INSECTS OF MICRONESIA
INTRODUCTION

BY

J. LINSLEY GRESSITT
Entomologist, Bishop Museum

Bernice P. Bishop Museum
INSECTS OF MICRONESIA
Volume 1

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their appreciation.

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FOREWORD

The publication of Insects of Micronesia is the culmination of one of the most ambitious projects yet undertaken in the zoology of the Pacific area. The project involves the work of many specialists, and the cooperation of numerous institutions and agencies, both private and governmental. During the several years the project has been in operation many obstacles have had to be overcome; others must be overcome before publication of the series is brought to final completion. Yet I am sure that all those who have participated and who have so generously given their thought and effort will find great satisfaction in the finished product.

In accepting the responsibility for sponsoring the final stages of the Insects of Micronesia project, Bishop Museum is fulfilling its natural function. This function is essentially one of bringing stimulus and continuity of interest to Pacific research through the establishment of cooperative ties between the Museum's necessarily small staff and the scientists of other institutions. In publishing Insects of Micronesia, Bishop Museum hopes to play an increasingly productive role in Pacific entomology.

In this first volume of the series, J. Linsley Gressitt has provided a fitting introduction for the papers that are to follow. His Introduction is more than a technical preface; it presents a comprehensive survey of the natural history of Micronesia that will be of interest to a wide audience.

This foreword would be incomplete without an expression of personal appreciation to Dr. Gressitt. To him has fallen the burden of coordinating the work of the contributors to the series and of exercising general editorial supervision. The financial problems which have accompanied the project have been a principal concern that he has faced optimistically and cheerfully. It is a pleasure to acknowledge the contribution that he has made to furthering the cause of science in the Pacific.

ALEXANDER SPOEHR
DIRECTOR
BISHOP MUSEUM
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INSECTS OF MICRONESIA

INTRODUCTION

By J. LINSLEY GRESSITT
ENTOMOLOGIST, B. P. BISHOP MUSEUM

INTRODUCTION

"Insects of Micronesia" is to be a series with more than 115 authors, each a specialist who will cover a limited portion of the terrestrial arthropod fauna. We are fortunate in having the cooperation of these highly competent workers who represent about 50 institutions in some 13 countries. Their reports will be published in the order received. Volume numbers will be assigned for an approximate systematic arrangement, and an index will be prepared for each volume.

This introduction is the first of the series. It will be followed by a bibliography of Micronesian entomology and the systematic reports of the many collaborators. Later, a general summary of the fauna, stressing zoogeography and speciation, will be prepared.

ACKNOWLEDGMENTS

In addition to the work of the specialists, this series is based on the efforts of many people. To a considerable extent, the survey is based on collections assembled during 1947 to 1953 by the Pacific Science Board (National Research Council) with the financial support of the United States Office of Naval Research. In addition, much material was taken during World War II by American servicemen; and before the war, by Japanese under Teiso Esaki of Kyushu University and by the Bishop Museum. Since the war, material has been collected by the U. S. Commercial Company, by the Trust Territory of the Pacific Islands, and by the Government of Guam, as well as by the Pacific Science Board. Since this project was taken over from the Pacific Science Board by the Bishop Museum at the beginning of 1953, the National Science Foundation, Washington, D. C., has awarded Bishop Museum two grants, for the period 1953 to 1957.

Bishop Museum is greatly indebted to the Pacific Science Board, the United States Office of Naval Research, the National Science Foundation, Dr. Teiso Esaki, and the collaborating specialists, for their important contributions toward the completion of this undertaking.
In connection with various aspects of planning for this series, and in the preparation of this introduction, I am indebted to Alexander Spoehr, Director of Bishop Museum, and to Harold J. Coolidge, C. E. Pemberton, R. I. Usinger, C. F. W. Musebeck, E. A. Chapin, W. H. Anderson, E. H. Bryan, Jr., L. D. Tuthill, D. E. Hardy, R. H. Van Zwaluwenburg, H. S. Dybas, J. F. Gates Clarke, J. G. Franclemont, Harold Morrison, P. A. Adams, R. M. Bohart, R. J. Goss, N. L. H. Krauss, R. W. L. Potts, K. V. Krombein, P. J. Darlington, R. L. Wenzel, E. S. Ross, H. K. Townes, R. G. Oakley, D. H. Johnson, and S. F. Glassman. I am particularly indebted to E. H. Bryan, Jr. for his help with the geography section, and to F. R. Fosberg for assistance with the sections on flora and vegetation. Harold St. John, F. A. McClure, and Marie C. Neal have also read the section on plants. Preston E. Cloud, Jr. and Ted Arnow have kindly provided information on geologic history; C. E. Palmer has advised on meteorology, particularly air currents; Walter C. Brown has helped with information on the herpetological fauna; S. H. Elbert, Henry Hedges, Donald Heron, Shigeru Kaneshiro, Francis B. Mahoney, Frank Mahony, David Ramarui, Edmund Gilmar, and Fabian Faruk have helped with spellings of place names; and K. L. Maehler, R. P. Owen, J. W. Beardsley, and G. D. Peterson gave special assistance on economic entomology. Several of the above-mentioned persons have kindly loaned photographs, and these are acknowledged in the captions. Many officials of the Trust Territory of the Pacific Islands have also helped in many ways.


For patient assistance at the Bishop Museum I am indebted to Setsuko Nakata and to Dorothy Rainwater, who also drew the maps.

For help in distributing the various collections I am grateful to a number of the above-named individuals and to most of the entomological staff members of the United States National Museum and the Section of Insect Identification of the United States Department of Agriculture. I should particularly like to acknowledge the help of Teiso Esaki, K. Yasumatsu, E. A. Chapin, O. L. Cartwright, J. F. Gates Clarke, B. D. Burks, R. L. Doutt, R. L. Wenzel, and H. S. Dybas. For helping to make available additional collections, I am also indebted to others, including W. J. Gertsch, Shizuo Kato, Hitoshi Hasegawa, Nodoka Hayashi, H. S. Wallace, C. R. Joyce, C. F. Clagg, R. P. Owen, Amy Suehiro, L. M. Chilson, E. J. Ford, Jr., and Miss Shui-chen Chiu, as well as a number of the collaborators.
Gressitt—Introduction

COLLABORATORS

The following list includes specialists with whom tentative arrangements have been made. Some groups have not yet been assigned.

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Arnott, R. H., Jr.
Auerbach, Stanley
Balfour-Browne, J.
Barber, H. G.
Barnard, J. L.
Barr, W. F.
Beier, Max
Bequaert, J. C.
Bobart, R. M.
Brennan, J. M.
Brown, W. L.
Burks, B. D.
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Cartwright, O. L.
Carvalho, J. C. M.
Chapin, E. A.
Chujo, Michio
Clarke, J. F. Gates
Clench, H. K.
Darlington, P. J., Jr.
Douett, R. L.
Drake, C. J.
Dybas, H. S.
Emerson, A. E.
Esaki, Teiio
Eshig, E. O.
Fennah, R. G.
Franclemont, J. G.
Frick, K. E.
Gillow, L. R.
Goodnight, C. J.
Gressitt, J. L.
Gurney, A. B.
Hagen, K. S.
Hardy, D. E.
Harmston, F. C.
Hoffman, R. L.
Hopkins, G. H. E.
Ishii, Tei
James, M. T.
Kato, Shizuo
Kessel, E. I.
Kohls, G. M.
Krombein, K. V.
Kulzer, Hans
Kurosawa, Yoshihiko
Lallemand, V.
Leech, H. B.
Liefteinck, M. A.
Lopes, H. de Souza
Matsuda, Ryuchi
Mesnil, L. P.
Michelbacher, A. E.
Miller, M. A.
Mills, H. B.
Morrison, Harold
Nakane, Takehiro
Newell, I. M.
Paramonov, S. J.
Park, Orlando
Pope, R. D.
Pritchard, A. E.
Quate, L. W.
Ray, Eugene
Reln, J. A. G.
Remington, C. L.
Richards, O. W.
Roewer, C. Fr.
Ross, E. S.
Ross, H. H.
Sabrosky, C. W.
Sanderson, M. W.
Scheerpeltz, Otto.
Seevers, C. H.
Shaw, F. R.
Shiraki, Tokuichi
Shirozu, Takashi
Skinner, F. E.
Smith, Marion R.
Snyder, F. M.
Sommerman, K. M.
Stannard, L. J., Jr.
Steel, W. O.
Steyssal, G. C.
Stone, Alan
Strohecker, H. F.
Takahashi, Ryoichi
Tokunaga, Masaaki
Tuthill, L. D.
Usinger, R. L.
Van Zwollvenburg, R. H.
Ward, Ronald
Watanabe, Chihisa
Wenzel, R. L.
Werner, F. G.
Wharton, G. W.
Wheeler, M. R.
Wirth, W. W.
Wittmer, Walter
Wood, S. L.
Wygodzinsky, Petr.
Yasumatsu, Keizo
Zimmerman, E. C.

