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ANT FAUNA OF FUTUNA AND WALLIS ISLANDS, STEPPING STONES TO POLYNESIA

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Abstract: The ants of Futuna and the Wallis Islands were studied for the first time during a field trip in 1965. A total of 36 species was collected from the two island groups, 22 of which are considered likely to be native and 14 introduced by man. No new species and therefore no endemics were encountered. The native fauna is quite rich for the land area occupied. It consists of species held in common with Melanesia or Samoa or both. From the latter fact, and from independent theoretical considerations based on a mathematical model of overseas dispersal, the islands are judged to be potentially important stepping stones for species invading the remainder of Polynesia. Also, note is made of the disproportionately important role of very small islands in the dispersal of a few species capable of dominating them.

The Wallis Islands and the nearby islands of Futuna and Alofi are among the few places in the world whose ant faunas have remained almost wholly unexplored to the present time. Previously only several isolated records due to Emery (1914) were available in the literature. The attraction for studying the islands is heightened by their strategic location: intermediate between Melanesia to the west, especially Fiji and the Solomon Islands, and Samoa to the east. From fig. 1 it can be seen that Melanesian species dispersing eastward into Polynesia are likely to increase their probability of colonizing the islands of Samoa, which hold the largest faunulae in Polynesia, by hopping along Futuna, Alofi, and the Wallis Islands. In planning this study we consequently asked whether the native species common to Melanesia and Samoa would also be found on the smaller, intermediate islands; and whether the Melanesian species that have not reached Samoa would prove to be absent also in the intermediate islands.

In 1965 Hunt visited the islands for the purpose of collecting ants and making ecological observations. He worked on Uvéa from 21 February to 3 March and 24 March to 9 April; on Futuna from 5 March to 20 March; and on the islets of Nuku Tapu, Nukuifala (Nuku Hifala), Nukuione, and Tekaviki, which rise from the eastern fringing reef of Uvéa, intermittently between 28 March and 1 April. A total of 382 accessions, representing many

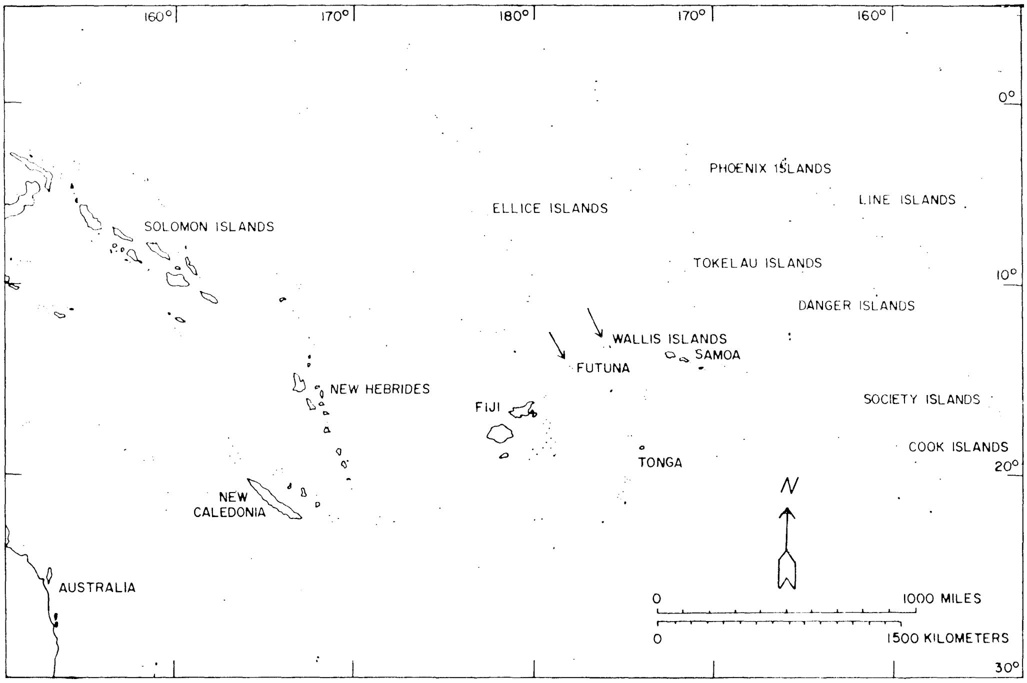

Fig. 1. Map showing the location of the Futuna and Wallis Islands.

more nest series, was made. The collections have been dry-mounted and placed in the Museum of Comparative Zoology, Harvard University. The classification of the material has been based on the recent monograph of the Polynesian ant fauna by Wilson & Taylor (1967).

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History and Environment of the Islands

The Wallis Islands, of which Uvéa is the central and principal member, contain a basaltic substructure believed to have been built to sea level by volcanic action sometime during the Tertiary. The emergent portion is relatively young, perhaps having been formed during the middle Pleistocene—on the order of a half million years ago—by further volcanic eruptions (Stearns 1945). The Futuna (or Hoorn) Islands, including Futuna and Alofi, are primarily of volcanic origin with some elevated reef limestone. No geologic dates have been suggested for this latter group of islands.

Uvéa is flat, with a maximum elevation (at Lulufakahega and Afala) of only 145 meters. Most of the land is either cultivated or carries very disturbed second growth. The summit of "Mount" Holo, for example, is covered by mango forest. In a few spots, such as Lalolalo and Lano, some well-preserved native forest still exists. Futuna, on the other hand, has a very rugged topography, with one peak (Mt Puke) rising to 797 meters. It is less densely settled than Uvéa, and human activities are moreover mostly limited to the coast. The interior of the island is covered chiefly by well-developed native forest.

The climate of both groups of islands is typical of the warm humid tropics. According to records kept by the Service Météorologique de la Nouvelle-Calédonie, the mean annual temperature at Mata-Utu, Uvéa, in 1950–58 was 27.0°C, with less than a 2° annual variation during most of the years. Diurnal variation was about 3° to 4.5° in November to March, and 4° to 6° in April to October, with a rare maximum of 10°. The absolute minimum temperature in the 9-year period was 20°, and the absolute maximum was 34.5°.

Rainfall at Mata-Utu in the same period was high. It averaged 2760 mm per year, with a mean number of days experiencing rainfall of 188. The driest year (1953) had 1478 mm in a total of 130 days of rainfall, while the wettest year (1954) had 3949 mm in 221 days of rain. The wet season, with rainfall exceeding an average of 200 mm per month, began slowly in October, reached a peak of 300 mm per month or more in March, and ended suddenly in April. The little dry season, with about 150 mm rainfall per month, ran from April to June. In June there was a slight, brief increase (the little wet season) to near 200 mm, then a steady decrease to the major dry season, which saw its nadir in August of less than 100 mm per month.

Some Zoogeographic Conclusions

In Table 1 the 36 species collected in Futuna and the Wallis Islands are partitioned according to faunistic origin. In Table 2 the native faunas of the islands together with those of Samoa are listed in parallel, together with an indication of which members are also known from Fiji and the Solomon Islands. Several interesting conclusions can be drawn from these data:

(1) The species densities of Futuna and the Wallis Islands are higher than most of the rest of Polynesia and in fact are comparable to those of Samoa.

Table 1. Areas and numbers of ant species of the islands studied.

