

## ADAPTIVE SHIFT AND DISPERSAL IN A TROPICAL ANT FAUNA

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### INTRODUCTION

The tropics have long been recognized as the site of maximum evolutionary activity on land. In tropical rain forests, evolution proceeds simultaneously in the largest number of species. A growing amount of evidence of diverse kinds also points to the rain forests, particularly those of continents and the large islands, as the "center" of evolution of a majority of major animal and plant groups, where these groups have diversified maximally in various stages of their phyletic history and out of which they have tended to spread into adjacent temperate and arid regions (Richards, 1952; Darlington, 1957).

According to the theory stressed by Darlington it is the Old World tropics specifically that form the principal evolutionary center of the vertebrates. Successful groups, achieving "general adaptation," send emigrant species out of the Old World tropics into temperate zones, where they may diversify secondarily and in time come to show zonation and radial dispersal of their own. From time to time faunal drift occurs across the region of the present-day Bering Straits. Movement across this barrier has been predominantly out of the Old World into the New. Once emigrant species reach the New World, further diversification may take place; this becomes especially probable if members of the group succeed in penetrating the Neotropical forests.

The nature of general adaptation and the dispersal mechanisms underlying major biotic movement is clearly one of the great problems of modern evolutionary theory. It appears that our knowledge has now reached the stage where finer analyses of these causal processes can and

should be undertaken. There is a need for a "biogeography of the species," oriented with respect to the broad background of biogeographic theory but drawn at the species level and correlated with studies on ecology, speciation, and genetics. In the present paper one such analysis is attempted in very preliminary form, dealing with the ponerine ants<sup>1</sup> of Melanesia. This fauna is unusually suitable for a study of the kind proposed. Melanesia, including New Guinea, has proven to be a peripheral or "recipient" zoogeographic and for ants, i.e., most of the present fauna has been derived ultimately from immigrations from southeastern Asia and Australia, while proportionately few Melanesian-centered groups have emigrated into these adjacent source areas. Hence dominant, successful groups can conceivably be distinguished in their early stages of expansion as they first enter Melanesia, and older resident elements can be studied to piece together details of the later history of invading groups. Theoretically, it should then be possible to characterize the early invading groups ecologically and to infer some of the attributes that have contributed to their successful dispersal, in short, the "attributes of success" associated with general adaptation.

### PATTERNS OF SPECIATION

Taxonomic analysis of the Melanesian ponerine fauna has revealed a remarkably

<sup>1</sup> The subfamily Ponerinae is one of eight subfamilies of ants (Formicidae) known from Melanesia. The species known constitute approximately one-fifth of the described ant fauna. Revisionary work on the Melanesian ants has been conducted at Harvard University during the past three years and is now virtually complete (Wilson, 1957 et seq.; Brown, 1958; Willey and Brown, ms.).

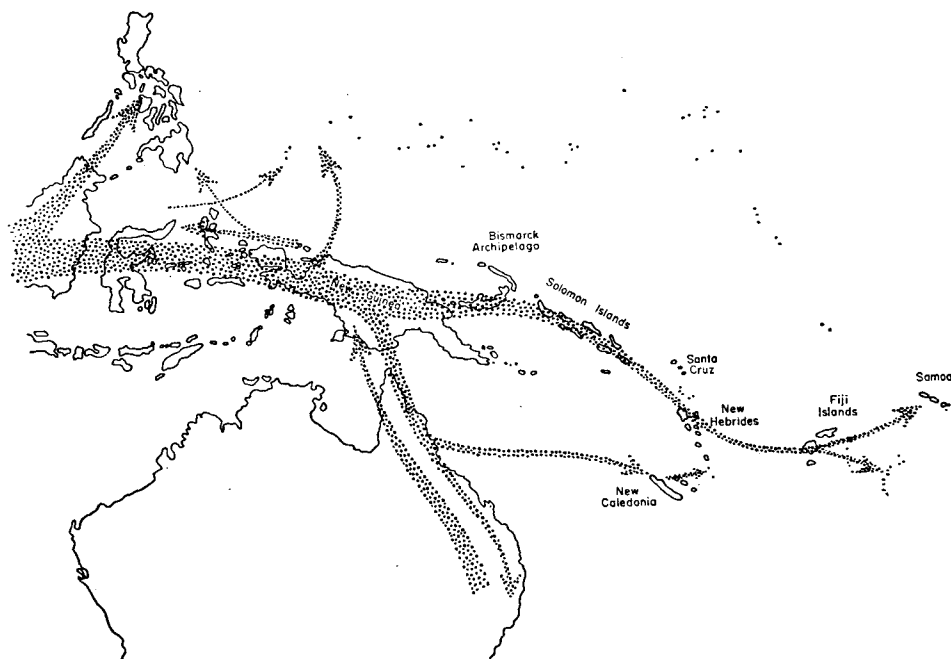


FIG. 1. Routes of dispersal in and out of Melanesia followed by the ponerine ants.

consistent order of zoogeographic patterns. These are summarized in the sections below.

(1) Most groups seem to invade New Guinea from southeastern Asia. Many of these also reach tropical Queensland, and a substantial part of the Queensland fauna is thus composed of Oriental stocks held in common with New Guinea. A few old Australian groups, lacking any apparent affinity with the Oriental fauna, also invade New Guinea. Occasionally, endemic Papuan groups move back in the direction of southeastern Asia but rarely if ever reach beyond the Moluccas and Philippines (fig. 1).

(2) From New Guinea a fraction of the invading stocks presses on to outer Melanesia. An ever-diminishing number reaches the Bismarck Archipelago, Solomon Islands, New Hebrides, and Fiji Islands. Progress along this route follows the classical "filter" effect that applies generally to the faunas of archipelagic chains with permanent water gaps. Some secondary radiation occurs in the various

island groups, especially the Fiji Islands, but there is at present no concrete evidence indicating any reverse movement of these precinctive species back toward New Guinea (fig. 1, table 1).

(3) Because radiation has been more extensive on the Fiji Islands, the fauna of this archipelago appears to be larger than that of the adjacent New Hebrides. However, this is true only in the sense that the total number of known species is larger. When species groups are counted instead of species, the fauna of the New Hebrides proves to be somewhat the larger. Since the number of species groups corresponds more closely to the actual number of original immigrant species, this estimate is to be considered a truer measure of relative accessibility of archipelagos to the mainland fauna (fig. 11, table 1).

(4) New Caledonia is faunistically very distinct from the remainder of Melanesia. Despite its proximity to the New Hebrides and Fiji Islands, it does not appear to have received any of its ponerine fauna

TABLE 1. List of the species of *Ponerinae* known from Melanesia, broken into species groups. Roman numerals after the names indicate evolutionary classification; lower case letters (a-f) indicate ecological distribution on New Guinea alone, referring specifically to the major habitats given in figure 9. Further explanation in text.

New Guinea	Bismarcks	Solomons	N. Hebrides	Fijis	Samoa
<i>Amblyopone australis</i> (I, f)		<i>A. australis</i> (I) <i>A. celata</i> (III)	<i>A. australis</i> (I)		
<i>Myopopone castanea</i> (I, ef)	<i>M. castanea</i> (I)	<i>M. castanea</i> (I)			
<i>Mystrium camillae</i> (I)					
<i>Prionopella majuscula</i> (III)	<i>P. majuscula</i> (III)				
<i>P. opaca</i> (? II, ef)					
<i>Platythyrea parallela</i> (I, cdf)	<i>P. parallela</i> (I)	<i>P. parallela</i> (I)			<i>P. parallela</i> (I)
<i>P. quadridentata</i> (II)					
<i>Rhytidoponera araneoides</i> (I, bc)	<i>R. araneoides</i> (I)	<i>R. araneoides</i> (I)			
<i>R. cellinodis</i> (III)					
<i>R. inops</i> (II, def)					
<i>R. gagates</i> (III)	<i>R. nexa</i> (III)				
<i>R. nexa</i> (III)					
<i>R. purpurea</i> (II, f)					
<i>R. abdominalis</i> (III, f)					
<i>R. aenescens</i> (III)					
<i>R. laciniosa</i> (III, ef)					
<i>R. rotundiceps</i> (III, f)					
<i>R. strigosa</i> (III, ef)					
<i>R. subcyanea</i> (III, e)					
<i>Gnamptogenys biroi</i> (II, f)					
<i>G. grammodes</i> (II, f)					
<i>G. macreles</i> (II, f)					
<i>G. major</i> (II, f)					
<i>G. cribrata</i> (II, e)		<i>G. malaensis</i> (II)			
<i>G. epinotalis</i> (II, f)		<i>G. albiclava</i> (III)			
		<i>G. crenaticeps</i> (III)		<i>G. aterrima</i> (III)	
		<i>G. lucida</i> (III)			
<i>Proceratium papuanum</i> (II, f)				<i>P. relictum</i> (III)	
<i>Discothyrea clavicornis</i> (II, f)		<i>D. clavicornis</i> (II)			
<i>Ponera biroi</i> (III, ef)					
<i>P. macradelphe</i> (III, f)	<i>P. biroi</i> (III)	<i>P. biroi</i> (III)		<i>P. eutrepta</i> (III)	
<i>P. punctiventris</i> (III, f)		<i>P. sororcula</i> (III)		<i>P. turaga</i> (III)	
<i>P. sororcula</i> (III, cd)					
<i>P. confinis</i> (I, ef)	<i>P. confinis</i>	<i>P. confinis</i>	<i>P. confinis</i>		
<i>P. pallidula</i> (II, ef)	(I)	(I)	(I)		

