

Ants of Tonga¹

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Abstract: This paper presents combined published, unpublished, and new ant records from 17 islands of Tonga representing all four island groups: Tongatapu (Tongatapu, 'Eua, 'Onevai, Pangaimotu), Ha'apai (Lifuka, Kao, Tofua, 'Uonukahahake, Nomuka, Nomuka-iki, Mango, Telekitonga), Vava'u (Vava'u, Nua-papu, Kapa), and the Niuas (Niuatoputapu, Niuafu'ou). These records increase the list of ants known from Tonga to 53 species. Ten species, including six undescribed species, are local endemics found only in Tonga or only in Tonga and Samoa: *Adelomyrmex* sp., *Camponotus conicus*, *Camponotus nigrifrons*, *Hypoponera* sp., *Monomorium* sp., *Ochetellus* sp., *Pheidole* sp., *Pristomyrmex* sp., *Strumigenys zakharovi*, and *Vollenhovia samoensis*. Another 21 species are broadly distributed Pacific natives: *Anochetus graeffei*, *Camponotus chloroticus*, *Hypoponera confinis*, *Monomorium liliuokalanii*, *Monomorium talpa*, *Odontomachus simillimus*, *Oligomyrmex atomus*, *Pheidole oceanica*, *Pheidole sexspinosus*, *Pheidole umbonata*, *Ponera incerta*, *Ponera tenuis*, *Pyramica dubia*, *Rogeria stigmatica*, *Solenopsis papuana*, *Strumigenys godeffroyi*, *Tapinoma minutum*, *Technomyrmex albipes*, *Tetramorium insolens*, *Tetramorium pacificum*, and *Tetramorium tonganum*. Finally, 22 species are not native to the Pacific region, but were brought to the region by human commerce: *Anoplolepis gracilipes*, *Cardiocondyla emeryi*, *Cardiocondyla nuda*, *Hypoponera opaciceps*, *Hypoponera punctatissima*, *Monomorium floricola*, *Monomorium pharaonis*, *Monomorium secbellense*, *Paratrechina bourbonica*, *Paratrechina longicornis*, *Paratrechina vaga*, *Pheidole fervens*, *Pheidole megacephala*, *Plagiolepis alluaudi*, *Pyramica membranifera*, *Solenopsis geminata*, *Strumigenys emmae*, *Strumigenys rogeri*, *Tapinoma melanocephalum*, *Tetramorium bicarinatum*, *Tetramorium lanuginosum*, and *Tetramorium simillimum*. The number of ant species now known from Tonga is much as would be expected based on the species-area relationship for the neighboring island groups of Fiji, Wallis and Futuna, and Samoa. Differences in ant species richness among these island groups is primarily due to a greater number of local endemics in the island groups with greater land area.

THE KINGDOM OF TONGA consists of about 170 islands with a total land area of ~700 km² spread across 350,000 km² of western Polynesia between 15–23° S and 173–177° W. Tonga is divided into four major island groups (from south to north): Tongatapu, Ha'apai, Vava'u, and the Niuas. Only about

40 of the Tongan islands are inhabited year-round.

Due to the difficulty and expense of travel to distant and unpopulated islands, most Tongan ant records come from the three largest and most accessible islands: Tongatapu, 'Eua, and Vava'u. On these islands, human activity has heavily impacted most flatter areas (Drake et al. 1996, Steadman and Freifeld 1998, Franklin et al. 1999). Tongatapu, by far the largest island of Tonga (259 km²), makes up 37% of the total land area of the kingdom. Tongatapu is very flat, tilting only slightly up to 30-m cliffs along the southern shore (maximum elevation, 82 m). About two-thirds of Tonga's 100,000 people live on Tongatapu. 'Eua, also part of the Tongatapu group, is the third largest island (87 km²) and

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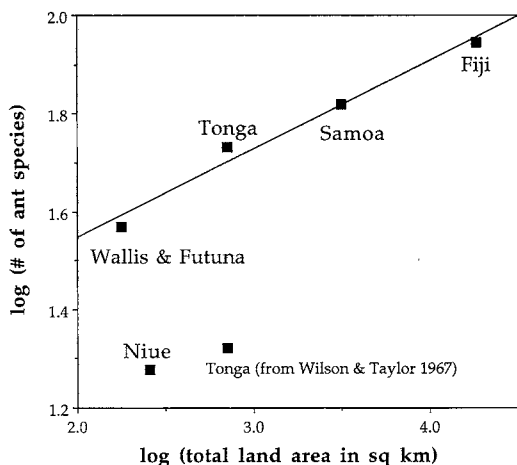


