunachweise für Ascension (*Pheidole teneriffana* FOREL, 1893, *Solenopsis* sp. 1, *Strumigenys emmae* (EMERY, 1890) und fünf Neunachweise für St. Helena (*Hypoconerops* sp. 1, *Linepithema humile* (MAYR, 1868), *Monomorium latinode* MAYR, 1872, *Monomorium* cf. *sechellense*, *Pheidole teneriffana*). Erstmals wurde die einzige von Tristan da Cunha bekannte Ameisenart bestimmt (*Hypoconerops eduardi* (FOREL, 1894)). Die Bestätigung von bereits bekannten Nachweisen fußte bei allen Arten auf Individuen, die 1995 oder später gesammelt worden waren, außer bei *Camponotus fabricator* (F. SMITH, 1858) und *Hypoconerops punctatissima* (ROGER, 1859) auf St. Helena. Nicht bestätigten konnten wir zwei weitere veröffentlichte Nachweise von Ascension (*Cataglyphis* sp., *Tapinoma* sp.) und einen von St. Helena (*Camponotus castaneus* (LATREILLE, 1802)).

Die meisten, wenn nicht überhaupt alle 20 Ameisenarten, die wir auf den Südatlantischen Inseln dokumentieren konnten, inklusive *C. fabricator*, ein vermeintlicher Endemit von St. Helena, sind wahrscheinlich in Folge menschlicher Aktivitäten auf die Inseln gekommen. Es ist allerdings nicht auszuschließen, dass einige Ameisenarten bereits vor der Ankunft der Menschen die Inseln besiedelt haben. Ein Kandidat für den Status einer nativen Art ist *Cardiocondyla mauritanica* FOREL, 1890, eine weitverbreitete, invasive Art, die wahrscheinlich aus Afrika stammt und auf Ascension in vielen, nicht vom Menschen besiedelten Regionen anzutreffen ist.

References

ASHMOLE, N.P. & ASHMOLE, M.J. 1997: The land fauna of Ascension island: new data from caves and lava flows, and a reconstruction of the prehistoric ecosystem. – *Journal of Biogeography* 24: 549-589.

- ASHMOLE, P. & ASHMOLE, M. 2000: St Helena and Ascension Island: A Natural History. – Anthony Nelson, Shropshire. 528 pp.
- BARQUÍN, J. 1981: Las hormigas de Canarias. Taxonomía, ecología y distribución de los Formicidae. – Colección Monograficas (Secretariado de Publicaciones de la Universidad de La Laguna) 3: 1-584.
- BOLTON, B. 1980: The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* MAYR in the Ethiopian zoogeographical region. – *Bulletin of the British Museum (Natural History) Entomology* 40: 193-384.
- BOLTON, B. 1982: Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). – *Bulletin of the British Museum (Natural History) Entomology* 45: 307-370.
- BOLTON, B. 1987: A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* MAYR (Hymenoptera: Formicidae). – *Bulletin of the British Museum (Natural History) Entomology* 54: 263-452.
- BOLTON, B. 1995: A new general catalogue of the ants of the world. – Harvard University Press, Cambridge, MA, 504 pp.
- BOLTON, B. 2000: The ant tribe Dacetini. – *Memoirs of the American Entomological Institute* 65: 1-1028.
- BREYTENBACH, G.J. 1986: Dispersal: the case of the missing ant and the introduced mouse. – *South African Journal of Botany* 52: 463-466.
- CREIGHTON, W.S. 1950: The ants of North America. – *Bulletin of the Museum of Comparative Zoology* 104: 13-585.
- DAHL, F. 1892: Die Landfauna von Ascension (Anhang zu Kapitel VII.) In: HENSEN, V. (Ed.): *Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 ausgeführten Plankton-Expedition der Humboldt-Stiftung*, Volume 1. – Verlag Lipsius & Tischer, Kiel & Leipzig, pp. 204-209.
- DALLA TORRE, K.W. von. 1893: *Catalogus hymenopterorum hucusque descriptorum systematicus et synonymicus*. Volume 7. Formicidae (Heterogyna). – W. Engelmann, Leipzig, 289 pp.
- DEYRUP, M., CARLIN, N., TRAGER, J. & UMPHREY, G. 1988: A review of the ants of the Florida Keys. – *Florida Entomologist* 71: 163-176.
- DEYRUP, M., DAVIS, L. & BUCKNER, S. 1998: Composition of the ant fauna of three Bahamian Islands. In: *Proceedings of the 7th Symposium on the Natural History of the Bahamas*. – Bahamian Field Station, San Salvador, Bahamas, pp. 23-31.
- DEYRUP, M., DAVIS, L. & COVER, S. 2000: Exotic ants in Florida. – *Transactions of the American Entomological Society* 126: 293-326.
- DLUSSKY, G.M. 1994: Zoogeography of southwestern Oceania (in Russian). In: PUZATCHENKO, Y.G., GOLOVATCH, S.I., DLUSSKY, G.M., DIAKONOV, K.N., ZAKHAROV, A.A. & KORGANOVA, G.A. (Eds.): *Animal population of the islands of Southwestern Oceania (ecogeographic studies)*. – Nauka Publishers, Moscow, pp. 48-93.
- DONISTHORPE, H. 1927: *British ants. Their life-history and classification*, 2nd edn. – George Routledge and Sons, London, 436 pp.
- DUFFEY, E. 1964: The terrestrial ecology of Ascension Island. – *Journal of Applied Ecology* 1: 219-251.
- EMERY, C. 1896: Saggio di un catalogo sistematico dei generi *Camponotus*, *Polyrhachis* e affini. – *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna* (5)5: 363-382.
- ESPADALER, X. in press: The ants of El Hierro (Hymenoptera, Formicidae). – *Memoirs of the American Entomological Institute* 78.
- ESPADALER, X. & BERNAL, V. 2003: Exotic ants in the Canary Islands, Spain (Hymenoptera: Formicidae). – *Vieraea* 31: 1-7.