TABLE 1—Continued

New Guinea	Bismarcks	Solomons	N. Hebrides	Fijis	Samoa
<i>P. papuana</i> (III)					
<i>P. pruinosa</i> (I, cdef)		<i>P. pruinosa</i> (I)	<i>P. pruinosa</i> (I)	<i>P. monticola</i> (III)	
<i>P. sabronae</i> (III, f)				<i>P. vitiensis</i> (III)	
<i>P. clavicornis</i> (I, def)					
<i>P. elegantula</i> (III, f)					
<i>P. selenophora</i> (III, e)		<i>P. clavicornis</i> (I)	<i>P. clavicornis</i> (I)	<i>P. colaensis</i> (III)	
<i>P. syscena</i> (III, f)					
<i>P. xenagos</i> (III, f)		<i>P. gleadowi</i> (I)			<i>P. gleadowi</i> (I)
<i>P. tenella</i> (III, f)					
<i>P. huonica</i> (III, f)					
<i>P. petila</i> (III, e)					
<i>P. szabo</i> (III, e)	<i>P. ratardorum</i> (III)	<i>P. ratardorum</i> (III)	<i>P. ratardorum</i> (III)		
<i>P. szentivanyi</i> (III, e)					
<i>P. tenuis</i> (III, f)					
<i>Brachyponera</i> <i>arcuata</i> (I)		<i>B. croceicornis</i> (I)			
<i>B. croceicornis</i> (I, cdef)					
<i>Mesoponera manni</i> (I, f)		<i>M. manni</i> (I)			
<i>M. papuana</i> (II, e)					
<i>Trachymesopus</i> <i>crassicornis</i> (III, f)		<i>T. crassicornis</i> (III)			
		<i>T. sheldoni</i> (III)			
<i>T. darwini</i> (I)		<i>T. darwini</i> (I)	<i>T. darwini</i> (I)		
<i>T. stigma</i> (I, cdef)	<i>T. stigma</i> (I)	<i>T. stigma</i> (I)	<i>T. stigma</i> (I)	<i>T. stigma</i> (I)	<i>T. stigma</i> (I)
<i>Ectomomyrmex</i> <i>aciculatus</i> (II, e)		<i>E. acutus</i> (II)			
<i>E. acutus</i> (II)	<i>E. acutus</i> (II)	<i>E. aequalis</i> (II)			
<i>E. exaratus</i> (II, e)					
<i>E. scobinus</i> (II, e)					
<i>E. simillimus</i> (II, e)					
<i>E. striatulus</i> (II, ef)					<i>E. insulanus</i> (II)
<i>Bothroponera</i> <i>incisus</i> (?)					
<i>B. obesus</i> (?)					
<i>Cryptopone butteli</i> (I, ef)	<i>C. butteli</i> (I)				
<i>C. fusciceps</i> (II, ef)		<i>C. fusciceps</i> (II)			
<i>C. testacea</i> (I, e)		<i>C. testacea</i> (I)			
<i>C. motschulskyi</i> (III, def)					
<i>Diacamma rugosum</i> (I, cdef)					

TABLE 1—Continued

New Guinea	Bismarcks	Solomons	N. Hebrides	Fijis	Samoa
<i>Myopias cribriceps</i> (III, e)					
<i>M. della</i> (III, e)					
<i>M. concava</i> (III, ef)					
<i>M. foveolata</i> (III)					
<i>M. gigas</i> (III, e)					
<i>M. julivora</i> (III, e)					
<i>M. levigata</i> (III, f)					
<i>M. lorlai</i> (III, f)					
<i>M. media</i> (III, f)					
<i>M. ruthae</i> (III, e)					
<i>M. xiphias</i> (III)					
<i>M. latinoda</i> (II, f)					
<i>M. tenuis</i> (?III, cdef)					
<i>M. tyllion</i> (?III, ef)					
<i>Leptogenys</i>					
<i>bituberculata</i> (II, ef)				<i>L. foveopunc-</i> <i>tata</i> (II)	
<i>L. drepanon</i> (II)			<i>L. hebrideana</i> (II)	<i>L. fugax</i> (II)	
<i>L. indagatrix</i> (II, f)				<i>L. humiliata</i> (II)	
<i>L. papuana</i> (II)				<i>L. letilae</i> (II)	
<i>L. triloba</i> (III, f)				<i>L. navua</i> (II)	
				<i>L. vitiensis</i> (II)	
<i>L. breviceps</i> (II, ef)					
<i>L. caeciliae</i> (III, f)					
<i>L. optica</i> (III, ef)					
<i>L. diminuta</i> (I, cdef)	<i>L. diminuta</i> (I)	<i>L. diminuta</i> (I)			
<i>L. nilens</i> (II)		<i>L. oresbia</i> (II)			
<i>L. purpurea</i> (II, f)		<i>L. foreli</i> (I)	<i>L. foreli</i> (I)		
<i>L. foreli</i> (I)	<i>L. emeryi</i> (III)	<i>L. truncata</i> (III)			
<i>L. keysseri</i> (III, f)					
<i>Odontomachus</i>					
<i>latissimus</i> (II)					
<i>O. liniae</i> (II, f)					
<i>O. malignus</i> (I, a)					
<i>O. imperator</i> (II)		<i>O. emeryi</i> (II)			
<i>O. montanus</i> (II)	<i>O. malignus</i> (I)	<i>O. malignus</i> (I)		<i>O. angulatus</i> (II)	
<i>O. opaculus</i> (II, f)					
<i>O. papuanus</i> (I, ef)					
<i>O. rufithorax</i> (II)					
<i>O. saevissimus</i> (I)					
<i>O. tauerni</i> (II)					
<i>O. aciculatus</i> (III)					
<i>O. aeneus</i> (III)	<i>O. simillimus</i> (I)	<i>O. simillimus</i> (I)	<i>O. simillimus</i> (I)	<i>O. simillimus</i> (I)	<i>O. simillimus</i> (I)
<i>O. cephalotes</i> (I, ef)					
<i>O. simillimus</i> (I, bcd)					
<i>O. nigriceps</i> (III, e)					
<i>O. testaceus</i> (III, ef)	<i>O. tyrannicus</i> (III)				
<i>O. tyrannicus</i> (III, f)					
<i>Anochetus cato</i> (III, f)	<i>A. cato</i> (III)	<i>A. cato</i> (III) <i>A. isolatus</i> (III)			

TABLE 1—*Continued*

New Guinea	Bismarcks	Solomons	N. Hebrides	Fijis	Samoa
<i>A. chirichinii</i> (III, ce)					
<i>A. fricatus</i> (III, e)					
<i>A. graeffei</i> (I, d)	<i>A. graeffei</i> (I)	<i>A. graeffei</i> (I)	<i>A. graeffei</i> (I)	<i>A. graeffei</i> (I)	<i>A. graeffei</i> (I)
<i>A. variegatus</i> (III)					
<i>A. vesperus</i> (III, d)					

from these islands. Rather, all endemic stocks appear to have come from tropical or subtropical Australia. This is true even in the cases of Oriental groups found both on New Caledonia and elsewhere in Melanesia; the New Caledonian species are in each instance most closely related to eastern Australian representatives of the invading Oriental group. Thus Oriental groups reaching New Caledonia, of which there are a goodly number, appear to have entered by way of eastern Australia. One species (*Amblyopone australis*) has spread from New Caledonia to the southern New Hebrides, thus providing a slender link between these two segments of the Melanesian fauna. The New Caledonian endemics show nearly every conceivable degree of evolutionary divergence from the cognate Australian species, from a clearly conspecific condition to a highly modified form approaching a distinct generic level (figs. 1, 4, 5, 6).

(5) Individual ponerine species and species-groups in Melanesia seem to show various steps in a sequence of expansion, diversification, and contraction. In fact, when the distributions and phylogenetic positions of all of the species are considered as a whole, the conclusion is almost inescapable that such a process is nearly universal in this group of ants. The steps are illustrated by the actual distributions of species shown in figures 2–8. These examples are admittedly selected, and the evolutionary history they are supposed to follow hypothetical. Yet virtually all of the patterns of the species groups fit somewhere within this unilat-

eral zoogeographic classification, and the evolutionary interpretation proposed seems to be the most reasonable and simple one within the limits of the existing evidence. Three classes of species can be distinguished, each representing a major step in the historical sequence.

*Stage-I species.* These are the species apparently in the process of expansion, either from southeastern Asia or Australia into Melanesia, or out of Melanesia back into the primary source areas, or out of New Guinea through most of the remainder of Melanesia. Thus two categories of Stage-I species are hypothesized: *primary*, including Oriental- or Australian-based species invading Melanesia (as well as Oriental-based species invading New Guinea and then Australia by way of New Guinea); and *secondary*, including Papuan species that are pushing well out into outer Melanesia or invading southeastern Asia or Australia. Stage-I species generally have continuous ranges and show little geographic variation, although non-geographic variation may be considerable (fig. 2).

*Stage-II species.* These are species which have differentiated to species level in Melanesia, i.e., are Melanesian precinctives, but which belong to species groups centered outside Melanesia, either in southeastern Asia or Australia. They represent stocks which are relatively recent invaders but which have been resident sufficiently long to diverge to species level (Figs. 3, 4).

*Stage-III species.* These are Melanesian precinctives belonging to Melanesian-centered species groups. That such