Island	Area (Square miles)	Number of species			
		Endemic	Native	Introduced	Total
Futuna	40	0	15	9	24
Uvéa	24	0	15	14	29
Nukuifala	0.02	0	4	7	11
Nukuione	0.02	0	5	6	11
Nuku Tapu	0.05	0	6	7	13
Tekaviki	0.01	0	1	2	3
All islands together	~64	0	21	15	36

Table 2. The combined species list of Fiji, Futuna, Wallis, and Samoa.

	Occurrence				Origin
	Fiji	Futuna	Wallis	Samoa	
PONERINAE					
Prionopelta kraepelini	—	—	—	X*	native
Cryptopone testacea	—	—	—	X*	native
Ponera colaensis	X̄	—	—	—	native
P. incerta	—	—	—	X*	native
P. loi	—	—	—	X̄	native
P. monticola	X̄	—	—	—	native
P. rugosa	X̄	—	—	—	native
P. swezeyi	—	—	—	X*	native
P. szaboi	—	X*	—	—	native
P. tenuis	—	—	—	X*	native
P. turaga	X̄	—	—	—	native
P. vitiensis	X̄	—	—	—	native
P. woodwardi	—	—	—	X̄	native
Hypoponera confinis	—	—	—	X*	native
H. punctatissima	X*	—	X*	X*	introduced
Trachymesopus stigma	X*	—	—	X*	introduced (?)
Platythyrea parallela	—	—	—	X*	native
Leptogenys foveopunctata	X̄	—	—	—	native
L. fugax	X̄	—	—	—	native
L. humiliata	X̄	—	—	—	native
L. letiliae	X̄	—	—	—	native
L. navua	X̄	—	—	—	native
L. vitiensis	X̄	—	—	—	native
Gnamptogenys aterrima	X̄	—	—	—	native
Proceratium relictus	X̄	—	—	—	native
Ectomomyrmex samoanus	—	—	—	X̄	native
Odontomachus angulatus	X̄	—	—	—	native
O. simillimus	X*	X*	X*	X*	native
Anochetus graeffei	X*	—	X*	X*	native
Cerapachys cryptus	X̄	—	—	—	native
C. majusculus	X̄	—	—	—	native
C. vitiensis	X̄	—	—	—	native
C. sculpturatus	X̄	—	—	—	native
Syscia silvestrii	—	—	—	X*	introduced
MYRMICINAE					
Strumigenys godeffroyi	X*	X*	X*	X*	native
S. jepsoni	X̄	—	—	—	native
S. jepsoni aff.	—	—	X*	—	native
S. malilei	—	—	—	X̄	native
S. nidifex	X̄	—	—	—	native

	Occurrence				Origin
	Fiji	Futuna	Wallis	Samoa	
S. rogeri	—	—	X*	X*	introduced
S. scelestus	X̄	—	—	—	native
S. szalayi	—	—	—	X*	native
S. wheeleri	X̄	—	—	—	native
Quadristruma emmae	—	—	—	X*	introduced
Trichoscapa membranifera	X*	—	X*	X*	introduced
Smithistruma dubia	—	—	—	X*	native
Pheidole aana	—	—	—	X̄	native
P. atua	—	—	—	X̄	native
P. caldwelli	X̄	—	—	—	native
P. colaensis	X̄	—	—	—	native
P. fervens	X*	—	—	X*	introduced
P. knowlesi	X̄	—	—	—	native
P. megacephala	X*	X*	X*	X*	introduced
P. oceanica	X*	X*	X*	X*	native
P. onifera	X̄	—	—	—	native
P. sexspinosa	—	X*	X*	X*	native
P. umbonata	X*	X*	X*	X*	native
P. vatu	X̄	—	—	—	native
P. wilsoni	X̄	—	—	—	native
Poecilomyrma senirewae	X̄	—	—	—	native
Adelomyrmex hirsutus	X̄	—	—	—	native
A. samoanus	—	—	—	X̄	native
Rogeria exsulans	—	—	—	X̄	native
R. rugosa	X̄	—	—	—	native
R. stoneri	X̄	—	—	—	native
R. striatella	X̄	—	—	—	nrtive
R. tortuosa	X̄	—	—	—	native
R. sublevinodis	X*	X*	X*	X*	native
Pristomyrmex mandibularis	X̄	—	—	—	native
P. mendanai aff.	—	—	X*	—	native
Archaeomyrmex cacabau	X̄	—	—	—	native
Tetramorium guineense	X*	X*	X*	X*	introduced
T. pacificum	X*	X*	X*	X*	native
T. simillimum	X*	—	X*	X*	introduced
T. tonganum	X*	X*	X*	X*	native
Romblonella scrobiferum	X̄	—	—	—	native
R. vitiensis	X̄	—	—	—	native
Triglyphothrix pacifica	X̄	—	—	—	native
T. striatidens	—	—	X*	—	introduced
Rhopalothrix elegans	X̄	—	—	—	native
R. procera	—	—	—	X*	native

	Occurrence				Origin
	Fiji	Futuna	Wallis	Samoa	
Monomorium destructor	—	—	—	X*	introduced
M. floricola	X*	X*	X*	X*	introduced
M. fossulatum	—	—	—	X*	introduced
M. minutum	—	—	—	X*	introduced
M. pharaonis	X*	—	—	X*	introduced
M. talpa	—	X*	X*	X*	native
M. vitiensis	$\overline{X}$	—	—	—	native
Solenopsis papuana	X*	—	X*	X*	native
Oligomyrmex atomus	X*	X*	—	X*	native
Vollenhovia samoensis	—	—	—	$\overline{X}$	native
V. pacifica	—	—	—	$\overline{X}$	native
V. sp.	—	X*	—	—	native
Cardiocondyla emeryi	—	X*	X*	X*	introduced
C. nuda	X*	X*	X*	X*	introduced
DOLICHODERINAE					
Iridomyrmex anceps	X*	—	X*	—	native
I. nagasau	$\overline{X}$	—	—	—	native
I. sororis	$\overline{X}$	—	—	—	native
Tapinoma melanocephalum	X*	X*	X*	X*	introduced
T. minutum	X*	X*	X*	X*	native
Technomyrmex albipes	X*	X*	X*	X*	native
FORMICINAE					
Plagiolepis alluaudi	X*	—	—	—	introduced
Anoplolepis longipes	X*	X*	X*	X*	introduced
Brachymyrmex obscurior	—	—	—	X*	introduced
Paratrechina longicornis	X*	—	X*	X*	introduced
P. bourbonica	X*	X*	X*	X*	introduced
P. minutula	—	—	—	X*	native
P. oceanica	$\overline{X}$	—	—	—	native
P. vaga	X*	X*	X*	X*	introduced
P. vitiensis	$\overline{X}$	—	—	—	native
Camponotus bryani	$\overline{X}$	—	—	—	native
C. chloroticus	X*	X*	X*	X*	native
C. cristatus	$\overline{X}$	—	—	—	native
C. dentatus	$\overline{X}$	—	—	—	native
C. flavolimbatus	—	—	—	$\overline{X}$	native
C. janus	$\overline{X}$	—	—	—	native
C. laminatus	$\overline{X}$	—	—	—	native
C. maafui	$\overline{X}$	—	—	—	native
C. manni	$\overline{X}$	—	—	—	native
C. maudella	$\overline{X}$	—	—	—	native
C. mayriella	$\overline{X}$	—	—	—	native

	Occurrence				Origin
	Fiji	Futuna	Wallis	Samoa	
C. navigator	—	—	—	$\overline{X}$	native
C. oceanicus	$\overline{X}$	—	—	—	native
C. reticulatus	—	—	X*	—	native
C. rufifrons	X*	—	—	—	native
C. schmeltzii	$\overline{X}$	—	—	—	native
C. vitiensis	$\overline{X}$	—	—	—	native

X marks the occurrence on the archipelago or island; $\overline{X}$ indicates that the species is an endemic; X* means that the species also ranges beyond Fiji, Futuna, Wallis, and Samoa. The species are also classified as to whether they are native to the western Pacific or were introduced by human commerce.