SCOPE AND AIMS

In terms of the area of the earth's surface, the land area of Micronesia and the number of species of insects is exceedingly small. Furthermore, the insect faunas of the probable source areas of the Micronesian fauna are insufficiently known. From this standpoint, it would seem more important to study first the fauna of the neighboring continental areas, such as New Guinea. But the fauna of such an area is so great, and so little has been collected, that such a project would be of tremendous proportions. However,
reasons other than the limited size of the Micronesian fauna and the availability of collections warrant this study.

The study of faunas of small islands is a fascinating one and presents great opportunity for the elucidation of such processes as evolution, speciation, dispersal, ecology, and related subjects. With isolated and limited faunas and small populations, phenomena can be observed or more accurately estimated in ways not possible with large, continental faunas. Furthermore, the faunas of small islands subjected to commerce are rapidly changing, and it is desirable to learn their status before they have been further transformed.

Economic considerations are also of great importance. Although this work is primarily systematic, available information on the immature stages, habits, ecology, and economic importance of the species will also be included. In any area, insects are of the greatest importance to agriculture and to public health; but introduced species may become extremely serious to the local economy of small islands, because of the scarcity of natural enemies or lack of competitors. Some striking examples of this have occurred in Micronesia during the post-war years. Micronesia, with its trans-Pacific air-route stops, is a connecting link between Asia and the Americas, with the consequent danger of the transportation of pests in either direction. In fact, several pests are known to have been carried in both directions, particularly with the increased air travel of recent years. Some have been carried from the Philippines to Micronesia, and others, from Hawaii to Micronesia. Several, such as the Oriental fruit fly, have probably been carried from Micronesia to Hawaii. Two of the most serious pests in the Mariana Islands were originally native to the Caroline Islands. Thus a knowledge of the insects already present in Micronesia, as well as the guarding against future movement of pests, is of paramount importance.

It is hoped that this series may prove helpful in the identification of future collections from Micronesia and that it may aid those studying the faunas of other parts of the Pacific, as well as those concerned with evolutionary and distributional problems.


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1 Dates in parentheses refer to Bibliography, page 207.
within the scope of the present series. Except possibly for Hawaii, Micronesia has the largest fauna of these areas.

The geographical area to be covered in this series is Micronesia in the broad sense, including the Marianas, the Carolines, the Marshalls and Gilberts, and also Ocean, Nauru, Wake, Marcus, the Bonins (Ogasawara Islands), and the Volcano (Kazan or Iwo) Islands. It thus covers much of the northwestern Pacific Ocean and includes practically all of the oceanic islands west of the 180th meridian and north of the equator, with a few south of the equator.

In addition to insects, this series embraces practically all terrestrial arthropods. All of the Arachnida, as well as the Chilopoda, Diplopoda, and Symphyla, will be included, and at least the terrestrial Isopoda and Amphipoda among the Crustacea.

The primary purpose of this introduction is to describe the environment of Micronesia, particularly as it relates to insects. Emphasis is on the geography and vegetation, with brief discussions of the geology, the climate and the various factors relating to the history of the islands and the means whereby insects are transported across water to these oceanic islands. An attempt is made to present a brief picture of the insect fauna in ecological terms. The principal records of economic insects for Micronesia have been assembled because these have not been brought together before, and because some records have only appeared in reports with very limited circulation. A list of Micronesian place names used in entomology is appended to help identify sources of specimens.

It is hoped that this introduction may serve to help the specialists studying the collections to picture the environment and more adequately identify the sources of the specimens, and to understand the climatic and other forces affecting the biota. It is also intended that the description of the environment will prove helpful to those using the systematic reports and to those who do future field work in Micronesia.

It is not intended to analyze the fauna and to treat of its origin and affinities in detail here, but merely to introduce these and related questions and to mention briefly the problems involved. An analysis of the fauna will be made at a later date, after many of the systematic papers have been written. Thus, the views here expressed on the origin, constitution, and zoogeographic relations of the fauna are preliminary and tentative. A more precise picture must await a thorough study of the collections.

The metric system is followed throughout the series. The following table may be convenient for conversion purposes.
Insects of Micronesia—Vol. 1, 1954

MEASUREMENTS

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<tr>
<td>1 meter (100 cm.)</td>
<td>3.2808 feet</td>
</tr>
<tr>
<td>1 kilometer (1,000 m.)</td>
<td>0.6214 statute mile</td>
</tr>
<tr>
<td>1 square kilometer (100 hectares)</td>
<td>0.3861 square miles (247.1 acres)</td>
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<tr>
<td>1 inch</td>
<td>25.4 mm. (2.54 cm.)</td>
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<tr>
<td>1 foot (12 inches)</td>
<td>0.3048 meters</td>
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<tr>
<td>1 statute mile (5,280 feet)</td>
<td>1.609 kilometers</td>
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<tr>
<td>1 nautical mile (6,080.20 feet)</td>
<td>1.850 kilometers</td>
</tr>
<tr>
<td>1 square mile (640 acres)</td>
<td>2.590 square kilometers</td>
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EQUIVALENTS

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WHAT IS MICRONESIA?

Micronesia (fig. 1) is an assemblage of a large number of small islands, the largest 50 kilometers long, scattered over a great area of the warmer part of the western Pacific Ocean. Some 2,400 islands in four major groups,—the Mariana, Caroline, Marshall, and Gilbert Islands—make up the greater part of Micronesia. Some nearby islands—the Bonin Islands, the Volcano (Iwo) Islands and Marcus Island, Wake Atoll, Nauru Island, and Ocean Island—are sometimes included in the area. In this work they are all treated as part of Micronesia. Politically, the islands now fall under several administrations. The largest portion is a trust territory administered by the United States. The Gilbert Islands and Ocean Island are part of the British Gilbert and Ellice Crown Colony. Nauru is a trust territory administered by Australia. Guam is a United States Territory. The Bonin Islands, the Volcano Islands, and Marcus are under provisional United States care.

Micronesia has been considered by some as an area comparable to Polynesia, hence a major division of the Pacific, and by others as a subdivision of Polynesia. It is perhaps more of an entity as a geographical area including oceanic islands, and as an ethnological unit, than as a zoogeographical unit. Polynesia, which in the ethnological sense includes approximately the rest of the oceanic islands of the Pacific, including Hawaii, is actually closely related to Micronesia. The ethnological relationship between the two is perhaps closer than that of either Polynesia or Micronesia to any other regions. The zoogeographical relationship between them is very close, whereas the geographical division is somewhat arbitrary, consisting, more or less, of the 180th degree of longitude. The “inner Pacific” has been divided into two distinct zoogeographical areas, Hawaii and Polynesia, the latter including Micronesia. This seems to define general relationships, inasmuch as the Hawaiian fauna is so different from those of the rest of the oceanic Pacific islands (Zimmerman, 1948). Recently the ethnological term Micropolynesia has been proposed by Spoehr as a more adequate term for anthropological classification of the region. In the ethnological classification, New Zealand forms part of Polynesia, but this is not true for zoogeographical and geological classifications.
Figure 1.—Map of western Pacific.
Micronesia extends over a vast ocean area of over 8,000,000 square kilometers, occupying a large part of the ocean between Japan at the northwest, New Guinea and the Solomons in the south, the Philippines in the west, Hawaii in the northeast, and the Phoenix and Ellice Islands to the southeast. Most of the islands are in a north-south chain between Japan and western New Guinea or in a west-east band between the southern Philippines and the central Pacific. The extent of Micronesia proper is from 131°E. to 177°E. longitude and from 3°S. to 21°N. latitude, or if the Bonin Islands are included, to 28°N.