FIGURE 1. Number of known ant species from Tonga in relation to total land area, compared with values for Tonga from Wilson and Taylor (1967), and for surrounding island groups.

the southernmost inhabited island of Tonga. 'Eua rises gradually from west to east in a series of terraces up to a 250- to 300-m eastern ridge (maximum elevation, 328 m) and then drops steeply down to the east coast (Drake et al. 1996). All people on 'Eua live on the west side of the island, and the steep eastern slope has much intact forest (Drake et al. 1996). Vava'u, the second largest Tongan island (104 km²), is hilly. The highest points of the island of Vava'u are Mount Mo'ungalafa (204 m) and Mount Talau (130 m). On Vava'u there are many areas of forest at various stages of regeneration from agricultural use (Steadman and Freifeld 1998, Franklin et al. 1999).

The ant fauna of Tonga is a mix of native Pacific species and exotic "tramp" species. Wilson and Taylor's (1967) review of the ants of Polynesia reported 21 ant species from Tonga. This is a low value compared with records from the immediately surrounding island groups (Figure 1): 88 ant species from Fiji to the west (Wilson and Hunt 1967), 37 from Wallis and Futuna to the northwest (Wilson and Hunt 1967, Gutierrez 1981 in Jourdan 1997), 67 from Samoa to the north (Wilson and Hunt 1967, Wilson and Taylor 1967; unpubl. data), and ~50 from south-

eastern Polynesia (Niue, the Cook Islands, and French Polynesia combined) to the east (Taylor 1967, Wilson and Taylor 1967, Morrison 1996a,b, 1997). In this study, I increase the list of ants known from Tonga to 53 species.

MATERIALS AND METHODS

In addition to published records of ants from Tonga, I searched for ant specimens from Tonga in the collections of several museums: the U.S. National Museum of Natural History (USNM) in Washington, D.C.; the American Museum of Natural History (AMNH) in New York; the Museum of Comparative Zoology (MCZ) in Cambridge, Massachusetts; and the New Zealand Arthropod Collection (NZAC) in Auckland.

Also, from 16 to 31 August 1995, I collected ants on the three largest islands (Tongatapu, 'Eua, and Vava'u), plus Lifuka and Kapa. Lifuka, the administrative center of the Ha'apai island group, is small, flat (11 km²; maximum elevation, 14 m), and highly disturbed throughout. Kapa is a small island (6.4 km²; maximum elevation, 96 m) in the Vava'u group.

I collected by visual search, turning over rocks and logs, stripping the bark off logs, and breaking logs apart, piece by piece. Many areas throughout Tongatapu and western 'Eua had the exotic big-headed ant, *Pheidole megacephala* (Fabr.), under almost every rock and log and virtually no other ants. In contrast, *P. megacephala* was much less common on Vava'u and Kapa, and rare on Lifuka. The primary objective of my collection was to document as fully as possible the diversity of ants in Tonga. I therefore usually skipped over most areas with extremely high *P. megacephala* density. Instead, I concentrated my collecting efforts in relatively undisturbed forests that had few or no *P. megacephala* present. I am currently preparing a more detailed, ecologically based account of these collections, documenting the impact of *P. megacephala* and other exotic ants in Tonga (unpubl. data).

I divided the Tongan ant species into three categories based on their distributions and

presumed origins, following Wilson and Hunt (1967): (1) local endemics, found only in Tonga or only in Tonga and Samoa, (2) broadly distributed Pacific natives, found continuously from the Indo-Australian area into Polynesia, and (3) exotic "tramp" species, distributed in the Pacific by recent human commerce.

RESULTS

I found published and unpublished records of ant species from numerous collections (Table 1) conducted on 17 Tongan islands representing all four island groups: Tongatapu (Tongatapu, 'Eua, 'Onevai, Pangaimotu), Ha'apai (Lifuka, Kao, Tofua, 'Uonukahake, Nomuka, Nomuka-iki, Mango, Telekitonga), Vava'u (Vava'u, Nuapapu, Kapa), and the Niuas (Niuatoputapu, Niuafou'ou).