(2) These high densities are due largely to the occurrence of native species on Futuna and the Wallis Islands whose ranges extend to but not much beyond Samoa. As detailed in Table 2, no less than 15 of the 26 native, non-endemic Samoan species also occur on Futuna and the Wallis Islands.

(3) There are no endemic species represented in our collections. This is surprising in view of the fact that a total of nearly 20 endemic species is known from Rotuma and various islands in Samoa and Tonga, which archipelagos occur to the east of Futuna and the Wallis Islands.

(4) Uvéa, the largest and central member of the Wallis group, has a native fauna very similar to that of Futuna. The number of species is the same in each: 15. On the other hand a few differences in the species lists exist; perhaps the most notable is the occurrence of *Camponotus reticulatus* as a common species in the Wallis Islands and its apparent absence on Futuna. This disparity is probably due to the chance pattern of colonization, a conclusion that will be discussed in more detail later in the systematic portion.

(5) In contrast to the relatively uniform picture presented by native species, Uvéa contains 14 known tramp species while Futuna has only 9. This disparity is probably due to the fact that the human population of Uvéa is larger, has cultivated more of the land, and carries on a more active foreign trade. Also, Uvéa is the main entrepot for the French islands north of New Caledonia. Futuna has much less traffic, most of which comes by way of Uvéa.

(6) The small islands of the Wallis group (Nukuifala, Nukuione, Nuku Tapu, Tekaviki) display a striking variation in species composition. This variation includes an exact complementarity in the ranges of *Pheidole megacephala* and *P. oceanica*, which species also tend to replace one another on small islands elsewhere in Polynesia (Wilson & Taylor 1967). It also includes the unexpected numerical abundance of *Solenopsis papuana* on Nukuione, together with the apparently unique occurrence of *Anochetus graeffei* on Nukuione and Nuku Tapu and of a species of *Pristomyrmex* on Nuku Tapu. The variation is very likely due in part to chance alone in the past order of colonization, an effect that Wilson (1961) has already referred to as "faunal drift" and advanced to account for similar peculiarities of distribution common throughout Polynesia.

The Stepping Stone Problem

Among the more useful results of the study is the discovery that Futuna and the Wallis Islands contain a large fraction (15/26) of the Melanesia-based native species that have reached Samoa. These islands are thus revealed to be potential stepping stones for ants and probably many other expanding animal and plant taxa as well. But how important have they been as actual source areas? More exactly, what is the probability that a propagule of a given species arriving on Samoa in the past came from the islands rather than all the way from Melanesia? This problem, which does not seem susceptible of an immediate empirical solution, can be attacked by an additional, more theoretical route. A simple model of overseas dispersal will now be constructed to that end, using the following symbols:

- w_r, width of the recipient island measured at a right angle to a line connecting it to the potential source island.
- w_1, width of the stepping-stone island.
- w_2, width of the more distant "source island."
- d_1, distance from stepping-stone island to recipient island.
- d_2, distance from "source island" to recipient island.

The areas of the three islands can be taken as roughly πw_r^2, πw_1^2, and πw_2^2 respectively. In concrete applications of the model only the true areas of islands 1 and 2 together with w_r are required. It is assumed that the number of propagules of a given species leaving a given island is roughly proportional to the number of individuals living on the island, which in turn increases linearly with the area of the island. In other words, the number of propagules leaving island i is αw_i^2, where α is a fitted constant. Even if this is only a very crude approximation it is acceptable, because we will be dealing with ratios rather than absolute values.

Of course most of the αw_i^2 propagules perish at sea. The number reaching a given distance *d* is determined by a dispersal distribution that is probably a characteristic of the species. If the probability of a given propagule perishing remains constant, as might be the case in passive dispersal in a constant wind, survivorship will approximate an exponential distribution; the number surviving after travelling the distance from one island to another will be

$$\alpha w_i^2 e^{-d_{i/\lambda}},$$

where λ is the mean dispersal distance. The probability that the right direction was taken by propagules travelling the correct distance is the ratio of the angle subtended by the width of the recipient island to 360°. The total number of propagules reaching the recipient island is therefore

$$n_i = \frac{2\tan^{-1}(w_r/2d_i)}{360^\circ}\,\alpha w_i^2 e^{-d_{i/\lambda}}.$$

We are interested in the probability that a given propagule landing on the recipient island came from island no. 1 (the stepping stone) rather than from island no. 2 (the main source island)—in other words $n_1/(n_1+n_2)$.

Let us now introduce another form of dispersal curve. In cases where propagules wander at random or are borne on some sea-going carrier, such as a floating log, which has a normally distributed persistence time, the dispersal distribution is probably more closely approximated by a normal distribution. A formula parallel to that for the exponential case can be developed from the expression

$$n_i = \tan^{-1}(w_r/2d_i)\alpha w_i^2\left[1-2\int_0^{d_i}\frac{1}{\sigma\sqrt{2\pi}}e^{-\frac{1}{2}\left(\frac{x}{\sigma}\right)^2}dx\right]. \qquad (3)$$

Notice again that since we are dealing with a ratio $[n_1/(n_1+n_2)]$, we do not need to know the absolute propagation rate of propagules; in other words, α cancels out. Similarly, so long as the 3 islands are aligned, variation in wind and current direction and velocity can be momentarily disregarded. Perhaps most important of all the terms in the 2 formulas that contribute most to propagule attrition are e^{-ax} and e^{-bx^2}. Clearly the rate of attrition for the second (normal) case is much higher than for the first (exponential) case.

Applying the model to the case at hand, island *r* can be all of Samoa or one of its islands. For present purposes it is enough to take Savai'i (the result would be about the same if another of the Samoan islands were taken or all were taken together). Island 1 is Uvéa or Futuna. Island 2 can be for our purposes all of Fiji. The parameters are then set as follows in miles for Futuna: $w_r=40$, $w_1^2=40$, $w_2^2=7083$, $d_1=340$, $d_2=500$. The parameters for the Wallis Is. are as follows: $w_r=40$, $w_1^2=40$, $w_2^2=7083$, $d_1=220$, $d_2=500$.

The proportion $n_1/(n_1+n_2)$ of propagules coming from Futuna (or Wallis), as opposed to Fiji, which arrive on Savai'i have been computed for various values of λ and are presented in Table 3. It can be seen that for all but the highest—and least likely—λ values, an overwhelming proportion of propagules should come from Futuna and Wallis, providing of course the species in question has been able to settle these stepping-stone islands in the first place. This is true for both the exponential and normal cases. Indeed, it is difficult to imagine *any* form of dispersal curve which, when fixed by low or moderate λ values, would yield a different qualitative result.