MAN IN MICRONESIA

The spread of insects and plants in Micronesia has been greatly facilitated by man's activities. The history of the early human migrations into the area is not known, but it is assumed that the ancestors of the Micronesians came primarily from southeastern Asia or the islands of Indonesia, and perhaps partly from Polynesia, Melanesia, the Philippines, or islands farther north. Possibly they came a few thousand years ago. There are extensive ancient ruins at Nanmatol on Ponape, and Lele on Kusaie (fig. 48, b), the histories of which are unknown. It is also possible that the Polynesians migrated eastward across Micronesia from Asia to the central Pacific.

These early immigrants, carrying various foods and plants in their canoes, inevitably brought with them insects such as ants, cockroaches, flies, and certain other household pests, including beetles and moths which attack dried foods; those insects associated with their plants; and body parasites. However, the number of species introduced by the earliest immigrants may have been quite small compared with what was brought by the later voyagers and traders.

The present Micronesians are not a homogeneous group, but represent varying degrees of the mixture of Asian and Polynesian elements, with some admixture of Melanesian blood. The Chamorros of the Mariana Islands are a fairly distinct group, with many customs derived from the Philippines. The Marshallese and the Gilbertese are each separate and moderately homogeneous groups, but the Caroline Islanders represent a wider diversity. On Kapingamarangi Atoll, the southernmost of the Carolines, the people are true Polynesians; and this island is now the westernmost outpost of the Polynesian peoples. Nukuoro Atoll, north of Kapingamarangi, also has Polynesian people; but they have mixed with Micronesians. The Banabans of Ocean Island and the people of Nauru, each a distinct group, have some Polynesian blood; but they have distinct languages, though Banaban is related to the Gilbertese language. The Banabans moved in early 1946 to the island of Rambi in the Fiji Islands, which they had purchased with phosphate royalties just before the war.
When domestic animals were taken to Micronesian islands, and when trade was instituted, still other pests were introduced. Likewise, arthropods, not directly related to man or his food or his animals and implements, were introduced accidentally. The fact that Guam has had much more trade with the outside world than other Micronesian islands correlates with a wider representation of genera and the presence on Guam of more of the widespread pests of man and agriculture.

Magellan discovered Guam in 1521. He called the islands the Ladrones, but later they were named the Mariana Islands, after Queen Marie Anna of Spain, wife of King Philip IV. Spain made claim to these islands and, eventually, to the Carolines and Marshalls. The Caroline Islands were named for King Charles II of Spain, though they were discovered by a Portuguese, Diego de Rocha, in 1526. Spain held title to all three groups for nearly four centuries, but during the first half of that period had almost no contact with the islands except for Guam and Saipan. Each year Spanish galleons sailed westward across the Pacific from Acapulco, Mexico, to Manila, stopping at Guam. Had their route around the world been from west to east, some of the introductions of Philippine insects to Guam might have taken place earlier. But as Guam is so far from Mexico, it is probable that few insects reached Guam from that direction. The Marshalls were discovered by the Spanish during the sixteenth century (Loyasa, 1526; Saavedra, 1529), but there is no record of their galleons having made regular stops in the Marshalls on their way to Guam. The Marshalls were rediscovered by the British in the eighteenth century. The southern Gilberts and northern Marshalls were sighted in 1765 and 1767, respectively, by Byron and Wallis, and the two island groups were named after two other British captains, Gilbert and Marshall, who explored both groups briefly in 1788. Nauru was discovered in 1798, and Banaba (Ocean), in 1804; both by the British.

During the eighteenth century, some ineffective efforts to send missionaries to the Carolines were made by the Spanish, but nothing else was attempted. Just before the middle of the nineteenth century, New England whalers started calling at the Marshalls and eastern Carolines, and American Protestant missionaries established headquarters at Kusaie and Ponape in 1852. Germany established a protectorate over the Marshalls in 1885. A Japanese warship visited Kusaie in 1884; and Japanese trade started with Ponape in 1890, with Truk in 1891. With the beginning of foreign trade, new diseases were introduced, and the advent of guns made warfare among the islanders more dangerous. Thus the native populations decreased rapidly. However, although some were killed during the second World War, modern medical treatment in recent years is producing a rapid increase in the population. Micronesians now number about 109,000, but this population could multiply a few times before the estimated former population would be regained.
After the Spanish-American War in 1898, Guam was ceded by Spain to the United States; and the rest of the Mariana Islands, with the Caroline Islands, were sold to Germany in 1899. The Gilbert Islands remained British. The Germans took considerable interest in Micronesia, sending missionaries and doing a little colonization and exploitation. The principal form of exploitation consisted of the planting of large numbers of coconut palms, using native labor and enforced planting quotas. The German administration operated from New Guinea, with local administrative centers in Ponape, Yap, Saipan, and the Marshalls. German trade was principally between Samoa and Saipan and between New Guinea and Ponape and Yap, so some insects were undoubtedly introduced by this means. More economic development was accomplished by the Germans in the areas under their control during the 16 years of their possession than by the Spanish during more than three centuries.

Japan joined the Allies in the first World War and seized Micronesia from Germany in 1914. In 1919 the area was awarded to Japan as a mandate from the League of Nations. Japan developed the islands much more than did the Germans, and colonized them extensively, particularly Palau and Saipan. A more diversified agriculture was developed and sugar cane, in particular, was extensively planted in the Marianas. The islands thus supplied large quantities of sugar and copra to Japan, in addition to phosphate, bauxite, dried bonito and alcohol. Extensive trade was carried on between Japan and Micronesia, especially through Saipan and Palau. There was also trade directly with Okinawa and the Bonin Islands, primarily to Saipan. The Japanese administrative center was at Koror in Palau, with branch stations at Saipan, Yap, Truk, Ponape, and Jaluit.

The Bonin Islands were discovered by Villalobos of Spain in 1543 and again by Japanese in 1593 and 1675. There were no native inhabitants; but the islands were colonized by a group of Hawaiians, Europeans, and Americans sent by the British Consul in Honolulu in 1830, and by Japanese both earlier and later, of which the early arrivals were unsuccessful. The islands were claimed in 1875 by Japan and remained Japanese until the end of World War II.

During the period preceding World War II the Japanese developed military or civil air bases in the Bonins, Iwo Jima, Marcus, Saipan, Tinian, Rota, Palau, Yap, Woleai, Truk, Ponape, Eniwetok, Kwajalein, Jaluit, Wotje, Maloelap, and Mili. Naval bases were established, principally at Truk, and at some of the other islands mentioned above. Regular sea-plane travel took place between Japan and Palau, via Saipan. The American commercial trans-Pacific sea-plane route called at Wake and Guam, between Hawaii and Manila. Thus opportunities for transport of insects increased greatly. There was further increase during World War II, with troop and supply movements...
in many directions; for example, from the Philippines, Malaya, and Indonesia to Micronesia, and later from New Guinea, the Solomons, New Hebrides, Fiji, Samoa, Hawaii, and other islands to Micronesia. In addition to opportunities for immigration of insects and plants from several directions, warfare greatly damaged crops and natural vegetation on many islands, thus changing the environment in several respects.

Islands where the vegetation suffered most—in several almost to the point of complete elimination—included Angaur, Peleliu and Iwo Jima, one or more islets each of Eniwetok (Eniwetok Is.),\(^2\) Kwajalein (Roi, Namur, and Kwajalein Is.), Jaluit (Jabor, Emidja and adjacent islets and the northern half of Jaluit), Wotje, Maloelap (Taroa Is.), Mili (Mili Is.), Butaritari (“Makin”), and Tarawa (Betio Is.). There was also considerable destruction on Saipan, Tinian, and Guam.

In 1944 and 1945 the United States retook Guam and occupied the Japanese Mandated Islands, which became the Trust Territory of the Pacific Islands under United Nations trusteeship. During that period the Gilberts were reoccupied by the British. Guam, Saipan, Iwo, Wake, Palau, Yap, Ulithi, Truk, Ponape, Kwajalein, Majuro, and Tarawa have become the principal centers served by commercial, military, or administrative transportation, both by air and sea travel. Eniwetok and Bikini have served as atomic bomb testing grounds. Other islands are visited, as a rule, by ships every two or three months. At Kwajalein, Guam, Wake, and Iwo Jima are based the principal direct plane connections with outside areas, particularly with Hawaii, Japan, Okinawa, and Luzon.