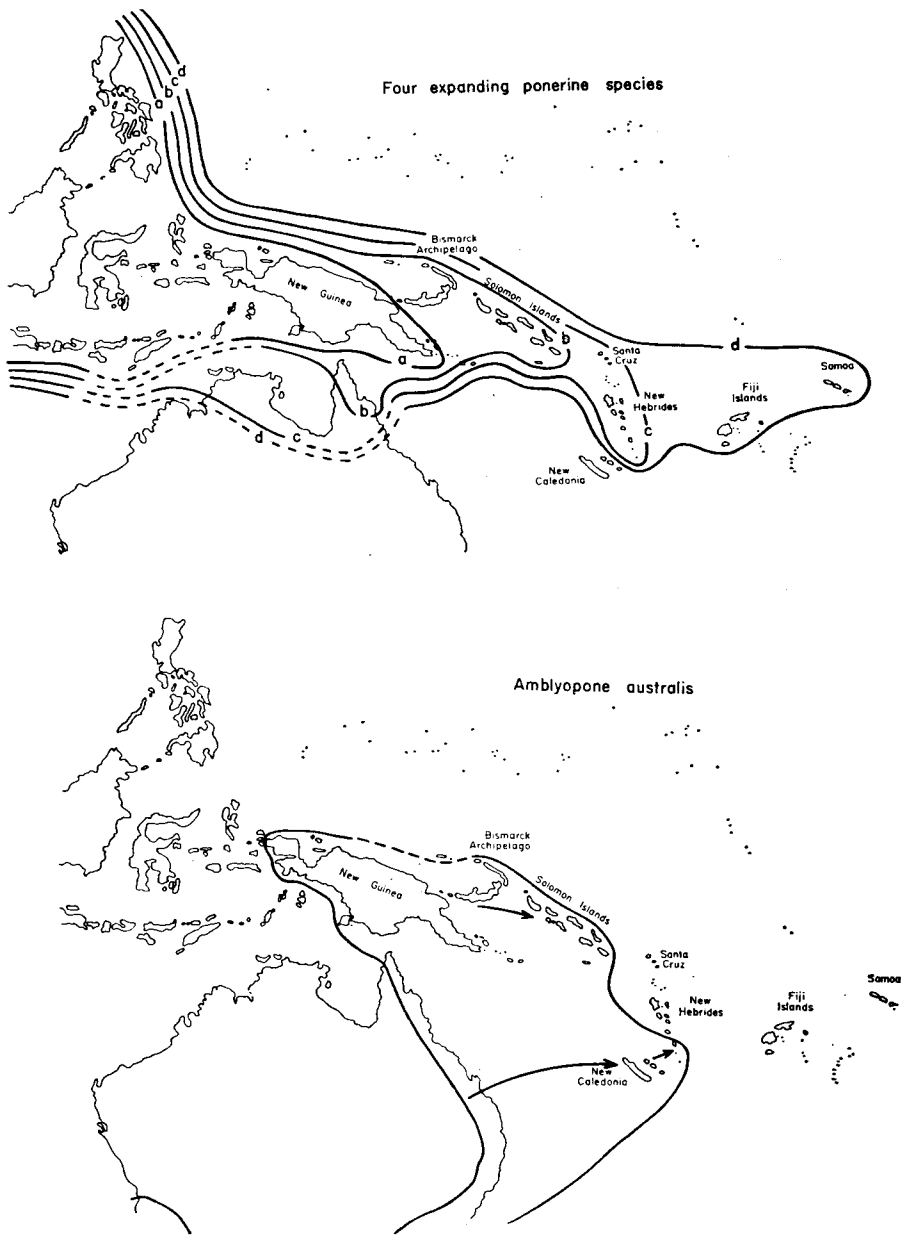


FIG. 2. Maximum known distributions of several Stage-I ponerine species. Upper: four unrelated species believed to represent successive stages of invasion from Asia; a, *Diacamma rugosum*; b, *Myopopone castanea*; c, *Trachymesopus darwini*; d, *T. stigma*. Lower: the range of *Amblyopone australis*, which has entered Melanesia from Australia in two places; a double entry is inferred from the fact that the Papuan-Solomons and New Caledonian-New Hebridean populations are marked by opposing trends in geographic variation.

In this and subsequent distribution maps the following qualifications should be noted. The precise limits of the species ranges in the Philippines, lesser Sundas, and lesser island groups such as the Louisiade and Manus Archipelagos are unknown. Dashed lines indi-

groups are ultimately Oriental or Australian in origin is suggested by the fact that groups in stages intermediate between II and III exist (e.g., groups of *Ponera selenophora* and *P. tenuis*). These have a few members with relict distributions outside of Melanesia that appear (within the framework of the present hypothesis) to be the last remnants of a contracting central (Asian or Australian) fauna (figs. 5-8).

Most Stage-III species have sufficient potency to continue diversifying, and some are able to expand out of Melanesia again, thus secondarily achieving Stage-I status (figs. 6, 7, 8, 12). Eventually, however, they probably enter upon a phase of irrevocable recession, their ranges contracting more and more until they can properly be labeled "relict" species (fig. 8). Presumably the next and final step for most is extinction, or extreme specialization, perhaps hastened by the inroads of freshly competing Stage-I and Stage-II species.

#### ECOLOGICAL ATTRIBUTES OF THE EXPANDING (STAGE-I) SPECIES

Using the zoogeographic criteria outlined in the preceding section, it is now possible to make a qualified distinction of those species that are in the early stages of expansion in or out of Melanesia. In the great majority of cases these belong to "dominant" Oriental- or Australian-centered species groups, i.e., groups that are relatively abundant, widespread, and diversified in the source areas. When ecological data gathered by the author during recent field work in New Guinea was analyzed, it was shown that Stage-I species in this area are characterized by (1) a proportionately greater concentra-

tion in marginal habitats, marginal in this case being defined specifically as open lowland forest, grassland, and littoral<sup>2</sup> (table 2, fig. 9) and (2) a greater ecological amplitude (table 3, fig. 10). Further, when the composition of the Melanesian fauna is broken down according to successive archipelagos, it was shown that a significantly larger proportion of Stage-I species occupies central Melanesia than is the case in New Guinea and the Fiji Islands (table 4, fig. 11). The evolutionary implications of these interesting correlations will now be considered.

#### DISCUSSION

If the zoogeographic sequence postulated here is correct, it seems to lead to the conclusion that ponerine species invade New Guinea, and outer Melanesia through New Guinea, by way of the relatively sparsely populated marginal habitats. When occasional Melanesian-based species succeed in expanding out of New Guinea into the Philippines or Australia, they apparently leave by the same adaptive route. This ecological attribute is the most significant one evident within the limits of the existing data.

It should be mentioned that there does not seem to be any other peculiarity in mode of dispersal or nest-site preference in Stage-I species that can account for their current expansion. These species include *Diacamma rugosum* and *Leptogenys foreli*, which have wingless queens, as well as many species that are presumed

<sup>2</sup> The central habitats are the "inner" rain forest, including denser lowland forest and montane (mid mountain) forest up to approximately 1000 meters elevation. Marginal habitats also have the smallest ponerine faunas in terms of absolute numbers of species.

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cate that the presence of the species anywhere in the island group under question is not known but believed likely. In most cases the precise limits of the ranges within larger archipelagos, such as the Solomon Islands and New Hebrides, are not known; where the entire archipelago is enclosed this can be taken certainly to mean only that the species occurs somewhere within the archipelago. Detailed locality data can be found in the revisionary basis of this article published elsewhere and cited in the bibliography.



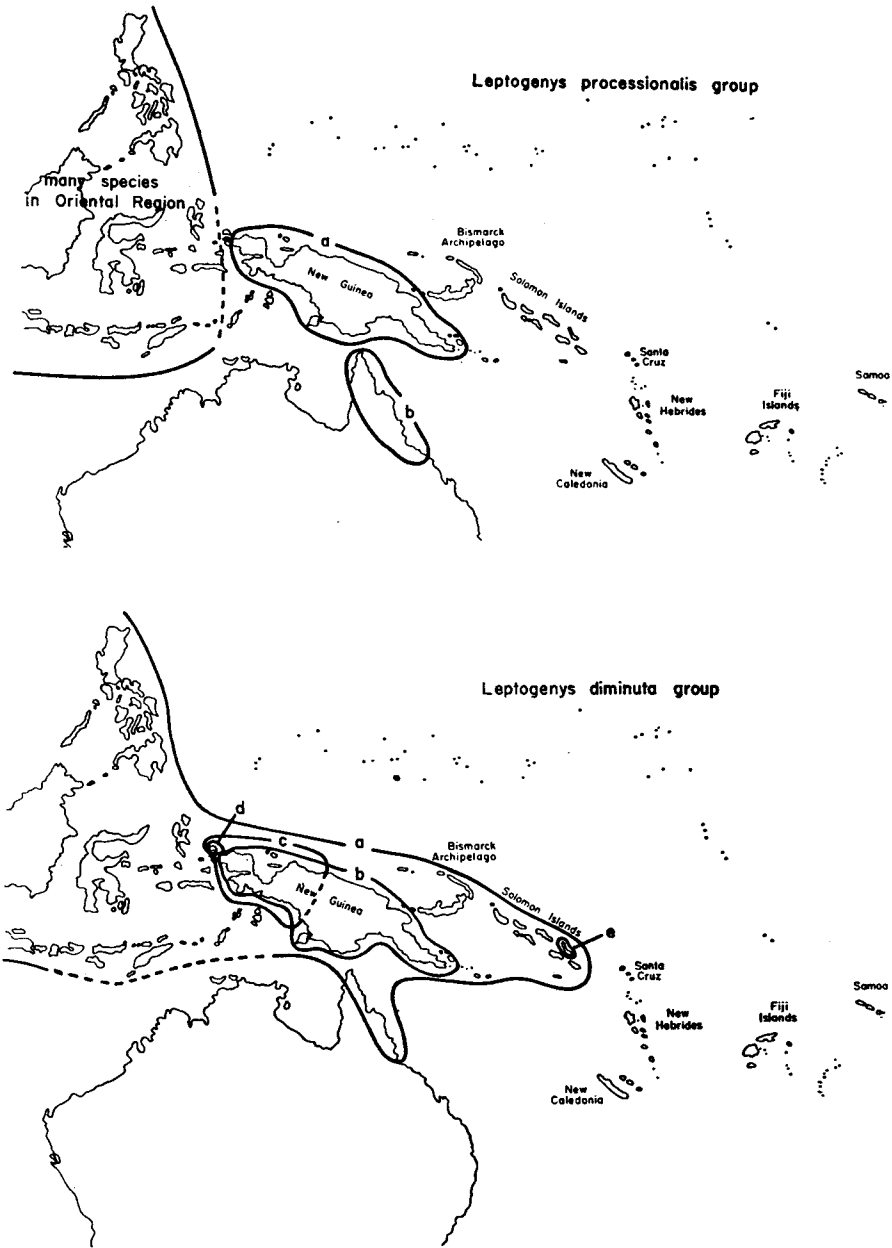


FIG. 3. Maximum known distributions of species in early Stage II. Upper: *a*, *Leptogenys breviceps*; *b*, *L. fallax*. Lower: *a*, *L. diminuta*; *b*, *L. purpurea*; *c*, *L. nitens*; *d*, *L. violacea*; *e*, *L. oresbia*.