By parallel reasoning, we can show that providing the Futuna and Wallis Islands, or any of the other intermediately positioned islands such as Niuafo'ou and Niuatoputapu, are capable of supporting a given set of species, the species will almost certainly colonize these stepping

Table 3. The probability $n_1/(n_1+n_2)$ that a propagule arriving on Savai'i came from Futuna (or Wallis) rather than from Fiji, assuming one or the other of two dispersal curves and a wide range of mean dispersal distances (λ) for various species.

Mean dispersal distance in miles (λ)	Exponential dispersal		Normal dispersal	
	Futuna	Wallis	Futuna	Wallis
0.01	>0.999999	>0.999999	>0.999999	>0.999999
0.1	>0.999999	>0.999999	>0.999999	>0.999999
1	>0.999999	>0.999999	>0.999999	>0.999999
10	0.999993	>0.999999	>0.999999	>0.999999
100	0.075971	0.173986	0.455888	0.968234
1,000	0.019107	0.016662	0.009369	0.030721
10,000	0.016587	0.012998	0.008173	0.025221

stones before they reach Samoa. It follows that such species will eventually come to Samoa by way of the stepping stones.

The Importance of Very Small Islands

The discovery of unexpected, deviant species compositions on the fringing islets of Uvéa has implications for the role of very small islands in dispersal. Three species (*Anochetus graeffei*, *Trichoscapa membranifera*, *Pristomyrmex* sp.) are known only from the islets. The phenomenon seems to be real in at least the case of the *Anochetus*, which replaces the related species *Odontomachus simillimus* on the islets and is replaced by it on Uvéa. Other species which are uncommon on the larger islands, such as *Solenopsis papuana*, *Triglyphothrix striatidens*, and *Rogeria sublevinodis*, proved unexpectedly abundant on the islets. Clearly, for a few species which are especially adapted to the islet environment or else thrive there in the lack of competition from ecological vicars limited to the larger islands, the islets serve as dispersal centers out of proportion to their relative areas.

Collecting Localities

Collecting localities are shown in the maps of fig. 2 and 3. In the maps and in the textual coverage of individual species, an alphabetical code to the localities on Futuna and Uvéa will be employed, as follows:

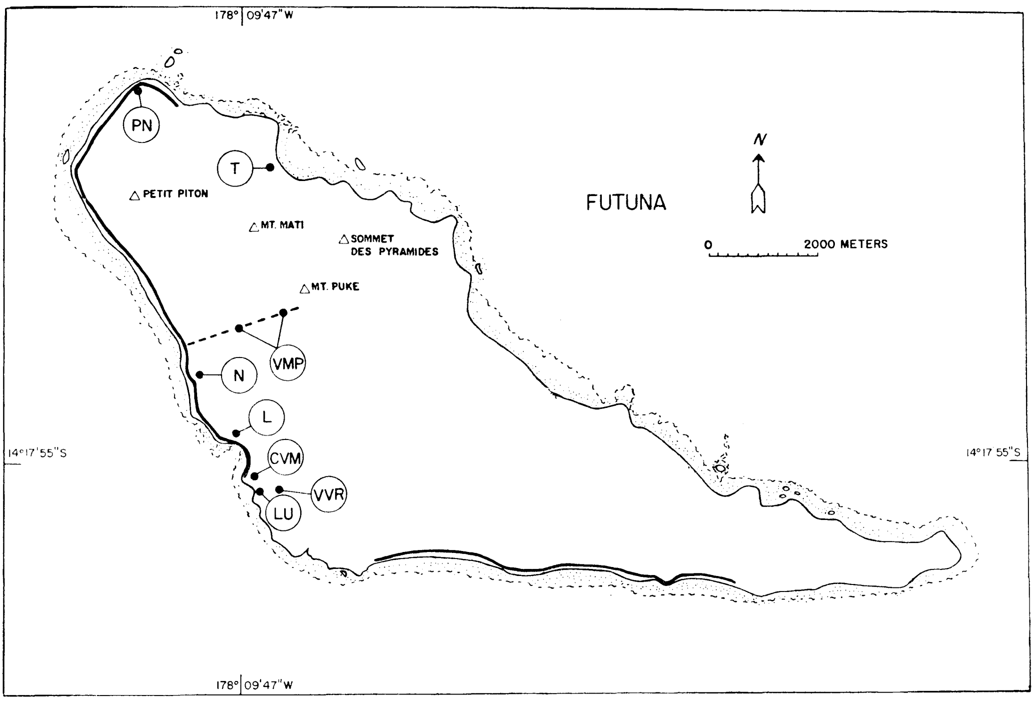

Fig. 2. Map of Futuna, showing the collecting stations in 1965.

FUTUNA

CVM.	Chapelle Vila Malia.
L.	Leava.
LU.	Luanuku.
L–LU.	Leava to Luanuku.
MO.	Mountain above the Molinhina, 65 m.

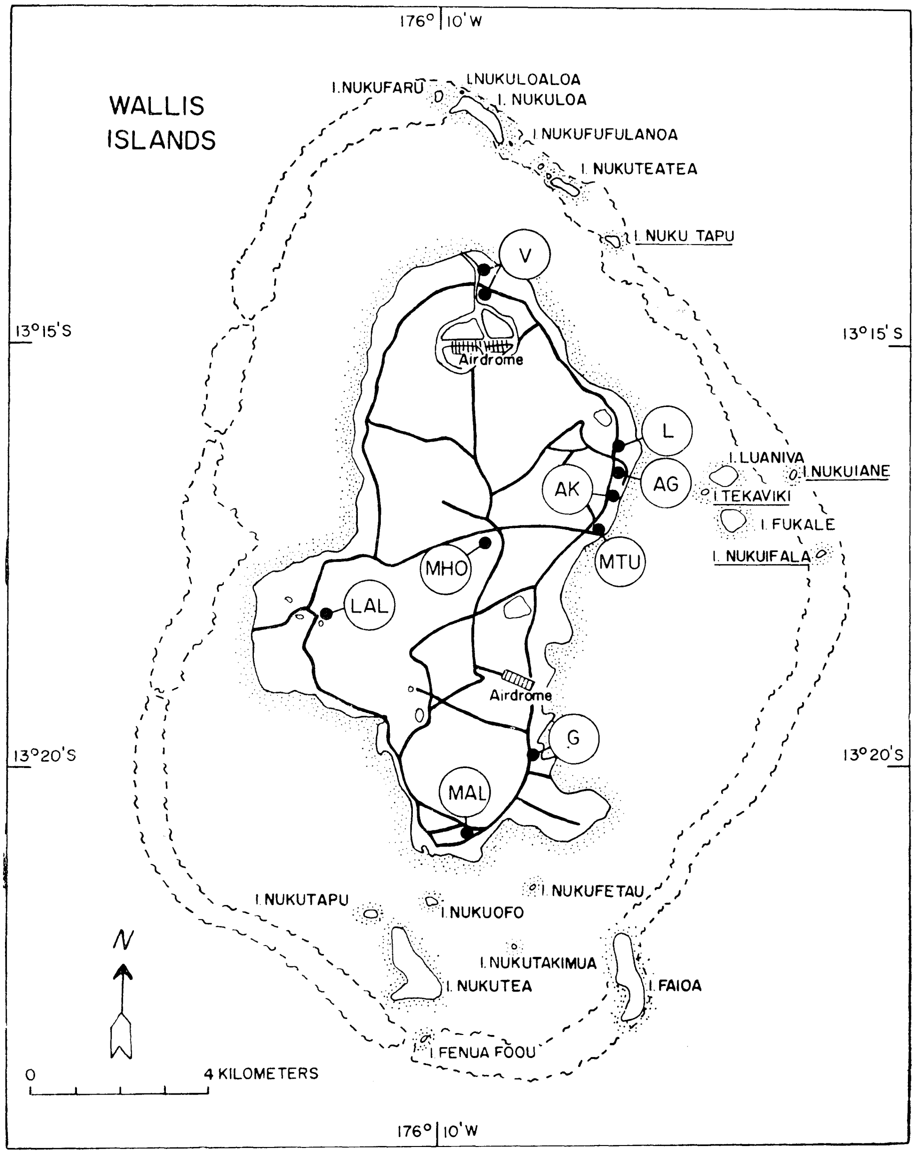

Fig. 3. Map of the Wallis Is., showing the collecting stations in 1965.