Agriculture in Micronesia differs from that in temperate climates. The number of crops cultivated is small, and domestic animals are few. The most important and most widespread crop is the coconut palm, which has been planted on practically every island with reasonably level land. Coconut groves fringe most of the islands and cover large areas of most of the low islands. Thus coconut cultivation has eliminated much natural vegetation, has facilitated the spread of coconut pests, and possibly on some islands has helped protect native vegetation from the establishment of new insects brought by commerce. The growing of sugar cane primarily on Saipan and Tinian before World War II has caused the second greatest disturbance of the indigenous vegetation. Agricultural settlements of Japanese on these islands and Palau, where pineapple, cassava, cane, cacao, coffee, and other crops were planted, have also disturbed native vegetation. Grazing has been another disturbing factor, although of lesser importance. Cattle are scarce on most islands, and goats have been introduced to only a few. Deer, rats, and giant African snails have changed conditions but are more serious to agriculture than to native

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\(^2\) For purposes of brevity, the abbreviations I. for Island and Is. for Islands will be used throughout this paper.
vegetation. Phosphate and bauxite mining have made changes (fig. 28, b) but have seriously affected only a few islands (Ocean, Nauru, Angaur, and Fais), and mining has been less important than agriculture and military operations.

Among early scientific expeditions to Micronesia may be mentioned several, most of which had more to do with botany or ornithology than with entomology:

1817 Russian ship _Rurick_, Captain Kotzebue, with Chamisso (1821) and Eschscholtz: Guam, Marshalls, western Carolines.
1819 French ships _Uranie_ and _Physicienne_, Captain Freycinet (1829-1839), with Quoy and Gaimard (1824-1826), and Gaudichaud-Beaupré: Guam, Rota, Tinian.
1823 Russian ship _Le Seniavine_, Captain Lutke, with Kittlitz (1836): Carolines.
1824 French ship _La Coquille_, Captain Duperry, with Lesson and Garnot (1829): Kusaie.
1828 French ship _Astrolabe_, Captain Dumont d'Urville (1834), with Quoy and Gaimard (1830-1835) and Hombron: Guam.
1838-1842 United States Exploring Expedition, Captain Wilkes (1844), with six ships.
1851-1853 Swedish ship _Eugenie_, Captain Virgin, with Kinberg: Guam (Skogman, 1854-1855).
1857-1859 Austrian ship _Novara_, Captain Wüllerstorff-Urbair, with Pelzeln.

The German Carl Semper (1873, 1881) studied Palau, particularly reef growth, in 1859 to 1861, and the German botanist Volkens visited the Carolines in 1899. In 1899 and 1900 the American botanist Safford (1905) collected on Guam. From 1908 to 1910 the German naturalist Krämer and others carried on extensive research in the Carolines, particularly in anthropology (Hambruch, 1932; Krämer, 1917; Thilenius, 1927).

The principal early Japanese botanist to work in Micronesia was Kanehira (1933), whose field work considerably preceded the start of Esaki's work in Micronesian entomology. The extensive insect collections made by the Japanese and Americans are mentioned under the section on field work.

ENTOMOLOGY IN MICRONESIA

This series on the insects of Micronesia is the outcome of the efforts of many people, a fact evidenced by the large number of authors and collectors listed. This project was started by the Pacific Science Board's Invertebrate Consultants Committee for the Pacific, earlier called the Insect Control Committee for Micronesia. Harold J. Coolidge, Executive Director of the Pacific Science Board, and C. E. Pemberton, chairman of the committee, are primarily responsible for initiating the project. However, earlier foundations had been laid.

From 1936 to 1940 Teiso Esaki and his associates made collections and investigations in the Japanese Mandated Islands, now the United States Trust Territory of the Pacific Islands. At least 81 published systematic reports by various workers, as well as writings on economic insects and zoogeography,
resulted from those trips (Esaki, 1940-1952). Some of the reports concerned subjects other than terrestrial arthropods. Much unstudied material from the collections at Kyushu University, Fukuoka, Japan is kindly being made available to the authors of the present series by Dr. Esaki. Approximately 2,200 species were taken in Micronesia by Esaki and his associates.

Previous to Esaki’s extensive undertaking, little had been done in Micronesia in the way of entomological investigations. During the period of Spanish rule almost nothing was done, except for the reporting of a few species, chiefly from Guam. Under the German administration scattered small collections were made, and these formed the basis for several reports and the descriptions of occasional new species. Prior to 1936 only about 300 insect species had been recorded from Micronesia, whereas some 1,200 species have now been described or recorded.

American contributions to the knowledge of Micronesian entomology commenced with miscellaneous short reports on insects from Guam published over a period from about 1911 to 1941. Most of these resulted from the collecting of D. T. Fullaway or were related to work done on Guam by economic entomologists or agriculturists, particularly S. R. Vandenberg. In 1936 an extensive survey of the insect fauna of Guam was made by O. H. Swezey and R. L. Usinger, aided for a short time by E. H. Bryan, Jr. These collections, with that made by R. G. Oakley in 1938, formed the basis of “Insects of Guam” (1942, 1946) published by Bishop Museum. Under the supervision of O. H. Swezey, 20 entomologists collaborated in this work in which about 737 species are recorded. In 1945 and 1946 G. E. Bohart and I made a collection on Guam, under the auspices of United States Naval Medical Research Unit No. 2. The Swezey-Usinger and Bohart-Gressitt collections each totaled about 1,000 species. It was originally intended that there should be a third volume of “Insects of Guam”; but as some manuscripts were delayed in preparation, they will be incorporated into the present series.

Additional material was collected during or just after the war in various parts of Micronesia by H. S. Dybas, R. M. Bohart, D. G. Hall, G. W. Wharton, S. F. Bailey, R. H. Baker, Ellsworth Hagen, E. H. Bryan, Jr., H. S. Wallace, C. K. Dorsey, David Frey, J. R. Stuntz and others (see field work). One of the best general Micronesian collections was made in 1946 by H. K. Townes and R. G. Oakley, under the auspices of the U. S. Commercial Company. E. Y. Hosaka collected some specimens under the same auspices. Many of the various collections were deposited in the United States National Museum, the Chicago Natural History Museum, the California Academy of Sciences, and Bishop Museum. All are being used in this study.

During the years 1947 to 1953 the Pacific Science Board sent entomologists to Micronesia to make the general entomological survey which forms the principal basis for this series. The plan was to have an entomologist spend
three or four months on each major island or island group. Participants in
this phase were P. A. Adams, R. M. Bohart, J. F. Gates Clarke, H. S.
Dybas, R. J. Goss, J. L. Gressitt, N. L., H. Krauss, and R. W. Potts. Marston
Bates, Ira La Rivers, R. L. Usinger, F. R. Fosberg, and E. T. Moul par-

ticipated in atoll ecology studies, principally under the auspices of the Pacific
Science Board. The collections were mounted at the Chicago Natural History
Museum, the Museum of Comparative Zoology, the California Academy of
Sciences, and Bishop Museum. In addition, entomologists sent to Micronesia
by the Board for studies of particular insect pests or problems included R. L.
D. B. Langford, K. L. Maehler, M. M. Ross, and R. P. Owen served as
entomologists or quarantine officers for the Navy, Guam, or the Trust Terri-

tory. Recently R. P. Owen and J. W. Beardsley, entomologists for the Trust
Territory, and G. D. Peterson, entomologist for Guam, have collected addi-
tional material. Some material from the Gilbert Islands has been furnished by
René Catala of New Caledonia. Other sources are mentioned in the section
on field work, in which are given short biographic sketches of collectors and
data on collecting localities (p. 193).

During the post-war period numerous beneficial insects have been intro-
duced to Micronesia for the control of serious pests, particularly with the
help of the Experiment Station of the Hawaiian Sugar Planters' Association
and the Territorial Board of Agriculture and Forestry in Honolulu.

ENVIRONMENT

GEOLOGY

Micronesia consists essentially of two principal lines of volcanic islands, one
north-south, the other west-east, and a large number of low coral islands
scattered along the west-east line and to the east in a northwest-southeast
direction. The north-south line has been called an arcuate, and the west-east
band a strewn, arrangement (Hobbs, 1945). Most of the volcanic islands are
just to the west of the sial, or andesite, line (Stearns, 1945) which marks the
easternmost extension of a hypothetical ancient Australasian continent and
the eastern boundary of Pacific volcanoes which extrude andesite and other
sial rocks instead of the basalt extruded by those to the east. The question
as to whether Truk is east or west of the sial line has been disputed, but
probably it is to the east, consisting as it does of basalt.