Published Ant Records

I found reliable published records of a total of 49 ant species from Tonga (Tables 1–3; Mayr 1870, 1876, Wheeler 1935, Wilson and Taylor 1967, Carver et al. 1993, Dlussky 1994a,b, Swaney 1994, Zakharov 1994, Stechmann et al. 1996).

Mayr (1870, 1876) listed 17 ant species from the "Tonga Islands" based on specimens at the Godeffroy Museum in Hamburg, Germany. Mayr (1870, 1876) gave no collector information for any specimen, and listed Tongatapu Island as the collection site for two species. I have assumed, perhaps erroneously, that all of Mayr's records came from Tongatapu (Tables 1–3). Wheeler (1935), in his review of the ants of Oceania, listed 16 species from Tonga, identical to Mayr's (1876) list except for the unexplained omission of *Tapinoma melanocephalum* (Fabr.).

Wilson and Taylor (1967) reported records of 21 ant species from Tonga, including Mayr's (1876) records, plus new records from three collectors: W. Cottrell-Darmer, G. P. Wilder, and N. L. H. Krauss (Tables 2 and 3). Wilson and Taylor (1967) deleted one species from Mayr's list: *Camponotus rufifrons* (Mayr). Although *C. rufifrons* is considered a valid Melanesian species (Bolton 1995), Wilson and Taylor (1967) concluded that the record of *C. rufifrons* from Tonga was a misidentification of *C. conicus* (Mayr).

Dlussky (1994a) listed ants collected during two visits to Tonga of the Soviet research ship *Kallisto* (Tables 2 and 3). In 1976–1977, Y. I. Chernov collected ants on Niuafou'ou in

TABLE 1
Collection Dates and Locales for Ants from Tonga

Collector (Source)	Collection Date	Island(s)
a. Unlisted (Mayr 1870, 1876)	<1870	T?
b. Cottrell-Dormer (Wilson and Taylor 1967)	<1914–<1935	T
c. Wilder (Wilson and Taylor 1967)	1923–1925	T, V, "Ha'apai"
d. Unknown (USNM)	1930	Niuafou'ou
e. Krauss (Wilson and Taylor 1967)	1956	T, E, V
f. Rogers & Rogers (NZAC)	1971	Niuatoputapu
g. Litsinger (NZAC)	1973–1974	T, E, V
h. Krauss (AMNH)	1974–1979	T, E
i. Watt (NZAC)	1975–1977	T, E, Niuafou'ou
j. Maddison (NZAC)	1975–1977	T, E
k. Chernov (Dlussky 1994a)	1976–1977	Niuafou'ou
m. Dlussky et al. (Dlussky 1994a)	1980	T, E, V, + many others
p. Stechmann et al. (1996)	1986	T
r. Carver et al. (1993)	1990–1992	T, E
s. Curio (pers. comm.)	1992	Niuafou'ou
t. Wetterer (this study)	1995	T, E, V, Lifuka, Kapa

Sources: USNM, U.S. National Museum of Natural History; AMNH, American Museum of Natural History; NZAC, New Zealand Arthropod Collection. Islands: T, Tongatapu; E, 'Eua; V, Vava'u.