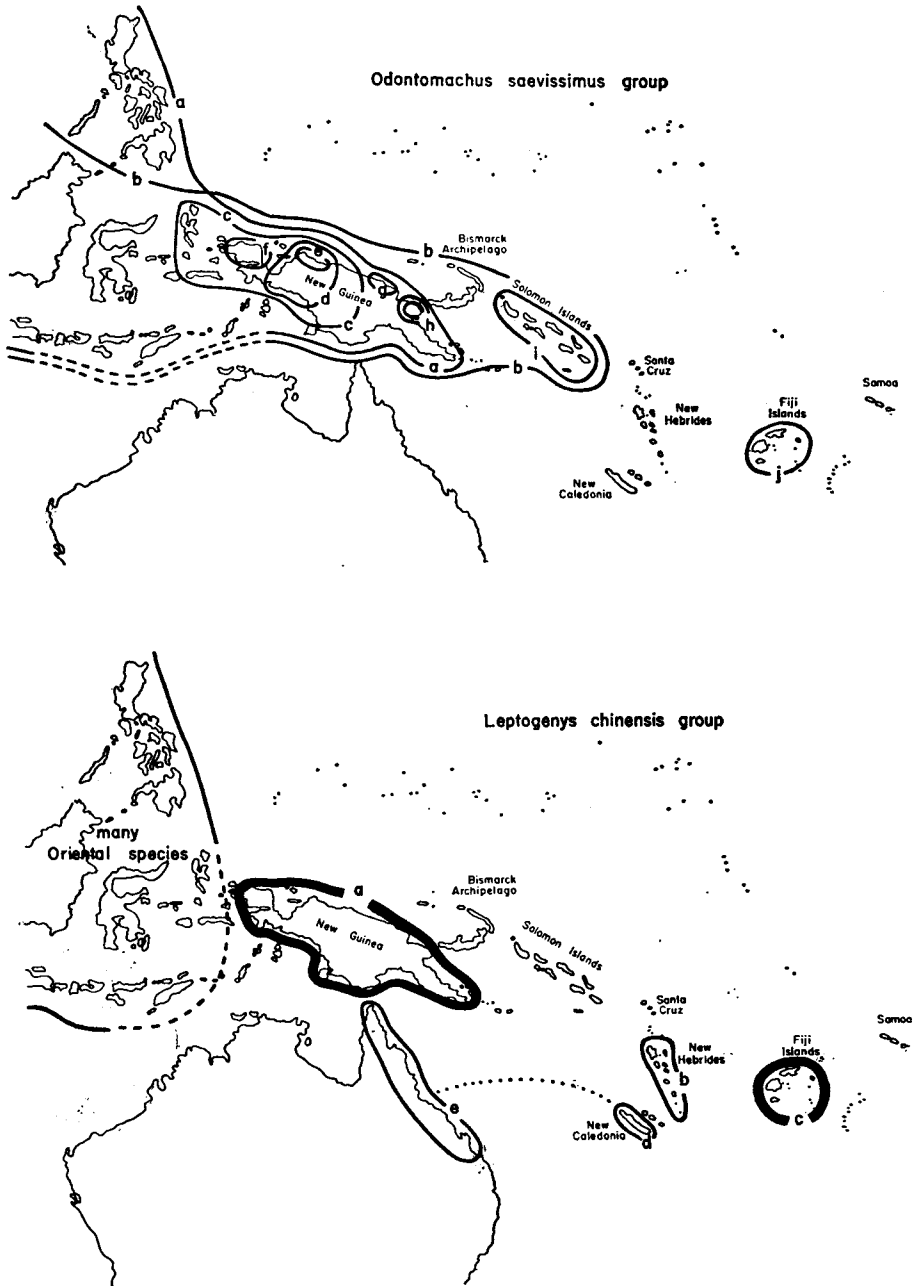


FIG. 4. Maximum known distribution of species in advanced Stage II. Upper: *a*, *Odontomachus rixosus*; *b*, *O. malignus*; *c*, *O. tauerni*; *d*, *O. rufithorax*; *e*, *O. lineae*; *f*, *O. imperator*; *g*, *O. opaculus*; *h*, *O. latissimus* and *O. montanus*; *i*, *O. emeryi*; *j*, *O. angulatus*. Lower: *a*, *Leptogenys bituberculata*; *L. drepanon*, *L. indagatrix*, *L. papuana*, *L. triloba* (the precise limits of these species on New Guinea is not indicated); *b*, *L. hebri-deana*; *c*, *L. foveopunctata*; *L. fugax*, *L. humiliata*, *L. letilae*, *L. navua*, *L. vitiensis*; *d*, *L. sagaris*; *e*, *L. anitae*. The dotted line suggests the close relationship of the New Caledonian *sagaris* and Australian *anitae*.

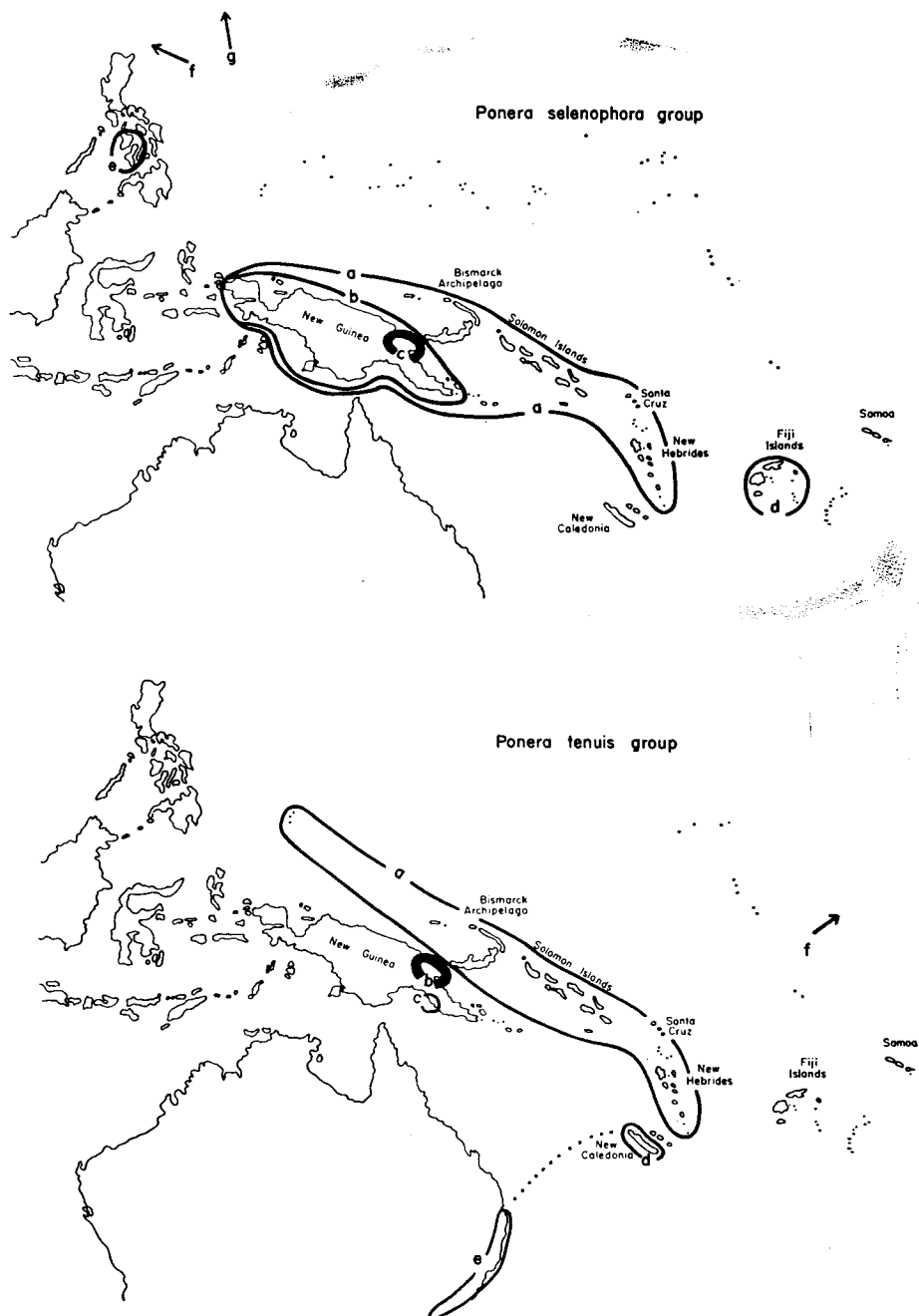


FIG. 5. Maximum known distribution of species in early Stage III, in which the Oriental source fauna has contracted and at present contains only a few relict species. Upper: a, *Ponera clavicornis* (ranked as a secondary Stage-I species); b, *P. selenophora*; c, *P. elegantula*, *P. syscena*, *P. xenagos*; d, *P. colaensis*; e, *P. oreas* (Philippines); f, *P. sinensis* (Hong Kong); g, *P. scabra* (Honshu). Lower: a, *P. ratardorum*, b, *P. huonica*, *P. petila*, *P. szaboi*, *P. tenuis*; c, *P. szentivanyi*; d, *P. caledonica*; e, *P. exedra* (Australia); f, *P. swezeyi* and *P. zwaluwenburgi* (Hawaii); g, *P. incerta* (Java). The dotted line suggests the close relationship between the New Caledonian *caledonica* and Australian *exedra*.