The north-south line is a continuation of the line of volcanic islands south
of Tokyo Bay which includes the Izu Shichito (Seven Islands). Within the
area under discussion are included the Bonin, the Volcano (Kazan or Iwo),
and the Mariana Islands. The Yap and Palau groups consist of an overlapping

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See Table 2 for altitudes of islands (p. 38).
at the southwest of the north-south and west-east lines. The latter continues eastward, after a long break without volcanic islands, to Truk, Ponape, and finally Kusaie. The Caroline atolls stretch along this west-east line, and southwestward from Palau almost to Waigiou, off the western end of New Guinea, and southeastward from Truk almost to the equator north of the Bismarcks. The Marshall and Gilbert atolls stretch from northwest to southeast, just east of the Carolines.

Some of the islands west of the sial line possess various old metamorphic rocks, such as schist, gneiss, or slate. These rocks are presumed to be lacking on islands east of the line, though a limited amount occurs in Truk (Bridge, 1948).

The Bonin Islands are of mixed volcanic rocks and limestone, something like the formations of the southern Marianas, but the Bonins are more rugged and lack great coraline plateaus and terraces. The Haha Jima group has andesitic lava, agglomerate, and Eocene nummulitic limestone; but the Chichi Jima and Muko Jima groups are rich in Boninite (andesite), with tuff, and Oligocene Lithothamnium limestone. Tayama considers the Bonins to represent a separate and older chain than that extending from Mount Fuji to the Volcano Islands. The Volcano Islands are entirely volcanic, with some active volcanoes, and with only limited coral growth below sea level. The northern Marianas are also entirely volcanic, if Farallon de Medinilla is included with the southern Marianas. Each island consists of one or more volcanic cones, all of them steep and with lava flows forming much of the slopes. Small cinder cones are present on some, and large craters exist on Pagan and Anatahan. Farallon de Pajaros, Pagan, and Asuncion are active volcanoes. Columnar basalt occurs in some of the thicker lava flows, often in cliffs or ridge tops.

The southern Mariana Islands are primarily limestone tablelands, resting on volcanic peaks which are only in part exposed. The limestone may be more than 200 meters thick. The conspicuous features of these islands are the limestone terraces, or benches, and tablelands. The terraces are eroded by wave action at different levels, indicating elevation at different periods. The older, higher terraces are much dissected by erosion above altitudes of 200 meters, and the lower terraces are much less dissected. Many of the terraces form broad flat surfaces around the islands. On Tinian, Rota, Agiguan, and the northern half of Guam the terraces form extensive flat uplands. Each terrace is bordered on the seaward side by steep terrace faces or bare rock cliffs which have been cut by waves. Lower terraces often have steep cliffs, sometimes overhanging the water. In northern Guam the high cliffs, which often drop nearly 200 meters, have narrow beaches at the bottom. The limestone bedrock is of two types: one is foraminiferal and coral, locally interbedded with tuff (volcanic ash) or with sandstone and shale; the other is mostly pure coral reef limestone. Often a red clay soil layer separates the two types. Volcanic rocks
crop out locally, except in central Saipan and the southern half of Guam. Here volcanics are dominant or practically the sole type. They are, in part, higher than the coral plateaus, though the highest volcanic peaks are again, in part, capped with coral limestone.

The Palau Islands have two principal types of formation: volcanic, and limestone formed by coral and calcareous algae (figs. 2, 20). The volcanic rocks are primarily andesitic, consisting of andesite, andesite transformed to bauxite, andesitic agglomerate with tuffaceous rock, and some manganese, zinc, and gold. The volcanic areas include practically all of Babelthuap, the western half of Koror, and most of Ngerkabesang and Malakal. On Babelthuap there are also areas of tertiary sediments, including raised beach deposits, shale, and some lignite. Raised limestone is found only in the extreme southern and southeastern tips on Babelthuap, mostly on portions separated from it by mangrove swamps. Wave-cut terraces have also been reported on Babelthuap and adjacent islands. The volcanic portions of Koror, and Ngerkabesang and Malakal, consist of andesitic agglomerate (Tayama, 1935b). The islands around them and to the south consist of raised reef limestone, in part raised to the height of 200 meters, which is nearly as high as Babelthuap.
Gressitt—Introduction

Angaur, the southernmost island, lying outside the barrier reef, is a raised atoll, with extensive phosphate deposits (Nugent, 1948).

Yap consists of ancient volcanic and sedimentary rocks and is without significantly raised limestone. The exposed rock consists largely of finely layered, dark green amphibole schist. Basaltic lava, granite, and granite-like rocks (gabbro and peridotite) penetrate the schist and locally displace it completely. Indurated gravel (conglomerate) and angular rock fragments (breccia) derived from schist and associated rocks are widespread. Red and yellow lateritic soils containing black iron oxide concretions are conspicuous on bare hilltops and upland areas, and some have been carried down by streams. Bauxite of high aluminum content is present in limited amount. Manganese, copper, iron, and asbestos are present, and nickel has been reported. Coral limestone covered with sand and gravel is reported from some of the low-lying portion of Yap (Bridge, 1946; Tayama, 1935c). The great width of the flat fringing reef (3 to 4 km. wide) of Yap is an indication that the island has been standing still for a long time (Davis, 1928), or sinking only at a rate which permits the coral growth to keep pace except in the sunken river valleys where the flow of fresh water retards coral growth.

Palau and Yap, therefore, have much in common, both being old, with metamorphic or sedimentary rocks and no recent volcanic activity.

Truk consists of a group of moderately high (up to 450 meters) volcanic peaks surrounded by the largest enclosing reef in the open Pacific. Early in the Tertiary Era extensive volcanic eruption produced two or three large piles of volcanic rock on the Caroline submarine ridge, forming volcanoes of the “shield” type similar to those of Hawaii, with gently sloping domes. Some fragmental material, agglomerate and tuff, is interbedded with the basaltic lava. All are rich in lime and iron and low in silica. Bauxite and schist are rare. There were two major periods of eruption at Truk, as at Ponape, Eocene and Oligocene. The earlier period produced normal basalt and the later period produced alkaline basalt containing nepheline (common to Truk, Ponape and Kusaie) with analcite and other unstable zeolitic materials, olivine basalt containing titaniferous augite, and an ultrabasic type of basalt. The interval between the two periods may have been quite long. After its development the Truk volcano was broken in places by faults, and it eroded to a wide shoal surmounted by the peaks that now form the islands in the lagoon. Terraces were cut by wave action during intermittent periods of submergence and emergence, with pleistocene deposits of beach gravel left on the terraces. These terraces were raised high above sea level before the start of a period of gradual submergence. Then valleys were drowned, forming reentrants in coast lines. Coral reefs grew up on the shoal, changing at its outer margin to a barrier reef, with some reef islets. Fringing reefs grew around islands in the lagoon, and isolated reefs developed. The latest change resulted in the ele-
vated coral reef limestone 1 to 2 meters above sea level. This may have been caused by uplift or, perhaps more likely, by the lowering of sea level in the Pacific (Daly, 1920), for this feature is common to many of the Micronesian islands. (Above mostly from Tayama, 1940.) A modification of this theory is that the present islands of Truk represent the peaks of a much larger island which had gradually sunk after a long period, following periods of emergence and submergence.

Ponape may have had a history somewhat similar to that of Truk. Its altitude is nearly twice as great (780 meters) as that of Truk, but its reef (fringing, with some islets) has a much smaller circumference. The interior consists of basalt, andesite, and other dark volcanic rocks, with smaller amounts of coarse (volcanic breccia) and fine (tuff) consolidated fragmental material produced by explosive eruptions. The composition is more or less uniform throughout the island. The basalt contains abundant zeolites. There are bold cliffs of columnar trap rock, particularly on Sokehs (Jokaj) in the north. The lower slopes and level areas consist largely of sand and gravel of water-worn volcanic fragments. There are also deposits of iron-rich concretions, the result of intense tropical weathering of rock and soil, particularly at some stream mouths. There is some bauxite and a little gold. Raised reef rock, mostly poorly bedded limestone, makes up eroded lower slopes between shore and steeper inland slopes, or forms discontinuous benches on the seaward-facing slopes along the coast. This limestone rarely rises to more than 30 meters above sea level. (See Tayama, 1936b.)