TABLE 2
Native Pacific Ants from Different Island Groups of Tonga

Species	Tongatapu				Niuas	Pacific Range	Origin
	Tongatapu	'Eua	Ha'apai	Vava'u			
Local endemics							
<i>Adelomyrmex</i> sp.		<u>mt</u>	<u>m</u>			-----	o
<i>Camponotus conicus</i>	<u>ae</u>	<u>em</u>				-----	ET
<i>Camponotus nigrifrons</i>	<u>ae</u>	<u>gjm</u>	<u>m</u>			-----	ET
<i>Hypoponera</i> sp.		t				-----	o
<i>Monomorium</i> sp.			t	t		-----	o
<i>Ochetellus</i> sp.	<u>mt</u>	<u>mt</u>	<u>m</u>			-----	o
<i>Pheidole</i> sp.		<u>mt</u>				-----	ET
<i>Pristomyrmex</i> sp.					f	-- S- --	o
<i>Strumigenys zakharovi</i>		<u>m</u>				-----	ET
<i>Vollenhovia samoensis</i>		<u>mt</u>				-- S- --	ES
Wide-ranging Pacific natives							
<i>Anocheilus graeffei</i>	<u>mt</u>	<u>m</u>	<u>mt</u>	<u>m</u>		MWS- CF	PO
<i>Camponotus chloroticus</i>	<u>aecht</u>	<u>em</u>	<u>cmt</u>	<u>cemt</u>	<u>fk</u> s	MWSN- --	PO
<i>Hypoponera confinis</i>		e				M- S- CF	PO
<i>Monomorium liltuokalanii</i>	t	<u>hm</u>			f	M- S- CF	OR
<i>Monomorium talpa</i>	t	<u>m</u>	<u>m</u>	<u>mt</u>		MWS- - F	NG
<i>Odontomachus similimus</i>	<u>abemt</u>	<u>mt</u>	<u>mt</u>	<u>emt</u>	<u>fk</u> s	MWS- - F	PO
<i>Oligomyrmex atomus</i>		<u>m</u>	<u>m</u>		f	MWS- --	NG
<i>Pheidole oceanica</i>	<u>aimt</u>	<u>imt</u>	<u>m</u>	<u>gmt</u>	<u>ks</u>	MWSNCF	NG
<i>Pheidole sexspinos</i>	<u>m</u>	<u>m</u>	<u>m</u>	<u>mt</u>		MWSN- F	NG
<i>Pheidole umbonata</i>	<u>ajmrt</u>	<u>gmt</u>	<u>mt</u>	<u>mt</u>	<u>fk</u>	MWSNCF	NG
<i>Ponera incerta</i>	t	<u>mt</u>	<u>m</u>	t	f	M- S- --	PO
<i>Ponera tenuis</i>		<u>m</u>	<u>m</u>			M- S- --	NG
<i>Pyramica dubia</i>		<u>m</u>				M- S- --	OR
<i>Rogeria stigmatica</i>	<u>m</u>	<u>mt</u>	<u>mt</u>	<u>m</u>	f	MWS- CF	RE
<i>Solenopsis papuana</i>	<u>gm</u>	<u>mt</u>	<u>m</u>	<u>m</u>		MWS- CF	NG
<i>Strumigenys godeffroyi</i>	<u>m</u>	<u>mt</u>	t	<u>mt</u>	f	MWS- CF	PO
<i>Tapinoma minutum</i>			<u>m</u>	t		MWSN- F	PO
<i>Technomyrmex albipes</i>	<u>achjmr</u> t	<u>ehmt</u>	<u>mt</u>	<u>emt</u>		MWSNCF	PO
<i>Tetramorium insolens</i>		gt				M- SN- --	o
<i>Tetramorium pacificum</i>	<u>achmt</u>	<u>eghmt</u>	<u>mt</u>	<u>emt</u>	s	MWSNCF	PO
<i>Tetramorium tonganum</i>	<u>amt</u>	<u>mt</u>	<u>mt</u>	<u>mt</u>	<u>k</u>	MWSNCF	RE

Note: Records: a-t, authors/collectors listed in Table 1; underline, published record. Pacific Range: M, Melanesia and/or Micronesia; W, Wallis and Futuna; S, Samoa; N, Niue; C, Cook Islands; F, French Polynesia. Origin follows classification by Dlussky (1994a): ET, Tonga endemic; ES, Samoa endemic; RE, regional endemic; PO, pantropical of Asian origin; OR, Asian origin; NG, New Guinean origin; o, not included in Dlussky (1994a).

the Niuas. In 1980, G. M. Dlussky, A. A. Zakharov, and S. I. Golovatch collected ants on the islands of Tongatapu, 'Eua, and Vava'u, as well as an assortment of other Tongan islands in the Tongatapu group (Onevai, Pangaimotu), Ha'apai group (Nomuka, Nomukaiki, Mango, Telekitonga, 'Uonukahahake, Kao, Tofua), and Vava'u group (Nuapapu). Together, 46 ant species were collected by the two Soviet surveys, which brought the total number of ant species known from Tonga to

49. Two species that Dlussky (1994a) listed as *Pheidole euana* Dlussky and *Vollenhovia kallisto* Dlussky were, in fact, never described (G. Dlussky, pers. comm.), so these names are invalid. Dlussky (pers. comm.) could not definitively distinguish the *Vollenhovia* specimens from *Vollenhovia samoensis* Mayr. I therefore list these two species as *Pheidole* sp. and *Vollenhovia samoensis*. Dlussky (1994a) also reported two ant species from Tonga, *Adelomyrmex hirsutus* Mann and *Ochetellus sororis*