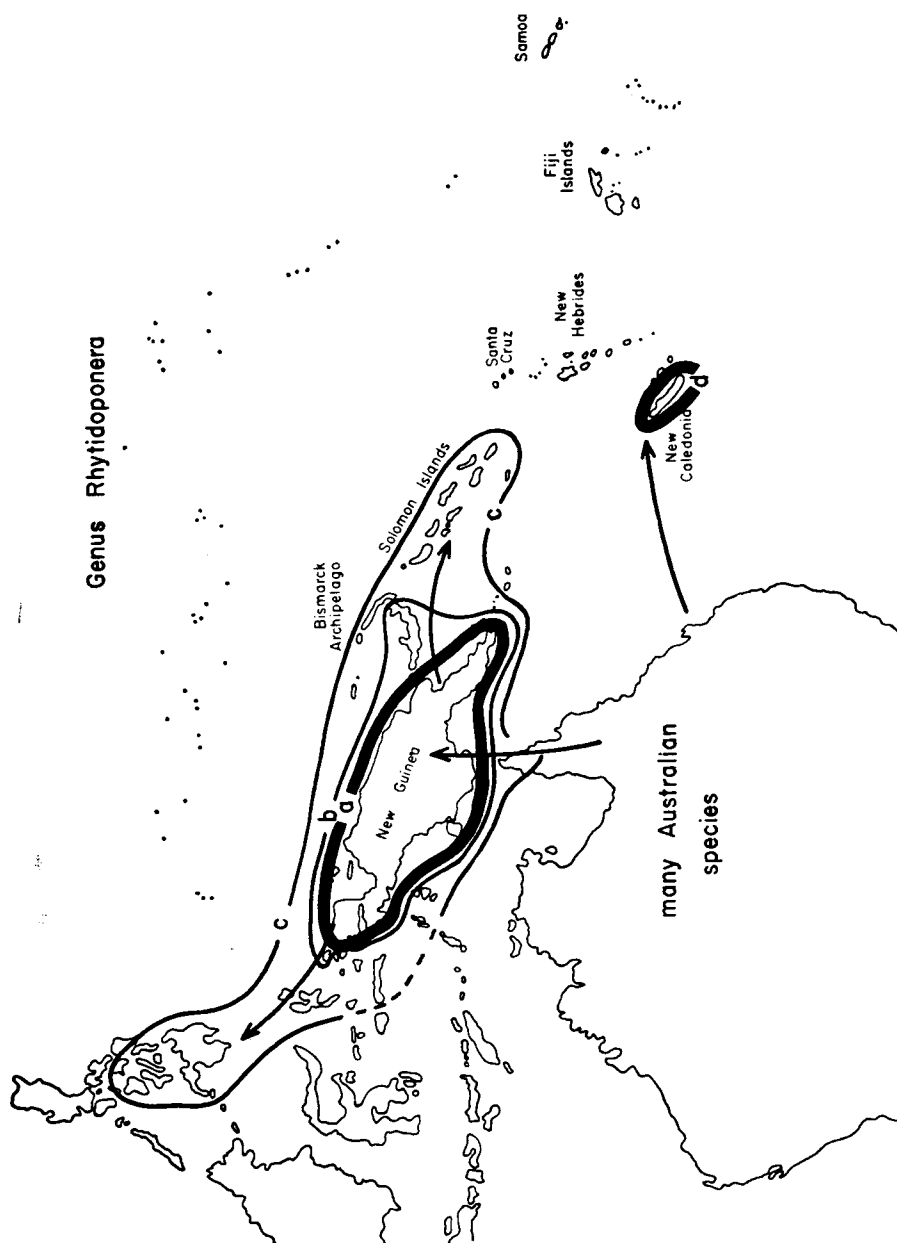


FIG. 6. The distribution of the genus *Rhytidoponera*, which is ultimately Australian in origin but which is differentiating and expanding secondarily out of New Guinea. Most of the Papuan species belong to Papuan-centered species groups and are classified in Stage III. *Rhytidoponera araneoides*, however, has expanded to the Philippines and Solomon Islands and is classified as Stage I (secondary). *a* represents the bulk of the Papuan species, which are confined to the New Guinea mainland; *b*, *R. nera*; *c*, *R. araneoides*; *d*, six endemic New Caledonian species, whose closest affinities are with Australian stocks.

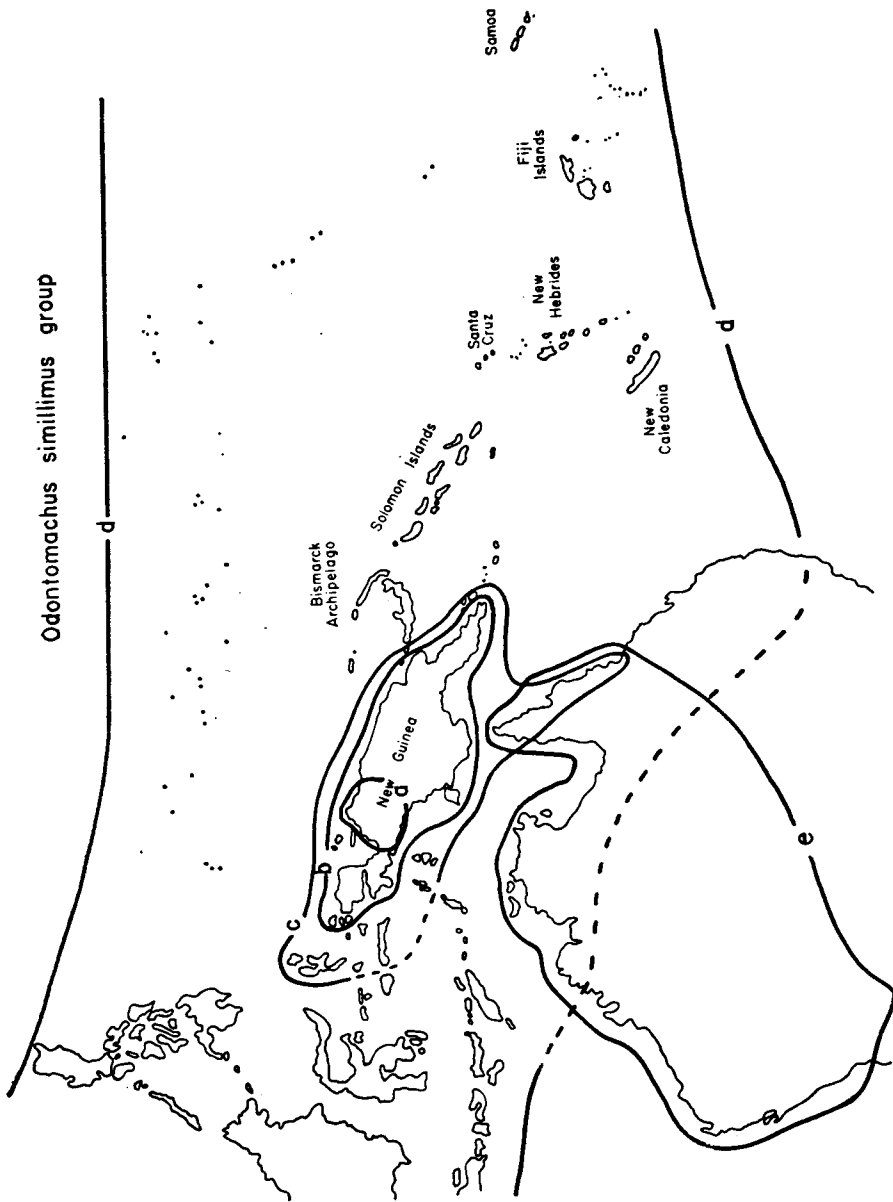


FIG. 7. Maximum known distributions of species of the *Odontomachus similimus* group. Classified variously in Stage I (secondary) or Stage III, depending on their present ranges. a, *O. aeneus*; b, *O. actulatus*; c, *O. cephalotes*; d, *O. similimus*; e, *O. ruficeps*. *O. similimus* (= *O. haematodus* auct.) ranges over most of the Pacific and has probably been transported through a large part of this area by man.

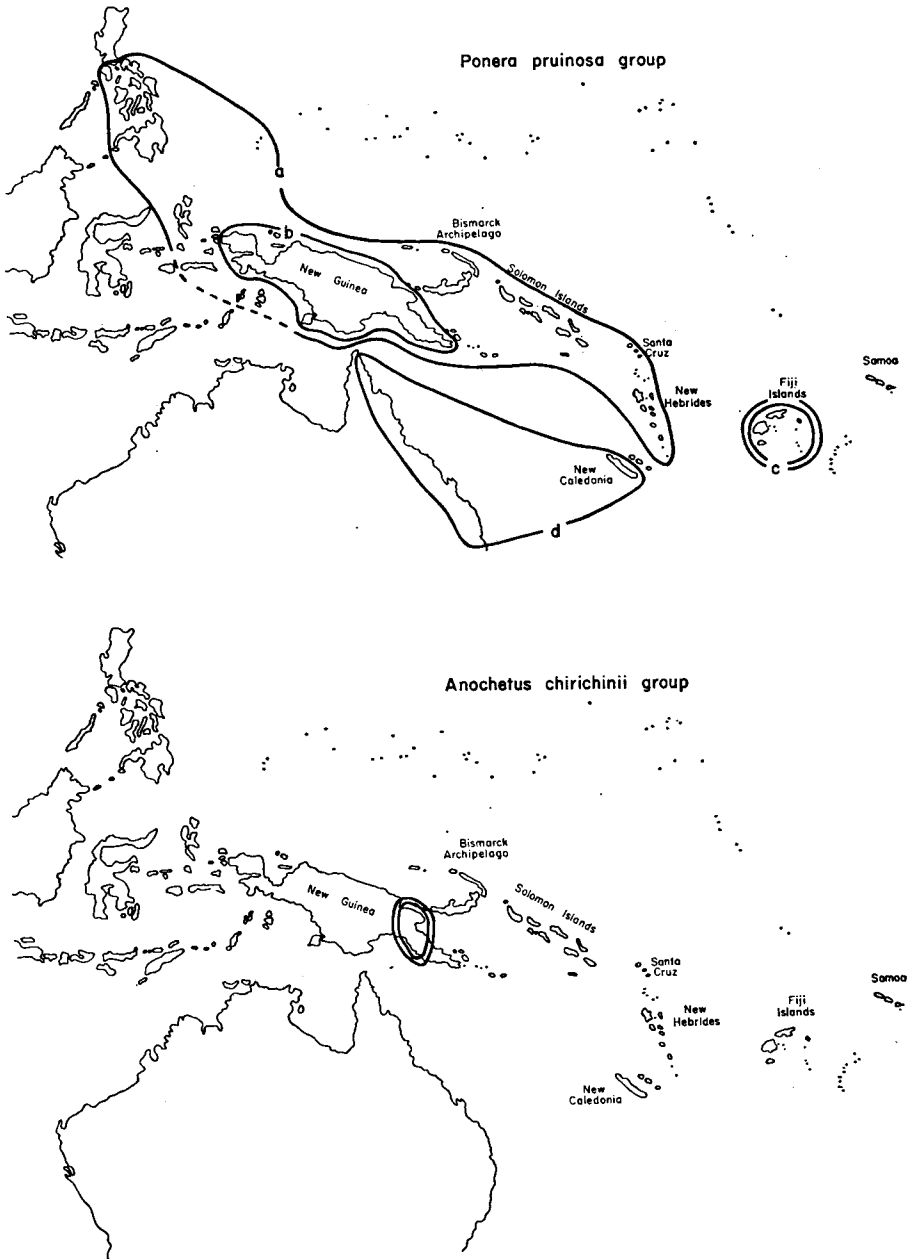


FIG. 8. Maximum known distributions of species in late Stage III. Upper: a, *Ponera pruinosa*; b, *P. sabronae*; c, *P. monticola* and *P. vitiensis*; d, *P. elliptica*. Lower: *Anochetus chirichinii* and *A. vesperus*. All of these species are classified in Stage III except *Ponera pruinosa*, which has expanded to outer Melanesia, the Philippines, and Palau. *P. elliptica* is not considered in the present analysis.