Kusaie is similar to Ponape but is steeper and smaller. Mount Matante (fig. 51, b) is younger and more volcano-like in form than the extremely narrow-crested ranges of the main portion of the island. Among Kusaie's deposits are clay, bauxite, and bat guano (or swiftlet guano).

The atolls of Micronesia are, in the main, typical coral atolls and include the second largest assemblage in the world. They also include the two largest atolls in the world, Kwajalein and Namonuito. Truk, the largest so-called "almost atoll," is not now considered an atoll. Until conclusions are drawn from the current extensive atoll research in the Pacific, it may be assumed that most of the Micronesian atolls owe their existence primarily to coral growth on slowly subsiding or stationary peaks of a great submarine plateau extending from just east of the sial line to almost the center of the Pacific. Those in the western Carolines may be associated with peaks of the folds along the edge of the ancient shelf of continental Asia. Presumably the islands that preceded these atolls were eroded to shoals or sank beneath the surface, and coral growth continued close to the surface, keeping pace with the sinking, or the coral grew from submarine peaks which never were islands.

North of most of Micronesia is a west-east band of drowned guyots, or truncated submarine mountains, extending from the Volcano Islands to the
central Pacific. Marcus Island, Wake Atoll, and Johnston Island are the only ones reaching the surface of the ocean, and most of them reach 3,000 to 4,000 meters above the ocean floor and 1,000 to 2,000 meters below sea level (Hess, 1946). These may also be compared with Tayama's "table reefs" and Caroline low islands (Tayama, 1935a).

In 1952 two drillings were made on opposite sides of Eniwetok Atoll down to volcanic basement rock consisting of olivine basalt (Ladd et al., 1953). These were the first borings to reach the basement rock of an atoll. One drilling reached basement at 1,405 meters below sea level; the other encountered basement starting at 1,266 meters. Above the basalt is limestone in various forms, including reef and dolomitic limestone and silt particles, and containing Eocene, Miocene, Pliocene, Pleistocene, and Recent Foraminifera, from bottom to top, as well as fossil corals, coral algae, and mollusks. Eocene corals apparently grew on top of the extinct volcano in less than 50 meters of water, and the Miocene and younger deposits contain only shallow-water forms. There were also traces of digested peat, though unidentifiable. These authors conclude that the volcano was elevated well above sea level before subsidence commenced. This evidence essentially supports Darwin's theory (1890) of atoll formation by gradual subsidence of volcanic islands.

In 1947 a drilling in Bikini Atoll 779 meters deep failed to reach basalt, as did the 1936 drilling to 432 meters at Kita Daito Jima. It was earlier known that coral rock extended at least to depths greater than 300 meters, as at Funafuti (Royal Soc. London, 1904), whereas coral is not capable of growth much deeper than 50 meters (Davis, 1928). Recently Cretaceous fossils were dredged from a sea mount east of Micronesia (Hamilton, 1953).

The islets on an atoll generally develop on the side from which the wind and currents come. Thus among the Carolines and the Gilberts, which lie in the westward equatorial current and the northeast trade wind belt, the islets are often concentrated on the eastern sides of the atolls. This is not so true of the Marshalls, which tend to have the islets more generally distributed. The geology and development of certain Marshall atolls, particularly Bikini, has received considerable attention (Emery, 1948; Ladd et al., 1950; Tracey et al., 1948), and much material is still in press (Emery et al., in press; Ladd, in press).

Among the conspicuous features of Micronesia are the very long lines of volcanic islands, the deepest ocean depths in the world, and the numerous coral atolls. The deepest ocean bottoms are all in the western Pacific and most are located near such volcanic continental island chains as the Kuriles, Japan, the Ryukyus, Formosa, and the Philippines. The great depths are correlated with great risings in the edge of the Asiatic continental shelf through volcanic action, and the consequent subsidence of sea bottoms parallel to and near the raised areas. (See Nugent, 1946, for a bathymetric chart.) The deepest
measured ocean depth is at the south end of the Mariana Trench, 10,860 meters, almost directly between Guam and Yap and not far northeast of Ulithi. Next is the Mindanao Trench, 10,537 meters deep, between Mindanao and Palau. For some time, most of the land areas of Micronesia have been dwindling in size from erosion or subsidence. The latter is evident on many of the high islands, except some of the northern Marianas and easternmost Carolines. On the other hand, the extensive raised coral limestone in the southern Marianas and Palau indicates that there have also been periods of subsidence beneath sea level, followed by high uplifting of accumulated coral limestone after some of the islands were originally raised as volcanoes. It is likely that the amount of land was once more extensive, in the western Carolines at least, because of the various sorts of continental rocks in Palau and, particularly, in Yap. Whether these islands were ever connected with Asia is a question on which opinions may differ among workers in various fields. The paucity of insects suggests that the connection, if any existed, was not continuous, or that the islands were later temporarily submerged.

Some geologists, some botanists, and Esaki (1950) state that both Palau and Yap are continental islands. Others, particularly biologists, consider all islands of Micronesia to be oceanic. Some of these differences of opinion may be based on differences of interpretation (Buxton, 1938; Hedley, 1899). For instance, a continental area temporarily completely submerged under the sea and then elevated again might be characterized differently by workers in different fields. Temporary immersion would not have the effect on rocks that it would on plants and insects. The factors for the latter are not identical, though most of the forces which disseminate plants and insects to oceanic islands are essentially the same. Palau and Yap have insects and plants which would appear to have great difficulty in passing over several hundred kilometers of water. However, had there been a direct connection between these islands and Asia or Papuasia, and had they never since been entirely submerged, it would seem likely that many more groups should be represented and that those present should exhibit a greater range of genera.

That greatly isolated oceanic islands may possess a large variety of species is exemplified in the Hawaiian Islands. However, in Hawaii the number of species ancestral to the present native fauna, that is, the number of natural introductions, was quite small and they arrived over a much longer period of time (Perkins et al., 1900-1913; Zimmerman, 1948). The number of species representing natural ancestral immigrants to Micronesia must be much larger than that for Hawaii. Not only does Micronesia's greater proximity to continental areas suggest this, but Micronesia has endemic species of far more higher categories than does Hawaii. Thus the fauna of Micronesia is a more balanced cross section of the insect world, although it also is incomplete. Actually, as Micronesia has few groups of insects not found on
some of the other oceanic islands, the presence in Palau or Yap of certain
groups not generally found on isolated oceanic islands or atolls should not
be taken as conclusive evidence that these are continental islands.

Geologic Age

Most of the islands of Micronesia either developed during the Tertiary Era
or are quite recent. In general, the high islands are older, probably for the
most part pre-Pleistocene, and the low islands are younger; that is, Recent or
late Pleistocene. In the Volcano Islands and the northern Mariana Islands,
vulcanism is still active; but it has not occurred in the southern Marianas or
the Carolines since the Miocene or earlier. Assuming that the majority of the
islands of Micronesia have been relatively stable tectonically for the last several
million years, it is reasonable to conclude that most islands more than 30
meters above sea level and not consisting of Pleistocene volcanics are proba-
bly pre-Pleistocene in age. The Mariana Islands, from Medinilla south; the
Palau Islands, including Peleliu and Angaur; and the Yap group have ap-
parently been at least partly above water since before Pleistocene time and
developed earlier, perhaps even as far back as Middle or Upper Miocene or
earlier. This indicates an age of between 1 million and 20 million or more
years, but it is quite likely that most of these islands are less than 10 million
years old. Yap and Palau are older than the southern Marianas, and the
volcanic rocks of Palau may have originated between the Eocene and the
Miocene. The limestone rocks of Palau are Plio-Pleistocene. The metamorphic
rocks of Yap are presumably pre-Tertiary, but there are some Miocene vol-
canic beds and a little Pleistocene limestone in Yap (Cloud and Arnow, per-
sonal communications).

The high islands of the central and eastern Carolines, east of the sial
line—Truk, Ponape, and Kusaie—have a different history; but they were
probably formed in two periods of volcanic activity, the first Eocene and the
second Oligocene. The only limestone above sea level is recent reef lime-
stone, which may be related to a recent fall in sea level. Presumably all the
low areas of the high islands may have been submerged in the late Pleistocene.