TABLE 3
Pantropical Exotic Ants from Different Island Groups of Tonga

Species	Tongatapu					Pacific Range	Origin
	Tongatapu	'Eua	Ha'apai	Vava'u	Niuas		
<i>Anoplolepis gracilipes</i>	amrt	t	mt	emt	ks	MWSNCF	PA
<i>Cardiocondyla emeryi</i>	hmt	hmt	mt	t	k	MWSNCF	PA
<i>Cardiocondyla muda</i>	aemt	m	m	mt	fk	MWSNCF	PA
<i>Hypoponera opaciceps</i>	gt	imt	m	t		M- S- CF	PN
<i>Hypoconera punctatissima</i>	mt	et	mt	t		MWS- - F	PA
<i>Monomorium floricola</i>	ahjmrt	hmt	mt	mt	fs	MWSNCF	PO
<i>Monomorium pbaraonis</i>	abm					M- S- - F	PO
<i>Monomorium sechellense</i>		t		m		M- S- C-	OR*
<i>Paratrechina bourbonica</i>	ekt	t		t		MWS- CF	PO
<i>Paratrechina longicornis</i>	cehrt	mt	mt	mt	fs	MWSNCF	PO
<i>Paratrechina vaga</i>	aehmrt	eghmt	mt	emt	k	MWSNCF	PO
<i>Pheidole fervens</i>	b	et		e		M- - CF	OR
<i>Pheidole megacephala</i>	hjmrpt	t	t	mt	d	MWSNCF	PA
<i>Plagiolepis alluaudi</i>	mt	m	mt	mt		M- -NCF	PA
<i>Pyramica membranifera</i>		m			f	MWS- - F	PA
<i>Solenopsis geminata</i>	beghmrt	eghmt	mt	emt	s	M- - CF	PN
<i>Strumigenys emmae</i>			mt			M- S- - F	PA
<i>Strumigenys rogeri</i>	gmt	mt	mt	mt		MWS- - F	PA
<i>Tapinoma melanocephalum</i>	abhmr	hmt	mt	emt	ks	MWSNCF	PO
<i>Tetramorium bicarinatum</i>	aemrt	m	m	et	k	MWS- CF	PA
<i>Tetramorium lanuginosum</i>			m		f	MWS- CF	PO
<i>Tetramorium simillimum</i>	bmrt	mt	mt	t		MWSNCF	PA

Note: Symbols as in Table 2. PA, pantropical of African origin; PN, pantropical of Neotropical origin. *, species in Dlussky (1994a) subsequently synonymized with a more wide-ranging species.

(Mann), otherwise known only from Fiji (Mann 1921). I believe, however, that these specimens are probably undescribed Tongan endemics, which I list as *Adelomyrmex* sp. and *Ochetellus* sp. (see later in Results for explanation).

Swaney (1994), in her travel guide to Tonga, described observations of "long-legged ants," the common name for *Anoplolepis gracilipes* (Smith), on Niuafu'ou in the Niuas attacking newly hatched chicks of the endemic Niuafu'ou incubator bird (*Megapodius pritchardii* Gray). Swaney's (1994) reference brought to my attention unpublished records of ants collected by E. Curio on Niuafu'ou in 1992 (see in a later section). Stechmann et al. (1996) recorded seven ant species tending aphids on Tongatapu in 1986. Carver et al. (1993) recorded 11 species of ants tending aphids on Tongatapu in 1990–1992.

Museum Specimens

In the USNM, I found one specimen of *Pheidole megacephala* collected on Niuafu'ou in the Niuas in October 1930. The collector's name was not recorded. This is by far the earliest record of *P. megacephala* in Tonga.

In the AMNH, I found ant specimens that N. Krauss collected on Tongatapu and 'Eua in 1974, 1978, and 1979 (Tables 1–3).

In the MCZ, I found Tongan ant specimens collected by W. Cottrell-Darmer (no date) and by N. Krauss (in 1956) that were previously listed by Wilson and Taylor (1967). In addition, N. Krauss collected *Tapinoma melanocephalum* on Vava'u in February 1956, a record not included in Wilson and Taylor (1967).

In the NZAC, I found ant specimens from four collections: W. Rogers and G. Rogers collected ant species on Niuatoputapu in the

Niuas between March and September 1971; J. A. Litsinger collected on Tongatapu, 'Eua, and Vava'u in 1973 and 1974; P. Maddison collected on Tongatapu and 'Eua from 1975 to 1977; J. C. Watt collected on Tongatapu, 'Eua, and Niuafu'ou in the Niuas in 1975 and 1977 (Tables 1–3).