TABLE 2. *Partition by evolutionary stage of the Ponerine fauna in six major New Guinea habitats*

Habitat	Stage I	Stage II	Stage III	Total	$\chi^2$	P*
a. Littoral	1 (1.0)**	—	—	1	0	
b. Savanna	2 (1.0)	—	—	2	0.41	
c. Monsoon forest	8 (0.8)	—	2 (0.20)	10	0.81	
d. Lowland rain forest (marginal)	9 (0.69)	1 (0.08)	3 (0.23)	13		
e. Lowland rain forest (interior)	12 (0.27)	13 (0.29)	20 (0.44)	45	8.08	<0.02
f. Montane rain forest	15 (0.24)	20 (0.32)	27 (0.44)	62	0.17	

\* P indicates the probability that the evolutionary and ecological characteristics in two adjacent rows are independent. It is given here in the single instance where it is "significantly" small (<0.05).

\*\* Italicized numbers in parentheses are the proportions with respect to evolutionary stage.

to conduct normal nuptial flights.<sup>3</sup> Stage-I includes a larger proportion of species nesting in open soil and beneath stones, as opposed to rotten wood and trees, than

do Stages II and III, so that it is not easy to account for the greater dispersal of Stage-I species by means of a differential rate of "rafting."

<sup>3</sup> The existence of a normal nuptial flight is no guarantee of a relatively high potential dispersal rate, since the organization of the flight itself may be of such a nature as to limit greatly this rate. In the Nearctic myrmicine species *Pheidole sitarches*, mating takes place on the ground directly beneath the swarms of males, and the queen does not attempt to fly afterward, so that the species range can be advanced within a generation only over the distance by which the males are able to form their swarms (Wilson, 1958c). If similar behavioral phenomena occur in Indo-Australian species, they can presumably normally cross water gaps only if the gaps are less than the distance over which the swarms can be formed.

TABLE 3. *Partition by evolutionary stage of species occurring in various numbers of major habitats in New Guinea \**

Number of habitats occupied	Stage I	Stage II	Stage III	Total
1	5 (0.09)	19 (0.33)	33 (0.58)	57
2	6 (0.30)	6 (0.30)	8 (0.40)	20
3	2 (0.40)	2 (0.40)	1 (0.20)	5
4	6 (1.0)	—	—	6

\* On the basis of two classes, occupants of a single habitat vs. occupants of multiple (2, 3, 4) classes,  $\chi^2 = 16.62$  and  $P = 0.001$ .

TABLE 4. *Partition by evolutionary stage of the species comprising the Ponerine faunas of various of the Melanesian Archipelagos and Samoa*

Place	Stage I	Stage II	Stage III	Total	$\chi^2$	P
New Guinea Mainland*	24 (0.22)	35 (0.31)	53 (0.47)	112	10.52	0.005
Bismarck Archipelago**	10 (0.56)	1 (0.06)	7 (0.38)	18	1.67	
Solomon Islands**	18 (0.49)	7 (0.19)	12 (0.32)	37	3.83	
New Hebrides**	9 (0.82)	1 (0.09)	1 (0.09)	11	11.10	0.001–
Fiji Islands*	3 (0.18)	7 (0.41)	7 (0.41)	17		0.002
Samoa**	5 (0.83)	1 (0.17)	—	6	8.69	0.01–
						0.02

\* The New Guinea and Fijian faunas do not differ significantly from each other in proportionment by evolutionary stage;  $\chi^2$  is only 0.64.

\*\* The faunas of central Melanesia (Bismarcks, Solomons, New Hebrides) and Samoa do not differ significantly from each other in proportionment by evolutionary stage;  $\chi^2$  between New Hebrides and Samoa is 0.87.

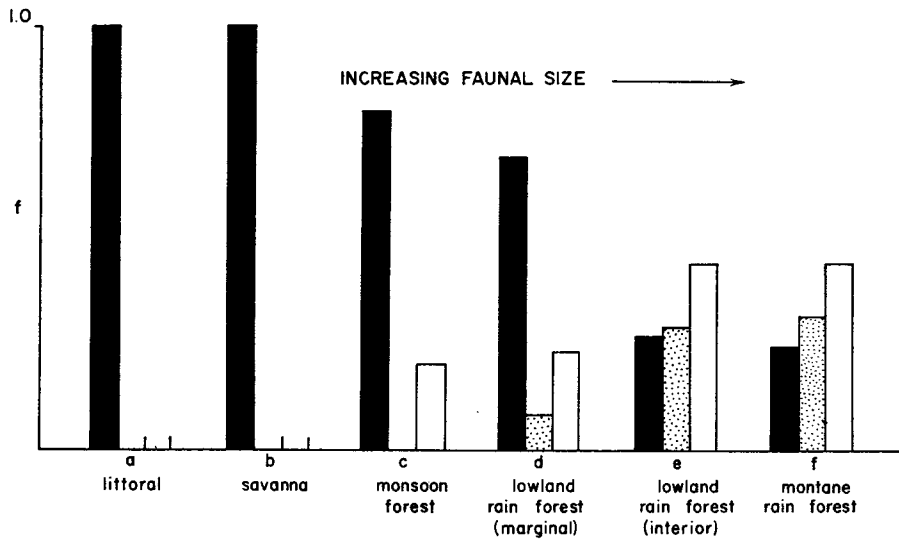


FIG. 9. Partition by evolutionary stage of the ponerine faunas of various major habitats in New Guinea. Black, Stage-I species; stippled, Stage II; blank, Stage III. See table 2.

Is it possible that faunal movement occurs through marginal habitats simply be-

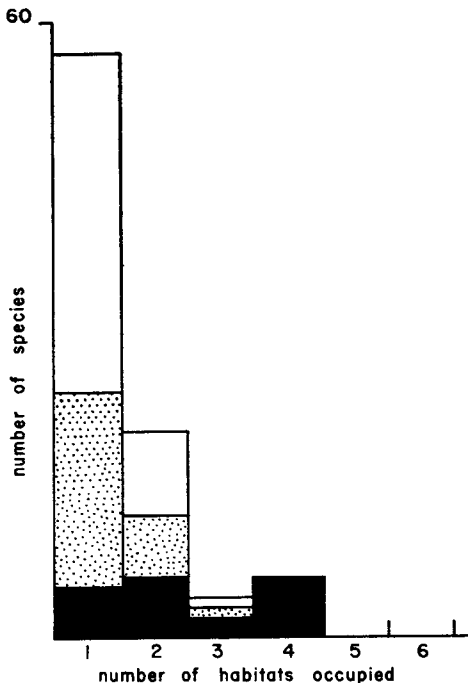


FIG. 10. Relationship of evolutionary stage and number of habitats occupied in the New Guinea fauna. Conventions as in figure 8. See table 3.

cause these habitats are more often nearer the coast? The present pattern of vegetation on New Guinea does not lend strong support to such a view. It is true that mountains, and montane rain forest, containing the largest number of ponerine species, are predominantly inland. But it is also generally true that where rainfall is sufficient to maintain lowland rain forest, this forest extends right to the coast, and where rainfall is not sufficient, grassland and monsoon forest extend far inland. It does not seem possible to invoke the slightly greater geographic accessibility of marginal habitats as the deciding factor in the marked preference of Stage-I species for these habitats.

Perhaps a stronger possibility to be considered is that the fauna of the marginal habitats is more prone to dispersal by wind and water, since it is more open to the action of wind currents and tends to be distributed differentially near waterways, e.g., "open aspect" rain forest predominates along streams in forested areas. There is at the present time insufficient evidence to test the validity of this supposition. If anything, two characteristics of Stage-I species, the common occurrence