N.	Nuku.
PN.	Pointe Nord.
T.	Tuatafa.
VMP.	Trail, Vaisei to Mt Puke, 400 m.
VVR.	Valley of Vaikélékélé River, 65 m.

UVÉA

AG.	Agricultural Station, Akaaka to Liku.
AK.	Akaaka.
G.	Gahi.
LAL.	Lalolalo, near lake.
LMA.	Road between Laalofiva and Mt Afala.
LNO.	Lano.
MAL.	Malaefoou.
MTU.	Mata-Utu.
MHO.	Mt Holo, 100 m.
V.	Vailala, Hihifo District.

In cases where more than 1 colony was collected at a given locality, the number of accessions is given in parenthesis after the code letters. Thus, AK(3) means that 3 collections, representing at least 3 colonies, were made at Akaaka, Uvéa.

Ponera szaboi Wilson

FUTUNA: MO.

A single worker has been tentatively identified as *P. szaboi*, a species previously known to range from New Guinea to the Solomon Islands (Rennell). It is smaller and more lightly sculptured than any of the numerous specimens of the closely related *P. tenuis* recently examined by R. W. Taylor from Samoa (Taylor, pers. commun). Additional worker material will be required to establish its identity with certainty.

Hypoponera punctatissima (Roger)

UVÉA: V.

Two workers found under the bark of a rotting coconut log belong to this pantropical tramp species.

Odontomachus simillimus Fr. Smith

FUTUNA: N, stray workers from native garden. PN, dealate queen on ground in second-growth forest. VMP (4), stray workers from ground and leaf litter in second-growth and mature forest. UVÉA: AK, stray workers on ground in native taro patch. LAL (2), mature forest, under rotting log, and stray workers in clearing, mostly on ground but several seen on low vegetation also. LNO(3), nesting in ground under rotting log. MTU(3), nest under rotting log in taro patch, winged queens 25-27.II strays at base of tree. V(2), under mango in open field, stray from under log.

This large species is the most widely distributed of the Indo-Australian *Odontomachus*, ranging as far east as Samoa. A notable feature of its distribution in the Wallis Is. is its apparent restriction to Uvéa. Despite its abundance on this large, central island, it was not encountered on the 4 smaller islands examined on Uvéa's fringing reef. On the other hand, *Anochetus graeffei*, the species most closely related to *O. simillimus* in the Wallis Is. was found *only* on the smaller islands.

Anochetus graeffei Mayr

NUKUIONE (2). Nesting in rotting logs. NUKUTAPU (3).

The species was found only on the 2 small islands of the Uvéa fringing reef listed above. It apparently replaces the larger, related *Odontomachus simillimus* there. Workers were relatively common in leaf litter.

Strumigenys godeffroyi Mayr

FUTUNA: CVM, nest in rotting log, second-growth forest. L(3), nest and strays in rotting wood on ground, second-growth forest; under bark of dead but not rotten log, 6 cm diameter. LU, nest in rotting log, coconut grove. L-LU, on foliage, mature forest in valley of small stream. MO, nest in rotting branch on ground, second-growth forest. N, strays on piece of rotting wood, edge of mature forest. PN(2), nest in rotting log in second-growth forest, strays from surface of rotting log, secondary forest. VMP, strays on ground in mature forest. NUKUIFALA: strays under bark of rotting log. UVÉA: G, strays in rotting coconut on ground. LAL(2), nest in dead hollow twig in leaf litter, strays under rotting log, mature forest. MHO(3), nest in rotting log, mango forest, strays under dead log in leaf litter and in open leaf litter.

This species is the most widely ranging member of its genus in the Indo-Australian area, and there is no reason at present to doubt that it is native to Futuna and the Wallis Islands. The ecological records given above indicate that, as in other parts of its range, it can occupy a variety of major habitats but is still restricted mostly to nesting in rotting wood and foraging in leaf litter and crevices in soil.

Strumigenys rogeri Emery

UVÉA: MHO(2), nest in small dead twig in leaf litter and strays in leaf litter, mango forest at summit of Mt Holo, 100 meters.

This tramp species, which originated in Africa, is common in other parts of Polynesia.

Strumigenys sp.

UVÉA: MAL, sifted from soil and leaf litter.

Two workers belong to an unknown member of the Melanesia-based *jepsoni* group. According to W. L. Brown (*in litt.*) the species might be an undescribed endemic of the Wallis Is., but so little material of the group is available from other islands as to make such a conclusion very premature at this time.

Trichoscapa membranifera (Emery)

NUKUIONE: nest in rotting log about 1 meter in length.

This pantropical tramp species apparently originated in Africa and has also been recorded from Samoa and Micronesia. Elsewhere it has proven to be ecologically the most variable of the dacetine ants, nesting in rotting logs and soil in both moist (mesophytic) forest and moderately dry, open, cultivated fields.

Pheidole megacephala (Fabricius)

FUTUNA: L(13), nesting under coconut shell, in rotting stump, in dead tree limb on live tree 8 m from ground, and in pebbly soil on grounds of Jessop's Hotel; another nest near hospital, under bark of fallen tree, containing at least 4 queens; abundant in vicinity of town, foraging in files on ground, low vegetation, and trees on lawns and in coconut groves. LU, nesting in rotting stump. N(3), strays in leaf litter collected in tree fork, in open ground in cultivated area, and on foliage in overgrown coconut grove. NUKUIFALA: workers attracted to food. TEKAVIKI (8): the dominant ant on this small island; workers were foraging over open ground, on low vegetation, and on trunks of trees; nests were found in a rotten coconut and in a hollow branch on ground, and in a rotting tree trunk. UVÉA: MAL(7), nest in stem of dying banana plant; foraging workers abundant in open areas and walls of buildings and on vegetation in surrounding cultivated areas. MTU(5), nest in rotten palm stump in second-growth woods; other nests on hotel grounds; an abundant ant in the village and in surrounding cultivated areas. MHO(2), strays under rotting logs and on ground in mango forest. V(2), nests in rotting stumps.

This well-known pantropical tramp species originates from Africa and is a dominant ant through much of the remainder of Polynesia. In Futuna and the Wallis Islands it is especially abundant around human dwellings, where it is a pest both in and out of doors. The colonies are diffuse, contain multiple queens, and emigrate readily. On several occasions, workers began moving brood into sacks of moist leaf litter kept overnight for sorting.