Fais consists of raised limestone of Plio-Pleistocene age, plus recent reef
deposits. Tayama (1935a) considers Fais a raised table reef rather than a
raised atoll.

The low islands and atolls, according to a current thesis, are very young
and, in large degree, probably owe their existence as habitable areas to a fall
in sea level of 2 meters or a little less that began, roughly, about 3,000 years
ago (Daly, 1920). Others, like Kwada in Kwajalein and some islets in
Ulithi, may be somewhat older, but perhaps not more than 10,000 years old
(Cloud, personal communication). Continuous change is going on, with atoll
islets being added to or divided or eliminated by regular weathering and bad storms. In 1907 an islet of Woleai Atoll was completely eliminated by a typhoon.

According to the above-mentioned theory, the relative ages of the high and low islands of most of Micronesia are very different, most of the high islands being at least 1,000 times as old as most of the low islands. Therefore the actual degree of endemism on the low islands is an interesting question. Most of the high islands are probably less than one-third the age of the Hawaiian Islands and somewhat younger than Samoa.

The traces of peat in the Eniwetok borings (Ladd et al., 1953) suggest that land and vegetation may have existed on the atoll in early periods, and this may or may not contradict the theory of the youthfulness of the low islands. It is obviously possible that ancient atolls on the now further sunken bases may have been completely submerged or otherwise destroyed until additional coral growth and the accumulation of debris on the surface of the reef formed new atoll islets.

SOILS

The soils of Micronesia are not very complex, and fall into several simple groups. First of all, they may be divided into the soils of high islands and of low islands. The former are more complex, having volcanic or coralline or mixed volcanic and coralline origin. Those of the low islands have an almost purely limestone derivation. On the young volcanic and young coral islands, actual soil or even sand may be extremely rare. The principal high island soils are lateritic in nature; that is, they developed by decomposition of rock under warm and humid, or tropical, conditions.

Many of the soils in western Micronesia are red, both those formed by decomposition of andesite and those formed from elevated reef limestone. The coralline soils are fine-textured and claylike, but they contain pieces of undecomposed coral. Their water-holding capacity is slight. The volcanic soils are often fine clays. The mixed volcanic-coralline soils are fine-grained heavy clays. In Yap some are red and some are yellow, and some contain black iron oxide concretions. In Yap and Palau soil may be thin and poor in some bauxite areas or on higher land. Where grass is burned annually on volcanic land in areas of higher rainfall, humus does not accumulate and soils are poor. Volcanic or sedimentary soils tend to be richer than coralline soils, where vegetation is not burned and, particularly, where alluvial deposits accumulate.

The soils on the eastern Caroline high islands are largely reddish brown to blackish, consisting of weathered basalt. In the forests, humus accumulates and there are also alluvial deposits. Muck develops in taro swamps, and peat develops in mangrove swamps. On the coastal strand and away from
mangrove, the soil may be mixed coral sand and alluvium on a coral gravel base, or it may be almost entirely coralline and resemble atoll soils.

Atoll soils are extremely young, if the theory of an approximate 2-meter drop in sea level a few thousands years ago (xerothermic period) is correct. The original materials on an atoll are loose, or rarely consolidated, and consist mainly of calcium carbonate, with some magnesium carbonate and a little pumice. There is constant weathering through solution by rainwater and the flushing away of solutes by tides. However, plants and animals add humus. Sea birds are particularly important as they add nitrogen and phosphorus; and crabs, insects, and legumes are quite important, and possibly also blue-green algae. Atoll soils (Stone 1951a, 1953; Fosberg, in press) consist primarily of three types: (1) Shioya, the most widespread, of slightly altered lime sands or gravels, sometimes with loam or silt; (2) Arno Atoll, well-drained, calcareous but dark, with high organic matter and up to 50 cm. deep, mostly in coconut groves; and (3) Jemo, containing phosphate in an indurated or hardpan horizon beneath a horizon of raw acid humus, formed only in Pisonia groves where sea birds nest. The phosphate is formed by the bird excrement, acidified by humus, dissolving in rainwater and precipitating when washed into the calcareous sand, which it cements (Fosberg, in press). Peat and muck deposits are rare on coral islands, but they occur in taro pits and mangrove. An extensive peat swamp exists on Washington Island in the central Pacific (Christophersen, 1927). In the Marshalls, there is also a minor coconut-pandanus peat (Stone, 1953). Atoll soils do not retain water very well. The water table varies in water salinity and is usually only slightly above the sea level. It varies with the tides, and the fresh or brackish layer above the salt water is called the Ghyben-Herzberg Lens. This is thicker in the middle of an islet than near the shores.

CLIMATE

Micronesia has, in general, a rather warm and moderately humid climate. The temperature, humidity, cloudiness, and atmospheric pressure are relatively uniform. Rainfall and wind are more variable, both seasonally and geographically. There is also considerable local irregularity in rainfall from year to year. Hurricanes, or typhoons, are most common in the western part of Micronesia, with an average of 25 per year. They often originate between Guam and Palau in late summer and autumn, traveling westward or northward and striking Asia between the Philippines and Japan.

Micronesia lies between the southwestern part of the northeast trade-wind belt and the eastern fringe of the monsoon region. With the shift in the sun north and south over the area in summer, a similar shift in the position of the doldrums and of the equatorial or intertropical front takes place. Prevailing winds are from the east. In northern winter the winds over most of the area...
are largely from the northeast or east. In northern summer the northward movement of the doldrums and equatorial front involves winds from the south, including southeast trades, or calms. In the west there are northeast monsoon winds in summer. The monsoons develop from stagnated vortices from the general westward air currents, and some of these vortices become typhoons.

Though most of Micronesia is rather wet, Wake Atoll, the northern Marshalls, and the southeastern Gilberts are relatively dry. These are all low islands. The Carolines are, in general, quite wet. The high islands have greater precipitation than the atolls, for the mountains intercept the moisture-laden winds. Truk has less rain on the average than the other high islands of the Carolines, perhaps because it is between the trade-wind area to the east and the monsoon region to the west.

The distribution of rain during the year also varies geographically. In general, the maximum rainfall is in summer in northern Micronesia and in the northern winter, or rather evenly distributed, in southern Micronesia. Palau and Ocean Island have both summer and winter maxima. Jaluit and Ponape have rather uniform precipitation throughout the year, though Ponape has somewhat less from January to March. Kusaie has a rather uniformly heavy rainfall, though it is lighter during August to November on the east coast.

**Bonin Islands**

The Bonins are drier and somewhat more stormy than most parts of Micronesia. Winds are fairly strong, and thunderstorms are frequent. Wind is mostly from the northwest from December to February and from the east or northeast from July to October. The temperature is higher than for similar latitudes in most parts of the world because of the warm Kuroshio Current. Average temperatures range from 16.7° C. (62° F.) in January and February to 26.7° C. (80° F.) in August. Coconuts ripen in the Bonins, though they do not ripen in Hong Kong, which is five degrees farther south. The average annual rainfall is about 1,550 mm. (61 in.). There is no marked wet or dry season, but the heaviest rainfall is in December, January, and March to August.

**Volcano Islands**

Iwo Jima is drier than the Bonins, and a little warmer, but otherwise similar. Average temperatures range from 24.4° C. (76° F.) to 28.3° C. (83° F.). The average annual rainfall is 1,395 mm. (55 in.). There are about six typhoons per year. Wind directions are about the same as for the Bonins.