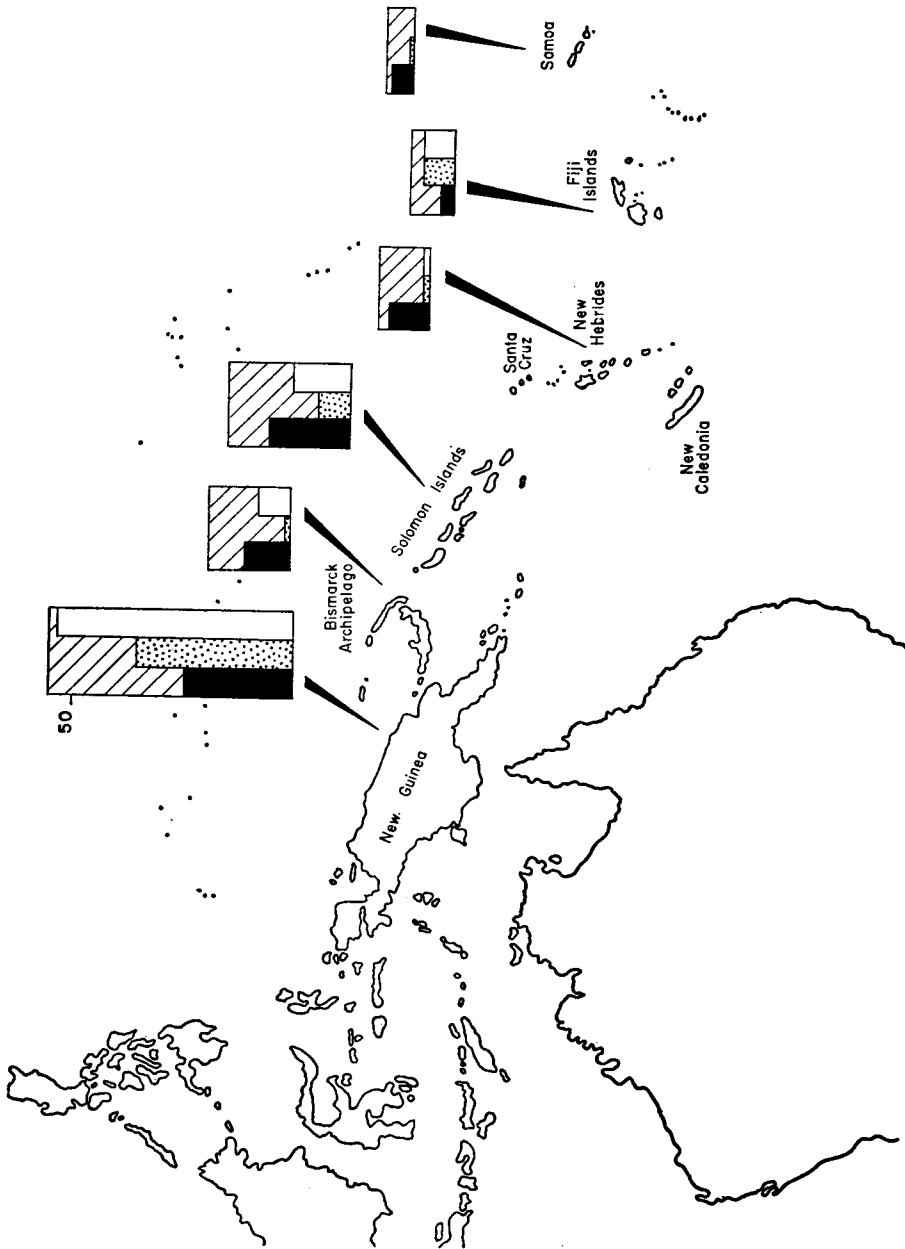


FIG. 11. Number of species groups and partition of species by evolutionary stage in the faunas of various Melanesian archipelagos. Hatched column represents the number of species groups; otherwise conventions are as in figure 9. The size of the Bismarck fauna as given is probably not indicative of its true relative size, since it is the most poorly explored; it is probably larger than that of the Solomons. See table 4.

of flightless queens and the common preference of soil as a nesting site, seem to weigh against regarding such an explanation too seriously at this time. Furthermore, there is some direct evidence, to be considered below, that the resident Stage-II and Stage-III species play a role in keeping Stage-I species out of the inner rain forest habitat.

It might also be argued that parts of the Celebes-Moluccan corridor, including some of Celebes itself and Buru, are drier and more "marginal" in their vegetation cover, hence posing a filter that has favored species adapted to marginal habitats. Again the evidence is not adequate to evaluate this possibility, and it may not be soluble until ecological studies are carried out in the Celebes and Moluccas. At least it is known that vast areas of these islands, including the entire island surfaces in some cases, are covered with dense rain forests, thus seeming to provide excellent stepping-stones that would allow a true rain forest fauna to cross over to New Guinea.

If the provisional interpretation adopted here is true, that different dispersal mechanisms and purely geographic phenomena are not sufficient to account for the marginal-habitat effect, one is inclined to turn to features of the biotic environment within Melanesia for a more complete explanation. There is likely significance in the fact that marginal habitats, containing as they do the smallest number of species, offer the least diversified biotic resistance. It is in fact the hypothesis advanced here that Stage-I species, by penetrating marginal habitats initially, are "flanking" the competition of the resident fauna rather than undertaking a "frontal assault" on it. The ant fauna of the inner rain forest does indeed present the appearance of a formidable closed "association." The species are very numerous (over 160 at the lower Busu River alone) and highly specialized to fill, in the aggregate, almost every imaginable niche available to ants. Moreover, the absolute composition of local faunas, as well as the

relative abundance of individual species, changes over distances as short as 12 kilometers, producing a "kaleidoscope effect" in the total faunal structure (Wilson, 1958d). In short, the potential competition offered by the resident inner rain forest fauna is very great at any given locality, and its overall effect may be greatly heightened by the spatially and temporally shifting nature of the total faunal structure, which would serve to thwart the extension of any local adaptation achieved by the first invading populations.

Now the question must be raised, if Stage-I species normally enter by way of marginal habitats, why has there not been a faunal buildup in these habitats, eventually closing them to further invasion? There is abundant evidence to indicate that species do not linger long in the marginal habitats. By the time they have differentiated and achieved Stage-II status, they usually have succeeded in penetrating the deep rain forest habitat.<sup>4</sup> Moreover, there is some indication that Stage-I species enter deep rain forest wherever competitive forms are relatively scarce. Thus *Rhytidoponera araneoides* is restricted to marginal habitats in New Guinea, but is apparently abundant in deep rain forest in the Solomon Islands, where the ponerine and myrmicine fauna is significantly smaller. On the Huon Peninsula of New Guinea, which has one of the largest and most diversified ponerine-myrmicine faunas of any comparable area in the world, *Odontomachus simillimus* (= *haematodus* auct.) is limited to marginal habitats. In the vicinity of the Brown River, Papua, with a local fauna only slightly larger than half that of local

<sup>4</sup> For the Ponerinae the most favored type of habitat in the New Guinea lowlands is what I have described elsewhere as "medium aspect" rain forest (Wilson, 1958d). Within this habitat most Stage-II and Stage-III ponerine species nest on the ground in rotting logs at the "zorapteran" and "passalid" stages of decomposition and prey on small arthropods. Microhabitat and nest-site choice is more variable in the mountain rain forests.

faunas on the Huon Peninsula, *O. simillimus* is moderately abundant in primary rain forest as well as marginal habitats. On Espiritu Santo, New Hebrides, which has a depauperate fauna, *O. simillimus* is one of the dominant ants on the floor of primary rain forest.

At this point the possibility should be considered that the invasion of Melanesia by way of the marginal habitats is a recent, unique event and not a continuing historical process, as supposed. This would be true if the coming of man, or else extensive drying of parts of New Guinea during the Pleistocene independent of man, had been necessary to open marginal habitats sufficiently for the Stage-I species to invade. In the author's opinion it is highly unlikely that such a circumstance existed. Even if at various geologic periods there were no savanna or monsoon forest, there would always be extensive rain forest border, and within the rain forest abundant patches of open-aspect, second-growth vegetation resulting from the fall of large trees, stream erosion, and landslides. Anyone who has worked in primary tropical forest is

familiar with the extensiveness of these phenomena. Native cultivation on New Guinea has undoubtedly greatly increased the extent of marginal habitats, and along with it the size of Stage-I populations, but if its effects were to be obliterated overnight, there would still be sufficient marginal areas to support large Stage-I populations. The same is probably true if all savannas and monsoon forests present in New Guinea today were to be replaced by continuous rain forest; there would remain abundant patches of open-aspect vegetation within the forest.

For invading (Stage-I) species, entering New Guinea by the marginal habitat route, there is a strong selective pressure to penetrate the inner rain forest (see fig. 12). Apparently they must achieve this adaptive shift in a relatively short time or face extinction, either through unfavorable environmental changes or under the pressure of newly invading competitor species. In evidence is the fact that there are relatively few old endemic species in the marginal habitats and even fewer that appear to be confined to them. This situation poses something of a paradox,

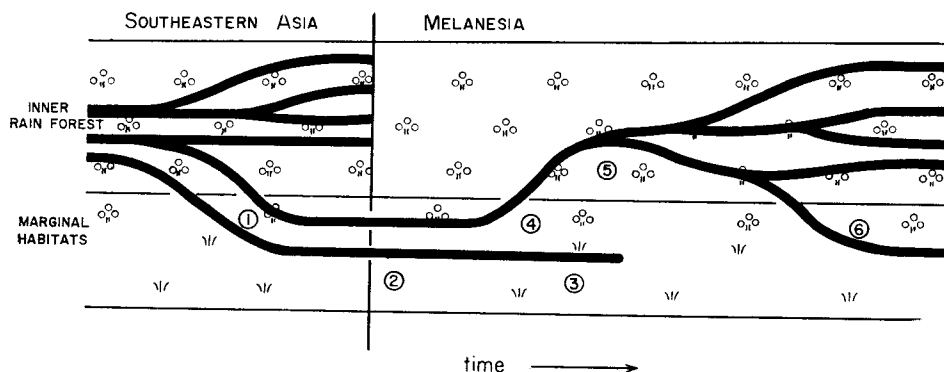


FIG. 12. Schematic representation of the hypothesized evolution of ponerine species groups in Melanesia, in this case tracing the history of groups derived ultimately from Asia. (1) Species or infraspecific populations adapt to marginal habitats in southeastern Asia, then cross the water gap to New Guinea and colonize marginal habitats there (2). In time these Stage-I species either become extinct (3) or invade the inner rain forest of Melanesia (4). Having successfully adapted to the inner rain forest, they diverge to species level (5), thus entering Stage II. As diversification continues in Melanesia, the source fauna in Asia may be contracting, so that in time the group as a whole becomes Melanesian-centered and its Melanesian species are classified as Stage III. A few of the New Guinea species may re-adapt to the marginal habitats (6) and expand back out of New Guinea, thus entering Stage I secondarily.

for it is true that the marginal habitats support (at least at present) large populations of ants. For the period of their tenure in the marginal habitats, the Stage-I species appear to be relatively abundant. What, then, causes their frequent extinction and the resultant selective pressure to shift into the deep rain forest habitat? Two causal phenomena can be hypothesized: (1) the environment of the marginal habitats, both physical and biotic, is more variable and capricious; (2) historically the marginal habitats have been limited in size and diversity of available niches, so that resident populations have tended to remain genetically relatively homogeneous and hence more vulnerable to the deleterious effects of rapid environmental change. (It should be noted that while the marginal habitats have fewer niches, it is thought that these niches tend to remain more open than is the case in rain forest, because of greater fluctuations in population size of resident species.)