Residents of Mata-Utu stated to Hunt that the species was unknown in the village prior to World War II. It is perhaps no coincidence that the first *P. megacephala* were noted at about the time of the war, when 2,000 American military personnel were stationed on Uvéa.

There is a perfect replacement pattern on the 4 smaller Wallis Is. studied with reference to *P. oceanica*. *P. megacephala* occurs on Nukuifala and Tekaviki, while *P. oceanica* occurs on Nukuione and Nuku Tapu. On the other hand, the 2 species are widely sympatric on the larger island of Uvéa as well as on Futuna.

Pheidole oceanica Mayr

FUTUNA: CVM(5), 2 nests in rotting logs, secondary forest; workers foraging on ground, feeding on coconut meat. LU, foraging in file on trunk of coconut tree, coconut grove. MO(2), strays in leaf litter, second-growth forest. N(3), strays on ground and low vegetation, mature forest. PN(4), nests in rotting logs, second-growth forest; workers foraging on ground and on vertical rock surface. VMP(4), nest under moss on tree trunk, mature forest; strays on ground and vegetation, savanna and mature forest. VVR, nest in rotting log, mature forest. NUKUIONE (3): strays on rotting logs. NUKU TAPU (4): 3 nests under rotting logs, strays under coconut on ground. UVÉA: LAL(5), 2 nests in rotting logs, mature forest, workers foraging on ground and vegetation, ♂ with workers 2.IV. MTU. V, foraging in open area, light secondary forest.

This native Indo-Australian species ranges from Melanesia east to the Society Is.

Pheidole sexspinosus Mayr

FUTUNA: LU, stray under log in coconut grove. L-LU(3), 3 nests in rotting logs, second-growth forest. VMP. VVR(3), nests under bark of tree and in rotting logs, mature forest. UVÉA: MHO(2), nest under bark of branch 2.5 cm in diameter on ground, mango forest, stray workers feeding on piece of coconut meat.

This is the most wide-ranging member of the exclusively Indo-Australian subgenus *Pheidolacanthinus*. *P. sexspinosus* extends from New Guinea east to the Marquesas. On Futuna and the Wallis Islands, as on the nearby islands of Samoa, it is mostly limited to forests.

Pheidole umbonata Mayr

FUTUNA: CVM, workers feeding on coconut meat, secondary forest. LU(3), nest under stone, and workers foraging on ground, coconut grove. N(4), nest in fern roots in tree fork, strays foraging on moss, coconut grove. PN, nest in rotting stump, secondary forest. VMP(9), nest in soil at base of tree, several nests in rotting wood, strays in leaf litter and on surface of rotting logs, mature forest. NUKUIFALA (2): strays from leaf litter and soil. UVÉA: AG(2), under bark of rotting tree trunk, native garden. G(4), nest in rotten coconut on ground, strays on ground and soil, coconut grove. LAL(4), strays on ground, mature forest. LNO(4), strays on ground, advanced secondary forest. MTU(4), nest in soil in hollow part of tree, strays on soil. V(6), strays on ground and rotting logs.

P. umbonata is a small native species which ranges from New Guinea to Samoa.

Solenopsis papuana Emery

NUKUIONE (8): nesting and foraging in rotten logs. UVÉA: MTU(2), nesting in small piece of rotting wood on ground beside path through taro patch.

S. papuana is the most wide-ranging Indo-Australian member of the genus, occurring sporadically from New Guinea to Samoa. The exceptional abundance of the species on the islet of Nukuione, where it was the most frequently collected ant, is in sharp contrast to its relative scarcity elsewhere in its range.

Oligomyrmex atomus Emery

FUTUNA: N, a single minor worker from beneath bark of a rotten piece of wood, mature forest on hillside above mission.

This tiny native Indo-Australian species ranges from New Guinea to Samoa.

Monomorium floricola (Jerdon)

FUTUNA: CVM, colony nesting in twig (about 12 mm in diameter) on tree, secondary forest. L, nest under bark of recently fallen tree in village. LU, workers from rotting wood in standing tree trunk. MO(4), nests in rotting log, strays on tree trunk, secondary forest. N, on low vegetation in native garden. PN, colony nesting in hollow liana, secondary forest. VMP, nest in small piece of rotting wood, savanna. NUKUIFALA: strays on trunk of tree. NUKU TAPU (2): nesting and foraging on rotting log. UVÉA: AG, on trunk of dead tree in native garden. AK, strays on banana stem in native garden. G(2), nest in rotten coconut on ground, strays on trunks of coconut palm, coconut grove. LNO, nest in dead stem, advanced secondary forest. MAL. MTU(4), 2 colonies nesting in dead branches of tree, workers foraging on tree trunk and vegetation, taro patch. MHO(2), nest under bark of dead branch (about 8 cm in diameter in leaf litter), nest in dead branch on live tree, mango forest.

M. floricola is among the most widespread and generally abundant pantropical tramp species. It is found throughout Polynesia. On Futuna and the Wallis Islands its behavior is typical—it occurs in a wide variety of major habitats and nesting sites but prefers arboreal sites in gardens and open, second-growth woods.

Monomorium talpa Emery

FUTUNA: CVM, nest in rotting log, secondary forest. L-LU, colony nesting deep within rotting log, secondary forest. MO(3), an apparent colony and stray workers beneath stones, secondary forest. PN, nest in rotting log, secondary forest. UVÉA: MAL, leaf litter and soil, a single dealate queen,

M. talpa is an unusual member of its genus which occurs in rain forests from New Guinea to Samoa.

Vollenhovia sp.

FUTUNA: VVR, 2 colonies nesting under bark of rotting logs in mature forest, winged queens with workers 12.III.

We have seen additional material of this species from the Banks Is., New Hebrides, collected by Borys Malkin.

Tetramorium guineense (Fabricius)

FUTUNA: CVM(4), nesting in tree trunk, in tree stump, and in base of leaves of palm, workers foraging on foliage, secondary forest; apparently the most common ant at this locality. L, strays on stone wall at hospital. LU(2), strays under fallen, rotting coconut trunk, coconut grove. MO, nesting under bark of dead (but not rotten) tree stump, secondary forest. VMP, workers foraging on bracken in open "savanna." NUKUIFALA: nest in rotting log. NUKU TAPU(2). UVÉA: LAL, workers with ♂, 2.IV. MHO(3), 3 nests in rotting logs.

This pantropical tramp species occurs throughout the Pacific region. The colonies nest in a variety of temporary sites both around human dwellings and in disturbed native forest; the workers forage mostly on vegetation.

Tetramorium pacificum Mayr

FUTUNA: PN, strays (both workers and wandering dealate queens) on rotting stumps, secondary forest. VMP(3), nesting in rotting log and in top of tree fern, workers foraging on vegetation, mature forest. UVÉA: MHO(3), nesting in dead branch (8 cm diam.) on live tree, mango forest.

This species is the most widely distributed member of a group whose distribution is centered in Melanesia. It is probably native from New Guinea to Samoa, where it occurs in arboreal sites in native forests and groves of cultivated trees.

Tetramorium simillimum (Fr. Smith)

UVÉA: V, stray workers on floor of native house in village.

T. simillimum is an Africa-based pantropical tramp species that is widespread elsewhere in Polynesia. It is usually found in highly disturbed habitats.