The previously unpublished records of *Tetramorium insolens* (Smith) and *Pristomyrmex* sp. brought the total number of ant species known from Tonga to 51. This species of *Pristomyrmex* is currently being described by M. Chang at the mcz as part of his dissertation research.

Other Unpublished Ant Records

In 1992, E. Curio collected nine ant species on Niuafu'ou in conjunction with research on the endemic megapodes (E. Curio, pers. comm.; Tables 1–3). B. Bolton at the Natural History Museum in London identified Curio's specimens (E. Curio, pers. comm.).

New Ant Collection

I collected 42 ant species in Tonga (Tables 2 and 3), including five that did not match any published descriptions. I tentatively consider the undescribed *Pheidole* as the same as Dlussky's (1994a) *Pheidole* sp., pending further study. Two other undescribed species, *Adelomyrmex* sp. and *Ochetellus* sp., are in the same genera as *Adelomyrmex hirsutus* Mann and *Ochetellus sororis* (Mann), reported by Dlussky (1994a). S. Cover distinguished my specimens from types in the mcz of these two Fijian species. Dlussky (pers. comm.), however, never compared the Soviet specimens with types. I therefore have tentatively assumed that the Soviet specimens were misidentified and are the same undescribed species as those that I found. Finally, I found two undescribed species, *Hypoponera* sp. and *Monomorium* sp., not reported by any previous collector. My new records raise the total number of ant species known in Tonga to 53.

I have donated all ant specimens I collected on Tonga to the mcz, with duplicates to be sent to appropriate collections in the Pacific and elsewhere.

Categories of Ant Species

Of the 53 ant species of Tonga, 10 species are known only from Tonga or from Tonga and Samoa, 21 species appear to be broad-ranged Pacific natives, and 22 appear to be exotic to the Pacific region (Tables 2 and 3). Wilson and Hunt (1967) considered *Monomorium minutum* Mayr an exotic tramp. Pacific specimens previously assigned to this species, however, have been reclassified as *Monomorium liliuokalanii* Forel (see Bolton 1995), which I categorized as a wide-ranging Pacific native.

DISCUSSION

Comparison of the Tonga Ant Fauna with Those of Neighboring Islands and Island Groups

The number of ant species now known from Tonga (53) is much as would be expected based on the species-area relationship of the neighboring island groups of Fiji, Wallis and Futuna, and Samoa, to the west and north. Comparing data from these four island groups on a log-log plot, the number of species (N_a) increases linearly with total land area (A) (Figure 1; least squares regression: $\log N_a = 1.177 + 0.183 \log A$, $R^2 = 0.98$). The increase in ant species with land area is primarily due to an increased number of local endemics in the island groups with greater land area (Table 4).

Niue, a solitary island directly east of Tonga, with only 19 known ant species, has fewer than half the number of species expected compared with the numbers known for Fiji, Wallis and Futuna, Tonga, and Samoa (Figure 1). It seems likely that, due to incomplete sampling, many inconspicuous ant species have been overlooked in Niue.

Endemic Ant Species in Tonga

Eight ant species are known only from Tonga and two species are known only from Tonga and Samoa. Mayr described two of these species (*Camponotus nigrifrons* Mayr in 1870; *Camponotus conicus* Mayr in 1876); Dlussky described one (*Strumigenys zakharovi* Dlussky in Dlussky 1994b). Five Tonga endemic spe-

TABLE 4
Number of Ant Species Known from the Islands and Island Groups of Tonga
and from the Surrounding Islands and Island Groups

Island/Island Group	Land Area (km ²)	Local Endemic	Pacific Native	Exotic Tramp	Total
Tongatapu	259	3	15	18	36
'Eua	87	8	20	19	47
Ha'apai group	109	4	17	17	38
Vava'u group	119	1	15	18	34
Niuas group	72	1	11	12	24
Wallis and Futuna	177	0	21	16	37
Niue	259	0	9	10	19
Tonga (total)	699	10	21	22	53
Samoa	3,132	15	27	25	67
Fiji	18,272	56	15	17	88

cies remain undescribed (*Adelomyrmex* sp., *Hypoponera* sp., *Monomorium* sp., *Ocnetellus* sp., and *Pheidole* sp.). *Vollenhovia samoensis* is known only from 'Eua and from Samoa. *Pristomyrmex* sp. is known only from Niuatoputapu and from Samoa.