Thus it is conceivable that the marginal habitats provide an opening for invading species while at the same time serving as an evolutionary trap for those that remain in residence. The islands of outer Melanesia may function in a similar fashion. As shown here, all of the archipelagos, with the single exception of the Fiji Islands, contain a higher proportion of Stage-I species than New Guinea. This youthful character of the fauna of central Melanesia may be due to the fact that these islands are geologically younger or less stable. But it may be also true that their smaller size and less diversified biota cause them to function also as evolutionary traps, "weakening" resident species and rendering them more susceptible to competition from subsequently invading species. The idea that oceanic islands do in fact have such a general effect on the evolution of endemic faunas has already been developed at some length by Mayr (1942, 1954) and Darlington (1957) and does not need further expression here.

Dobzhansky (1955) has recently summarized the population geneticist's view of the process of adaptation to diversified environments in the following rule: "Granted that genetic variability is an instrumentality whereby Mendelian populations master environmental diversity, one may expect that, other things being equal, populations which control a greater variety of ecologic niches will be more variable than those having a more limited hold on the environment." In a penetrating analysis extending over the past ten years, Dobzhansky and his colleagues have gone far to document just a phenomenon in the *Drosophila willistoni* group (da Cunha, Burla, and Dobzhansky, 1950; da Cunha and Dobzhansky, 1954; Birch and Battaglia, 1957; Dobzhansky, 1957; Townsend, 1958). Although the evidence is of a different and more limited kind, one is tempted to extend Dobzhansky's rule to include consideration of the evolution of the Melanesian ponerines. At first glance there appears to be a basic contradiction. If Stage-I species tend to be genetically impoverished, as suggested in the present paper, how is it that they occur in a greater array of major habitats than do old resident species? Would not greater ecological amplitude of this nature presuppose greater genetic diversification? The answer suggested by our much more extensive knowledge of *Drosophila willistoni* is that occurrence of a species or a population of a species in a wide range of major habitats (as defined here) does not of itself imply genetic diversity. If the habitats are marginal, or the distribution peripheral, the species (or population) may be relatively homogeneous. Of much greater importance are length of residence within the part of the range under consideration and the microecological diversification within the major habitats occupied. In the case of *Drosophila willistoni* it is the tropical forests and adjacent savannas of central Brazil that contain the largest number of inversion types and the highest percentage of in-

version heterozygotes. The Brazilian forests appear to be the center of the range of the species and also that part of the range to which resident populations are maximally adapted. In the case of the Melanesian ponerines, most of the Stage-I species are derived from Oriental stocks that are probably primarily rain-forest dwellers. In the case of these that have reached Stage-I status by expanding out of New Guinea by way of the marginal habitats, it is known with certainty that they belong to groups that are otherwise adapted to the inner rain forest. In making an adaptive shift to marginal habitats, the pioneer populations of these stocks are entering a peripheral, generally less favorable area, and it is probable that their genetic variability is correspondingly diminished. Furthermore, as Mayr (1954) has duly emphasized in his elaboration of the "founder principle" in speciation, pioneer populations such as those crossing water gaps in Melanesia are certain to have diminished variability, and the consequently narrowed "genetic environment" may have an accelerating effect on subsequent evolution.

With the foregoing theoretical background in mind, it is now possible to construct a model of the sequence of genetic events that have occurred in the colonization of Melanesia by the ponerine ants. Five steps can be conceived.

1. Prior to its invasion of New Guinea, the species occupies a central range, or permanent breeding area, probably composed mostly of deep rain forest, and on occasion marginal areas as well, in sum making up what Brown (1957) has referred to as the "maximum range." Brown has suggested the following events as being typical for animal populations: "Within the maximum range, the populations of the species normally undergo successive expansions into the less favorable areas, alternating with contractions into more favorable refuges. The expansions and contractions are the sequelae of inevitable density fluctuations affecting all or part of the species at one time."

2. Evolutionary changes accompany the continuing process of expansion and contraction. Populations occupying marginal areas will tend to adapt to the differing habitats found there.

3. Populations that are adapted to marginal habitats are now candidates for the colonization of New Guinea. Queens and colony fragments from both rain-forest and marginal-habitat populations probably disseminate from time to time across the water gaps to New Guinea, but generally only those adapted to marginal habitats are able to establish pioneer populations. The basis of this selection is the more open nature of the resident endemic marginal-habitat populations on New Guinea, containing fewer species and offering overall less competition to invading forms.

4. Having become established in New Guinea, the pioneer populations tend to remain genetically homogeneous because of the "niche-poor" condition of the marginal habitats. Their future is rendered further hazardous by the more intense fluctuations that occur in the marginal environments. Hence there is a strong selective pressure on these populations to penetrate the inner rain forest habitat.

5. If penetration of the inner rain forest is successful, new evolutionary opportunities are realized, and the populations tend to diversify and speciate. In time Group-II status is reached. With the further passage of time, however, the phyletic line will ultimately tend to diminish, as new, better adapted stocks penetrate the inner rain forest from outside. Occasionally, a species will break out of the inner rain forest habitat secondarily and expand out of New Guinea in the same fashion that the ancestral species entered, by way of the marginal habitat route. Such species, however, rarely if ever are able to push back beyond Australia or the Philippines.

#### SUMMARY

1. The zoogeography of the Melanesian ponerine fauna is preliminarily analyzed. Most of the fauna has apparently been

derived ultimately from Oriental stocks entering by way of New Guinea; some invading species are able to spread beyond this island to Queensland and outer Melanesia. A smaller part of the fauna has been derived from old Australian stocks that have entered by way of New Guinea or New Caledonia. Faunal flow from New Guinea through outer Melanesia has been unidirectional, with an ever diminishing number of species groups found outward from the Bismarcks to the Fiji Islands. New Caledonia draws almost all of its fauna from eastern Australia and has engaged in very little direct faunal exchange with the remainder of Melanesia.

2. A cyclical pattern of expansion, diversification, and contraction is hypothesized to account for later evolutionary events following initial dispersal. Following invasion of Melanesia (Stage I, *primary*), the pioneer populations may then diverge to species level (Stage II) and further diversify. Eventually the source populations outside Melanesia tend to contract, leaving the species group as a whole peripheral and Melanesian-centered (Stage III). Endemic Melanesian species occasionally enter upon a secondary phase of expansion (Stage I, *secondary*) but are rarely if ever able to push beyond Australia or the Philippines.

3. Stage-I species are characterized on New Guinea by their greater concentration in "marginal" habitats, including open lowland forest, savanna, and littoral. The central habitats, including denser lowland forest and montane forest, contain significantly larger faunas as well as a higher percentage of Stage-II and Stage-III species. Stage-I species are also characterized by their individual occurrence in a greater range of major habitats. Finally, these species make up a significantly higher proportion of the faunas of the archipelagos of central Melanesia, including the Bismarck Archipelago, the Solomon Islands, and the New Hebrides.

4. On the basis of these data it is suggested that ponerine species normally in-

vade New Guinea by way of the marginal habitats. Evolutionary opportunity is nevertheless limited in the marginal habitats, and there is a strong selective pressure favoring re-entry into the inner rain forest habitats. In general, Stages II and III, leading to the origin of the great bulk of the Melanesian fauna and its most distinctive endemic elements, are played out only in the inner rain forest.

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#### LITERATURE CITED

- BIRCH, L. C., AND B. BATTAGLIA. 1957. Selection in *Drosophila willistoni* in relation to food. *EVOLUTION*, 11: 94-105.
- BROWN, W. L. 1957. Centrifugal speciation. *Quart. Rev. Biol.*, 32: 247-277.
- . 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bull. Mus. Comp. Zool. Harvard*, 118: 175-362.
- DA CUNHA, A. B., H. BURLA, AND TH. DOBZHANSKY. 1950. Adaptive chromosomal polymorphism in *Drosophila willistoni*. *EVOLUTION*, 4: 212-235.
- DA CUNHA, A. B., AND TH. DOBZHANSKY. 1954. A further study of chromosomal polymorphism in *Drosophila willistoni* in its relation to the environment. *EVOLUTION*, 8: 119-134.
- DARLINGTON, P. J. 1957. *Zoogeography*. Wiley.
- DOBZHANSKY, TH. 1955. A review of some fundamental concepts and problems of population genetics. *Cold Spring Harbor Symp. Quant. Biol.*, 20: 1-15.
- . 1957. Genetics of natural populations XXVI: chromosomal variability in island and continental populations of *Drosophila willistoni* from Central America and the West Indies. *EVOLUTION*, 11: 280-293.
- MAYR, E. 1942. *Systematics and the origin of species*. Columbia University Press.
- . 1954. Change of genetic environment and evolution. In *Evolution as a process*. Allen and Unwin.
- RICHARDS, P. W. 1952. *The tropical rain forest*. Cambridge University Press.

- TOWNSEND, J. I. 1958. Chromosomal polymorphism in Caribbean island populations of *Drosophila willistoni*. Proc. Nat. Acad. Sci., **44**: 38-42.
- WILSON, E. O. 1957. The *tenuis* and *selenophora* groups of the ant genus *Ponera* (Hymenoptera: Formicidae). Bull. Mus. Comp. Zool. Harvard, **116**: 355-386.
- . 1958a. Studies on the ant fauna of Melanesia. I. The tribe Leptogenyini. II. The tribes Amblyoponini and Platythyreini. Bull. Mus. Comp. Zool. Harvard, **118**: 101-153.
- . 1958b. Studies on the ant fauna of Melanesia. III. *Rhytidoponera* in western Melanesia and the Moluccas. IV. The tribe Ponerini. Bull. Mus. Comp. Zool. Harvard, **118**: 303-371.
- . 1958c. Organization of a nuptial flight of the ant *Pheidole sitarches* Wheeler. Psyche, **64**: 46-50.
- . 1958d. Patchy distributions of ant species in New Guinea rain forests. Psyche (In press.)