Tetramorium tonganum Mayr

FUTUNA: LU, nesting in rotting stump, coconut grove. L–LU(4), nesting under back of slightly decayed log, workers foraging on logs and ground nearby, secondary forest. MO (6), nesting in dead branch on tree 1 m from ground, in dead branches on ground, workers foraging on ground, secondary forest. NUKUIFALA: strays under rotting log. NUKU TAPU (2): nesting at base of coconut frond, workers foraging on ground and exposed tree root. UVÉA: AG(4), workers foraging on and beneath bark of dead tree trunks in native garden. G(3), 3 colonies nesting in rotten coconuts on ground, coconut grove. LAL, workers on foliage, second-growth vegetation at edge of forest. MHO(4), 2 nests in rotting logs, workers foraging on ground, mature forest.

This species also occurs in, and is probably native to, Samoa and Tonga.

Pristomyrmex sp.

NUKU TAPU: a single worker from a rotting log.

This is the first record of the genus *Pristomyrmex* from Polynesia. The species is close to *P. mendanai* Mann of the Santa Cruz Islands, differing in having short, obtuse spines on the humeri (the humeri of *mendanai* are smoothly rounded) and in being more darkly colored. The Nuku Tapu species is not endemic to the Wallis Is. We have seen closely similar, probably conspecific workers from the east coast of Peleliu I., Palau Group, collected by H. S. Dybas in 1948. The species is possibly undescribed, but its further characterization will have to await revision of the genus.

Triglyphothrix striatidens (Emery)

NUKUIFALA (6): nesting in rotting log, in rotting palm stump, and in dead twig lying on ground, workers foraging on ground and on rotting log. NUKUIONE (2): strays in foliage. NUKU TAPU (3): strays from leaf litter and rotting log, in fringing mangrove and interior of island. UVÉA: AG(3), strays from surface and beneath surface of bark on dead, standing tree in native garden. LNO, workers foraging on gravel beside road. V, strays in soil accumulated in hollow of trunk of live coconut palm.

T. striatidens is an Oriental tramp species which occurs sporadically throughout the tropics. Its prevalence on the smaller of the Wallis Is. is noteworthy and may reflect a preference for islet environments. It has also been found to be a dominant ant on Clipperton, a small and very isolated island in the eastern Pacific (Taylor & Wilson 1962).

Rogeria sublevinodis Emery

FUTUNA: CVM, nest in rotting log, secondary forest. LU, strays under stone, coconut grove. L–LU, strays from top of rotting log, secondary forest. N, strays in soil from tree fork, mature forest. VMP(2), nesting in soil collected in tree, workers foraging on tree trunk, mature forest. NUKUIONE (5): nesting and foraging in rotting logs, winged queens with workers 31.III. NUKU TAPU: strays in rotting log.

R. sublevinodis replaces the related *R. stigmatica* Emery from Fiji to the Society Is. and is probably native to most or all of that peripheral region.

Cardiocondyla emeryi Forel

FUTUNA: N, workers foraging on low vegetation in unkept coconut grove. UVÉA: MTU(2), workers foraging on vegetation in second-growth woods next to taro patch and on surface of concrete conduit next to hospital.

This pantropical tramp species originated in Africa and occurs through most of the remainder of Polynesia. It is most commonly found in the most open, disturbed habitats, such as cultivated fields, lawns, and roads.

Cardiocondyla nuda (Mayr)

FUTUNA: N, strays on ground in banana-taro garden, steep hillside. VMP(3), strays on ground and piece of rotting wood, open bracken heath. NUKUIFALA: strays on open ground near island shelter. NUKU TAPU (2): strays on ground. UVÉA: AG(2), strays from foliage and trunk of dead tree in native garden. AK, strays on banana stem in native garden. MTU(3), strays on ground and foliage, second-growth native vegetation along foot-path.

This species has a similar origin, distribution, and ecology to that of *C. emeryi.*

Iridomyrmex anceps (Roger)

UVÉA: MTU, on ground beside road.

I. anceps is an Indo-Australian species whose easternmost records previously included Viti Levu, Fiji, and Aitutaku, Cook Is. Curiously, it has not been found on Samoa despite intensive collecting on that archipelago in recent years. Since foraging workers are quite conspicuous, the single record listed above indicates that the species is relatively rare in the Wallis Is.

Technomyrmex albipes (Fr. Smith)

FUTUNA: MO(2), nesting in rotting log and foraging in leaf litter, secondary forest. N(2), nest in rotting wood and in soil around roots of fern growing in tree fork, ♂ with workers 5–7.III. VMP(4), nesting in dead leaf stem and in crown of tree ferns, workers foraging in leaf litter, mature forest. UVÉA: LAL, foraging on foliage, small clearing in mature forest. MHO, nesting in dead branch of live tree, secondary forest. V, nest in rotting coconut, old field.

This species ranges more or less continuously from India to Hawaii.

Tapinoma melanocephalum (Fabricius)

FUTUNA: N, nesting in rotting stump, overgrown coconut grove. VMP, nesting under moss on tree trunk, mature forest. NUKUIONE: workers foraging on mangrove foliage. NUKU TAPU. TEKAVIKI: workers foraging on tree trunk. UVÉA: AG(6), nesting in rotting limb on tree 1.5 m from ground, strays on tree trunks, native garden; strays from foliage of second-growth vegetation next to garden; colonies with multiple queens. AK (2), nesting in soil next to rotten coconut husk, strays on banana stem, native garden. G, strays on vegetation, coconut grove. LNO(3), nesting in rotting branch and foraging on ground, advanced secondary forest. MAL, strays on foliage. MTU(5), foraging on vegetation near road. V(6), nesting under bark of rotting logs and stumps, old field.

This highly successful pantropical tramp species occurs throughout Polynesia. It nests in a wide variety of disturbed and native habitats and often invades human dwellings. The colonies are very vagile and typically contain multiple queens.

Tapinoma minutum Mayr

FUTUNA: LU, nesting in rotting stump, coconut grove. N(2), nesting in rotting tree stump and in rotting twig (2.5 cm diameter) lying on ground, overgrown coconut grove. UVÉA: AK, foraging workers on banana stem, native garden.

T. minutum is widely distributed through most of the Indo-Australian area, reaching as far east as Samoa.

Anoplolepis longipes (Jerdon)

FUTUNA: CVM(2), nesting in tree trunk, foraging on surface of rotting log, secondary forest. LU(3), nesting in rotting stumps and logs, foraging on vegetation and ground, coconut grove; one of the most abundant and widely foraging ant species at this locality. L-LU, foraging workers dominant everywhere on ground and vegetation. MO(10), 6 colonies nesting in dead wood of standing trees, workers foraging on the ground, on foliage and on tree trunks, dense secondary forest; the most abundant and widely foraging ant species at this locality. PN, strays on fallen tree trunk and on ground, secondary forest; relatively scarce at this locality. NUKUIFALA (4): numerous workers foraging on ground, vegetation, and tree trunks. NUKUIONE (6): workers foraging on ground, on rotting logs, and on vegetation; occurs in the fringing mangrove and is increasingly abundant inland; not as abundant overall as on Nukuifala. NUKU TAPU (4): nesting in rotting stumps, numerous workers foraging on ground, vegetation, and tree trunks in the mangrove and inland. UVÉA: AG(7), nesting in rotting stumps and logs, workers foraging on ground, vegetation, and dead trees, native garden; by far the most common ant species at this locality. AK, nesting in ground beneath palm stump, native plantation. G(4), nesting under stone and in rotten coconut shell on ground, workers foraging on ground and arboreally, coconut grove. MTU(4), workers abundant on ground and foliage in second-growth vegetation; probably the dominant ant at this locality. MHO(5), workers abundant on ground and vegetation, bracken "heath"; the most common ant species at this locality.