Only three of the local endemic ant species have been found on Tongatapu, and just one of these has been collected since 1956. In contrast, 8 of the 10 have been found on the nearby, smaller island of 'Eua, all of which species have been collected one or more times since 1980. The paucity of endemic species on Tongatapu may relate, in part, to its very flat topography, which offers little habitat variation and has allowed almost the entire island to come under cultivation. In addition, the highly destructive big-headed ant, *Pheidole megacephala*, now occurs in high densities over most of the island (unpubl. data). In contrast, the eastern slope of 'Eua has varied habitat, is too steep for cultivation, and has not yet been invaded by *P. megacephala*.

Native Pacific Ant Species in Tonga

According to the classifications of Wilson and Hunt (1967), 21 of the ant species found in Tonga are wide-ranging Pacific natives. However, it is not possible to determine reliably which are actually native to Tonga (i.e., predating humans) and which are more recent arrivals from other parts of the Pacific.

For example, Wilson and Taylor (1967) wrote that *Pyramica dubia* (Brown) is probably a tramp that originated in New Guinea and spread around the Pacific by human commerce. In further evidence of this uncertainty, Dlussky (1994a) placed the origin of *P. dubia* in Asia.

Four ant species that are native to the western Pacific region have invaded other parts of the world. One such "Pacific-native tramp" is *Technomyrmex albipes* (Smith), the "white-footed" ant, which is now found as an exotic in many areas, including New Zealand, Hawai'i, California, Florida, South Africa, India, China, Madagascar, and Saudi Arabia (Wilson and Taylor 1967, Wetterer 1997a, 1998, McGlynn 1999). In addition, *Tetramorium tonganum* Mayr is an exotic in Hawai'i and Brazil; *Tetramorium pacificum* Mayr is in Florida, Canada, Central America, and the Caribbean; and *Odontomachus simillimus* Smith is in the Caribbean (McGlynn 1999).

Dlussky (1994a) used a different classification scheme than did Wilson and Taylor (1967) and Wilson and Hunt (1967). Dlussky (1994a) proposed the geographical origin of species, but was not explicit about which species predated human arrival in Polynesia (see Tables 2 and 3). Dlussky (1994a) classified the 21 wide-ranging Pacific natives of Tonga as two regional endemics, seven species of New Guinean origin, two of Asian origin, and nine pantropical species of Asian origin

(Table 2). One species, *Tetramorium insolens*, was not found in Dlussky's (1994a) study.

Exotic Ant Species in Tonga

According to the classifications of Wilson and Hunt (1967), 22 ant species found in Tonga are alien tramp species not native to the Pacific, but brought to the region by human commerce. The scarcity of records from Tonga precludes dating the arrivals of exotic species precisely. However, seven of these invaders had already arrived in Tonga by the 1860s: *Anoplolepis gracilipes*, *Cardiocondyla nuda* (Mayr), *Monomorium floricola* (Jerdon), *Monomorium pharaonis* (L.), *Paratrechina vaga* (Forel), *Tapinoma melanocephalum*, and *Tetramorium bicarinatum* (Nylander) (Mayr 1870, 1876). Wilson and Taylor (1967) listed six additional tramp species in Tonga: *Hypoponera punctatissima* (Roger), *Paratrechina bourbonica* (Forel), *Paratrechina longicornis* (Latreille), *Pheidole fervens* Smith, *Solenopsis geminata* (Fabr.), and *Tetramorium simillimum* (Smith). It is possible that all five have been introduced to Tonga within the past 100 yr.

Nine exotic species now in Tonga were absent from Wilson and Taylor's (1967) list: *Cardiocondyla emeryi* Forel, *Hypoponera opaciceps* (Mayr), *Monomorium sechellense* Emery, *Pheidole megacephala*, *Plagiolepis alluaudi* Forel, *Pyramica membranifera* (Emery), *Strumigenys emmae* (Emery), *Strumigenys rogeri* Emery, and *Tetramorium lanuginosum* Mayr. Only one has an unpublished record predating 1967, *Pheidole megacephala*. Museum specimens, reported here for the first time, indicate that *P. megacephala* invaded the far north of Tonga by 1930. The first *P. megacephala* specimens from the main island of Tongatapu were collected by Maddison in 1975. The other eight exotic ant species not on Wilson and Taylor's (1967) list were all collected in Tonga for the first time in the 1970s or later. Although these late records could represent recent invasions, it is possible that these invaders came much earlier, but were simply not documented.