- ESPADALER, X. & LÓPEZ-SORIA, L. 1991: Rariness of certain Mediterranean ant species: fact or artifact? – *Insectes Sociaux* 38: 365-377.
- FOREL, A. 1879: Études myrmécologiques en 1879. – *Bulletin de la Société Vaudoise des Sciences Naturelles* 16: 53-128.
- FOREL, A. 1914: Le genre *Camponotus* MAYR et les genres voisins. – *Revue Suisse de Zoologie* 22: 257-276.
- HOLDGATE, M.W. 1965: The biological report of the Royal Society Expedition to Tristan da Cunha. Part III. The fauna of the Tristan da Cunha Islands. – *Philosophical Transactions of the Royal Society of London B* 152: 550-567.
- MAYR, G. 1886: Notizen über die Formiciden-Sammlung des British Museum in London. – *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 36: 353-368.
- MELLISS, J.C. 1875: St. Helena: A physical, historical, and topographical description of the Island, including its geology, fauna, flora, and meteorology. – Reeve, London, 426 pp.
- OLAFSSON, E. & RICHTER, S.H. 1985: Húsamaurinn (*Hypoponera punctatissima*). – *Náttúrufræðingurinn* 55: 139-146.
- SEIFERT, B. 2003a: The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae) – a taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi*, and *C. minutior* species groups. – *Annalen des Naturhistorischen Museums in Wien* 104B: 203-338.
- SEIFERT, B. 2003b: *Hypoponera punctatissima* (ROGER) and *H. schauinslandi* (EMERY) – two morphologically and biologically distinct species (Hymenoptera: Formicidae). – *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 75: 61-81.
- SMITH, F. 1858: Catalogue of the hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. – *British Museum, London*, 216 pp.
- TAYLOR, R.W. 1976: La faune terrestre de l'île de Sainte-Hélène. 7. Superfam. Formicoidea. – *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques* 215: 192-199.
- TAYLOR, R.W. & WILSON, E.O. 1961: Ants from three remote oceanic islands. – *Psyche* 68: 137-144.
- TRAGER, J.C. 1984: A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the Continental United States. – *Sociobiology* 9: 49-162.
- VOISIN, J.F. 1980: Notes on insects of Tristan da Cunha and Gough Island. – *Entomologists' Monthly Magazine* 116: 253-255.
- WETTERER, J.K. 1998: Nonindigenous ants associated with geothermal and human disturbance in Hawai'i Volcanoes National Park. – *Pacific Science* 52: 40-50.
- WETTERER, J.K. 2006: Ants (Hymenoptera: Formicidae) of Niue, Polynesia. – *Pacific Science* 60: 413-416.
- WETTERER, J.K., ESPADALER, X., WETTERER, A.L., AGUIN-POMBO, D. & FRANQUINHO-AGUIAR, A.M. 2006: Long-term impact of exotic ants on the native ants of Madeira. – *Ecological Entomology* 31: 358-368.
- WETTERER, J.K., ESPADALER, X., WETTERER, A.L., AGUIN-POMBO, D. & FRANQUINHO-AGUIAR, A.M. in press: Ants (Hymenoptera: Formicidae) of the Madeiran Archipelago. – *Sociobiology*.
- WETTERER, J.K., ESPADALER, X., WETTERER, A.L. & CABRAL, S.G.M. 2004: Native and exotic ants of the Azores (Hymenoptera: Formicidae). – *Sociobiology* 44: 1-20.
- WETTERER, J.K. & WETTERER, A.L. 2004: Ants (Hymenoptera: Formicidae) of Bermuda. – *Florida Entomologist* 87: 212-221.
- WETTERER, J.K. & WETTERER, A.L. 2006: A disjunct Argentine ant metacolon in Macaronesia and southwestern Europe. – *Biological Invasions* 8: 1123-1129.
- WILSON, E.O. 2003: *Pheidole* in the New World. A dominant, hyperdiverse genus. – *Harvard University Press, Cambridge, MA*, 794 pp.
- WILSON, E.O. & TAYLOR, R.W. 1967: Ants of Polynesia. – *Pacific Insects Monographs* 14: 1-109.
- YAMAUCHI, K., KIMURA, Y., CORBARA, B., KINOMURA, K. & TSUJI, K. 1996: Dimorphic ergatoid males and their reproductive behavior in the ponerine ant *Hypoconerina bondroiti*. – *Insectes Sociaux* 43: 119-130.