Anoplolepis longipes is a species of African origin that has spread through most of the Old World tropics by means of human commerce. From the data just presented, it is clear that in Futuna and the Wallis Islands it has a strikingly patchy distribution. Like certain other well-known tramp species, including *Pheidole megacephala* and *Iridomyrmex humilis*, it occupies only some of the localities accessible to it; but where it occurs, it is frequently the most abundant ant. Workers forage in (and appear to dominate) a surprisingly wide range of terrestrial and arboreal sites. Nests are built in a variety of major habitats as well, although the species prefers more vegetated areas. Hunt received the impression that on Futuna and Uvéa *A. longipes* occupied a range largely complementary in detail to that of the large ponerine *Odontomachus simillimus*, although no direct evidence of competitive replacement was obtained.

Paratrechina bourbonica (Forel)

FUTUNA: PN. NUKUIONE: workers foraging on mangrove trees. UVÉA: AK(2), colony nesting under fragment of palm tree, workers foraging on banana stem. MTU, stray workers from footpath in taro patch. (See comment below.)

The workers in 2 series listed above from Akaaka (acc. nos. 31, 38) and 1 from Mata-Utu (acc. no. 49) are actually intermediate in size (head width about 0.65 mm) and color between *P. bourbonica* and the closely similar *P. vaga*, raising the possibility that they are actually no more than large, dark *vaga*. Elsewhere in Polynesia, a small percentage of worker series are regularly indeterminate to either species (Wilson & Taylor 1966). More extensive collections, preferably with workers and ♂♂ associated, are needed to establish with certainty the presence of *bourbonica* on Uvéa.

P. bourbonica is an Indo-Australian species that has been spread by human commerce throughout the tropics.

Paratrechina longicornis (Latreille)

UVÉA: LAL(3), common, foraging in columns on tree trunks and forest floor, mature forest. MAL, workers foraging on ground and stone wall in front of medical dispensary. MTU(2), workers foraging on ground and dead tree in taro patch. V, workers foraging on floor of native house in village.

This Indo-Australian species has been spread throughout the warmer parts of the world by human commerce. It is even common in greenhouses in the temperate zones. In the tropics it occurs most commonly around human habitations, although occasionally colonies penetrate native forests such as the one at Lalolalo.

Paratrechina vaga (Forel)

FUTUNA: CVM(2), strays in rotting log and on foliage, secondary forest. L, strays on stone wall around garden. LU(3), 2 colonies nesting in rotting tree trunks, strays under stone, coconut grove. L–LU(3), nest in rotting logs, secondary forest. MO(3), nest in rotting branch 2.5 cm thick on ground, strays from vegetation and leaf litter, dense secondary forest, queens with workers 18.III. N(3), nesting in rotten coconut hull and strays on ground, coconut grove; strays on ground in banana-taro patch on steep hillside. PN(3), nesting in rotting logs, secondary forest. T(2), attending aphids and foraging on foliage in coconut grove. VMP(7), strays on vegetation in bracken heath; nesting in rotting log, and in small stick and curled dead leaf in leaf litter, workers foraging under moss and on surface of tree trunk and on vegetation, mature forest. VVR. NUKUIFALA (6): colonies nesting in dead palm stump and in dead hollow twig 10 mm in diameter, workers foraging on ground and foliage. NUKUIONE (2): on vegetation in mangrove and interior of island. NUKU TAPU. UVÉA: AK, stray on vegetation next to path. G, strays on low vegetation, coconut grove. LAL(6), nesting in rotting log and rotting twig in leaf litter, workers foraging on ground, beneath log, and on low vegetation, mature forest. LNO, stray workers on ground, advanced secondary forest. MAL, stray workers from tree trunk. MHO(4), 3 colonies nesting in small rotting branches (2.5–3 cm) in leaf litter, strays on ground, mature mango forest. V(2), nest in rotting coconut husk, old field; strays foraging on ground.

P. vaga is an Indo-Australian species that has become established, probably through human commerce, throughout almost all of Polynesia. It is clearly the most widespread and adaptable ant species in Futuna and the Wallis Islands. It is also often very abundant locally.

Camponotus chloroticus Emery

FUTUNA: L, ♂♂ only, 7.III. MO, nest in rotting tree branch on floor of secondary forest. N(3), nesting in rotting stump at edge of native plantation; ♂♂ and winged queens with workers 5-7.III. T, workers in company with aphids on lower leaf surface, shrubby vegetation in coconut grove. VMP (3), nesting in pieces of rotting wood and in rotting log, mature forest; ♂♂ with workers 9.III. TEKAVIKI: incipient colony, containing a single dealate queen and several minor workers, nesting in rotting branch stump of living tree. A careful search of the entire islet revealed only this single colony. UVÉA: LAL (2), incipient colony in knothole of rotting log, larger colony in rotting log, mature native forest. MTU(2), nesting in piece of rotting wood buried in soil and in dead branch on living tree, cultivated area; ♂♂ and winged queens with workers 25-27.II. MHO(3), incipient nest under bark of 5-cm-wide rotting wood fragment on ground, larger colony in rotting stump, dense mango grove. V(3), 3 colonies nesting in rotting stumps.

This species ranges, probably as a native, from Melanesia east as far as Tonga and the Danger Is.

Camponotus reticulatus Roger

NUKUIFALA (2): nesting in rotting stump, workers foraging on foliage. NUKUIONE (2): workers were moderately common on foliage in the outer portion of mangrove forest. Farther in and throughout interior of island, the species appeared to be replaced by *Anoplolepis longipes.* NUKU TAPU: foraging on and under mangroves. UVÉA: AG, workers foraging on flower heads in weedy vegetation next to native garden. LMA. LAL(2), workers on rotting log and low vegetation of mature forest. MTU(6), colonies nesting in rotting stump, workers foraging on ground and foliage in open area. MHO(4), strays on vegetation in second growth next to mango grove, on floor and low vegetation of mango grove. V(8), 7 nests in rotting stump in old field; ♂♂ and winged queen with workers 27.III.

This Melanesian species was previously known only from as far east as the Solomon Is. However its above-average dispersal powers were already indicated by the fact that it is among the most common ant species on Rennell Island, the most isolated member of the Solomon group. The absence of *reticulatus* from Futuna suggests that the Wallis Is. were colonized by a single, rare invasion by propagules that missed surrounding islands. This hypothesis is strengthened by the existence of the endemic *C. rotumanus* Wilson & Taylor on Rotuma, a species related to *reticulatus* and possibly even derived from it by another, earlier invasion.

In the Wallis Is., *reticulatus* behaves much as it does on Rennell. Where it occurs it tends to be abundant, occupying a wide range of native and disturbed habitats. It differs from the other species of *Camponotus* on the Wallis Islands, *C. chloroticus,* in an interesting and possibly significant way. During the day, when our collections were made, the workers ranged far from their nests in rotting stumps and logs to forage on the ground and foliage. At the same time *chloroticus* workers were distinctly more confined to the nest area. Very likely the latter forage nocturnally.

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