Dlussky (1994a) placed the 22 exotic ant species found in Tonga in four categories, according to their presumed origins (Tables 2

and 3): seven pantropical species of Asian origin, 11 pantropical species of African origin, two pantropical species of Neotropical origin, and one species of Asian origin. In addition, one species, classified by Dlussky (1994a) as *Monomorium fossulatum* Emery of Asian origin, has been synonymized with the much broader-ranging tramp species *Monomorium sechellense*.

It is striking that only two exotic ant species in Tonga are of New World origin: *Hypoponera opaciceps* and *Solenopsis geminata*. This, no doubt, relates to not only geographic proximity and ocean currents, but also traditional trade routes. Certainly in the future, more arrivals of ants from the New World can be expected.

Future of the Tongan Ant Fauna

Even with the new records published here, the ants of most of the 170 islands of Tonga remain relatively unknown. Only three islands, Tongatapu, 'Eua, and Vava'u, have been well sampled for ants. No doubt many undocumented native ant species persist on other Tongan islands. However, tramp ants, particularly *Pheidole megacephala*, appear to be rapidly exterminating native ants on Tongatapu and 'Eua (unpubl. data).

Although *Pheidole megacephala* specimens were collected on Tongatapu by Maddison in 1975, contemporary collections on Tongatapu by Litsinger (in 1973–1974) and Watt (in 1975–1977) did not include *P. megacephala*, suggesting that *P. megacephala* populations in the 1970s were limited. By 1995, however, *P. megacephala* dominated vast areas of Tongatapu, where it occurred in almost every log and under almost every rock (pers. obs.). The 1980 Soviet collection documented by Dlussky (1994a) recorded the first *P. megacephala* on Vava'u. In 1995, I made the first collections of *P. megacephala* in 'Eua and Ha'apai. At that time, *P. megacephala* was the dominant ant species over large parts of western 'Eua, but had a limited population on Lifuka in Ha'apai. The vast population expansion on 'Eua appears to have occurred in just 15 yr. The tiny *P. megacephala* population on Lifuka is probably even younger.

Although I found that *P. megacephala* was relatively uncommon in Vava'u, Kapa, and Lifuka, I predict that this ant will spread to dominate these islands as well.

Three destructive tramp ants known in the Pacific that have not yet been found in Tonga are *Linepithema humile* (Mayr), *Monomorium destructor* (Jerdon), and *Wasmannia auropunctata* (Roger). In Hawai'i, *Linepithema humile* is the primary pest ant at higher elevations (above 900 m) (Reimer 1994, Wetterer et al. 1998). It also has had a great impact on the native ants of Santa Cruz Island in the California Channel Islands (Wetterer et al. 2000). *Monomorium destructor* is known from many parts of the Pacific, including Samoa, the Cook Islands, and French Polynesia (Wilson and Taylor 1967). Mayor (1922:103) wrote of *Monomorium destructor* in the Florida Keys: "So voracious are these insects that we are obliged to swing our beds from the rafters and to paint the ropes with a solution of corrosive sublimate, while all tables must have tape soaked in corrosive sublimate wrapped around their legs if ants are to be excluded from them. These pests have the habit of biting out small pieces of skin, and I have seen them kill within 24 hours rats which were confined in cages." Perhaps the greatest threat, however, is *Wasmannia auropunctata*, which has become established in several Pacific island groups, including the Galápagos (Clark et al. 1982), Wallis and Futuna (Gutierrez 1981 in Jourdan 1997), New Caledonia (Jourdan 1997), the Solomon Islands (Fabres and Brown 1978), and most recently Vanuatu (Rapp 1999) and Hawai'i (Anonymous 1999). In areas where it invades, *W. auropunctata* can be a significant agricultural pest, both through stinging workers and through enhancing populations of Homoptera (Spencer 1941). In addition, *W. auropunctata* has direct negative impacts on native invertebrates and vertebrates (Fabres and Brown 1978, Lubin 1984, Jourdan 1997, Wetterer 1997b, Wetterer et al. 1999).

More thorough ant surveys of Tonga are certainly warranted. In addition, the collections of other museums, particularly the Bishop Museum in Hawai'i and the Austra-

lian National Insect Collection in Canberra, need to be searched for additional unreported ant specimens from Tonga to better understand the spread or loss of ant species.

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