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4 See Table 2 for altitudes of islands (p. 38).
Marianas Islands

The Marianas are in the transition zone between the monsoons and the northeast trade winds. The equatorial front may reach the southern Marianas between July and September, causing rainy and unsettled weather. From November to June, the weather is drier, with northeast winds. There is at least one typhoon per year. Breezes are fairly constant. The wet and dry seasons are not quite so pronounced on Saipan and Tinian as on Guam. The northern Marianas have less rainfall and cloudy weather than the large southern islands, but the higher, northern islands may be cloud-capped. Temperature ranges from 16.1° to 35° C. (61° to 95° F.), with the means from 23.0° to 29.4° C. (75° to 85° F.). Atmospheric pressure is fairly uniform, except when typhoons are near, and ranges from 756 to 760 mm. on Guam. It is slightly higher on Saipan. Relative humidity averages 84 percent in January and 90 percent in June on Guam, and 78 percent in winter and 84 percent in summer on Saipan. Rainfall averages about 2,286 mm. (90 in.) per year on Guam, 2,134 mm. on Saipan, and 1,524 mm. on Pagan. On Guam and Saipan more than two-thirds of the rain falls from July to October, and April is the driest month. Cloudiness is greatest from July through January and is greater over the islands than over the ocean. Fog and haze are rare. Winds in the southern Marianas are from northeast to east for nearly three-fourths of the year, particularly in the autumn and winter, with average force of 11 to 13 km/hr. (6 to 7 knots). In summer the winds are 6 to 8 km/hr. (3 to 4 knots); and they are from east-northeast in May and June, east-southeast in July, south-southwest in August, and southwest in September. On Pagan winds are from the east from the end of May to the middle of July, and from the west during the rest of the year. From November to May the upper winds are easterly to at least 5,000 meters high, with velocities of 28 to 37 km/hr. (15 to 20 knots). From July to October the easterlies continue with less velocity. Squalls and thunderstorms are frequent in summer and typhoons may occur from July to December, most often in November.

Caroline Islands

The temperature, relative humidity, rainfall, and degree of cloudiness are all high; the atmospheric pressure is uniform; and typhoons are occasional in the west. The Carolines are in the area of the doldrums belt, also called the equatorial or intertropical front. When the belt passes through the area, northward from May to July and southward from August to November, its movement is accompanied by stormy weather and heavy rain. These storms are generally of short duration and alternate with good weather. From December to May the winds are the northeast trades, with somewhat reduced humidity and with monsoon influence in the west.
The mean annual temperature is between 26.1° and 27.8° C. (79° and 82° F.), and the mean diurnal range is less than 6.5° (12° F.). In Palau the mean monthly temperature ranges from 26.7° to 27.3° C. (80° to 82° F.) and the extremes are 21.7° and 32.8° C. (71° and 91° F.). In Yap the means are also 26.7° to 27.8° and the extremes are 23.9° and 31.1° (75° and 88° F.). In Truk the monthly means are from 26.7° to 27.8° C. (80° to 81° F.) and the extremes are 21.1° and 32.8° (70° and 91° F.). In Ponape the monthly means are 25.6° to 27.8° (78° to 82° F.) and the extremes are 20° and 33.3° (68° and 92° F.). In Kusaie the monthly means are 26.7° to 27.8° (80° to 82° F.) and the extremes are 24.4° and 37.8° (76° and 100° F.). All of these figures are for close to sea level.

Atmospheric pressure is extremely uniform in the Carolines, and is slightly lower than in the Marshalls. It ranges from 755 to 764 mm. The average daily oscillation is 2 mm.

Relative humidity is high throughout the Carolines, and it is highest in Ponape and Kusaie. In Palau monthly averages are 77 to 84 percent; in Yap, 80 to 86 percent; in Truk, 80 to 86 percent; and in Ponape, 79 to 91 percent. The lowest humidity is generally in March and April.

Rainfall is fairly heavy in the Carolines; and it is greatest in Kusaie, Ponape, and Palau, particularly in the interiors of Kusaie and Ponape. The monthly means for the high island groups and for one atoll are presented in table 1.

Table 1.—Mean precipitation, Caroline Islands (in millimeters)*

<table>
<thead>
<tr>
<th>STATION</th>
<th>PALAU KOREK</th>
<th>YAP</th>
<th>LANGAHEK</th>
<th>TRUK ERTEN</th>
<th>PONAPE</th>
<th>KUSAIE LAR</th>
<th>KUSAIE MISSION</th>
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</thead>
<tbody>
<tr>
<td>Record, yrs.</td>
<td>9</td>
<td>20</td>
<td>4</td>
<td>7</td>
<td>10</td>
<td>9</td>
<td>10</td>
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<tr>
<td>January</td>
<td>222</td>
<td>161</td>
<td>164</td>
<td>145</td>
<td>268</td>
<td>391</td>
<td>483</td>
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<td>February</td>
<td>182</td>
<td>185</td>
<td>92</td>
<td>206</td>
<td>185</td>
<td>340</td>
<td>388</td>
</tr>
<tr>
<td>March</td>
<td>200</td>
<td>153</td>
<td>135</td>
<td>185</td>
<td>298</td>
<td>403</td>
<td>692</td>
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<tr>
<td>April</td>
<td>173</td>
<td>130</td>
<td>294</td>
<td>289</td>
<td>514</td>
<td>489</td>
<td>542</td>
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<tr>
<td>May</td>
<td>297</td>
<td>257</td>
<td>236</td>
<td>307</td>
<td>481</td>
<td>452</td>
<td>730</td>
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<td>June</td>
<td>306</td>
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<td>341</td>
<td>313</td>
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<tr>
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<td>153</td>
<td>322</td>
<td>399</td>
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<tr>
<td>October</td>
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<td>251</td>
<td>252</td>
<td>370</td>
<td>264</td>
<td>395</td>
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<tr>
<td>November</td>
<td>332</td>
<td>240</td>
<td>188</td>
<td>283</td>
<td>373</td>
<td>351</td>
<td>490</td>
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<tr>
<td>December</td>
<td>388</td>
<td>208</td>
<td>244</td>
<td>302</td>
<td>403</td>
<td>416</td>
<td>408</td>
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<tr>
<td>Annual</td>
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<td>3,024</td>
<td>2,645</td>
<td>3,235</td>
<td>4,514</td>
<td>4,477</td>
<td>6,472</td>
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</table>

* After Reed (1927).
The degree of cloudiness is high in the Carolines, averaging 75 to 80 percent and up to 90 percent in some parts, being highest on the high mountains. Fogs are rare except on Kusaie and Ponape. The dominant cloud type is cumulus.

The winds in the eastern Carolines are from the east from December through April, with an average velocity of about 16 km/hr. (over 8 knots). From May until November the winds are more from the southeast and average about 10 km/hr. (5 knots). These winds extend up to 5,000 meters, above which are the westerlies. In the west the wind is mostly from the east-northeast from November through April and averages about 13 km/hr. (7 knots). In May and June winds are from the east and are slower, and from July through October the winds are light and variable, with occasional squalls.

**Marcus Island**

Marcus, an isolated island, is relatively dry and windy. The annual precipitation is about 1,397 mm. (55 in.), the months from July to November having 125 or more millimeters each and the other months 50 to 100 mm. each. The mean annual temperature is 25.6° C. (78° F.), and the monthly means range from 22.8° (73° F.) in February to 27.8° (82° F.) in July, August, and October. There is an average of 3.7 tropical cyclones or typhoons and 5 extratropical cyclones per year. Clear days exceed cloudy days, and there is no fog. Surface winds are principally from the northwest to east in winter and from the east to south in summer. Winds at a height of 3,000 meters are primarily from the west in winter and from the south and southeast during the rest of the year. The ocean current is westward except in February, when it is southwestward; and the mean surface temperature of the ocean is 26.7° C. (80° F.).

**Wake Atoll**

Annual precipitation for Wake is only 600 to 900 mm. (24 to 35 in.), with September and October having over 100 mm. (4 in.) and the rest less. Mean annual (average) temperature is 26.9° C. (80.4° F.), with the monthly means ranging from 24.8° C. (76.6° F.) in March to 28.8° C. (83.9° F.) in August. The temperature extremes are 20° C. (68° F.) in March and 32.8° C. (91° F.) in August.

**Marshall Islands**

The climate of the Marshalls is uniformly tropical. The mean annual temperature is 27.2° C. (81° F.) and the sea water is uniformly about 28.3° C.
The maximum air temperature is about 34° C. (93° F.) and the minimum about 21.7° (71° F.). The ordinary diurnal range is only a few degrees. The precipitation is about twice as great in the southern Marshalls as in the north. At Jaluit, from 1894 to 1913, the mean annual rainfall was 4,039 mm. (159 in.), with the monthly means above 300 mm. from March to October and in December, and lowest in February with 216 mm. At Ujelang (in the northwest) for the same period the mean annual rainfall was 1,966 mm. (77.4 in.) and the monthly means were above 200 mm. from July through November and lowest in February, with 46 mm. At Kwajalein (2,032 mm.) the dry season corresponds to the period of maximum trade winds (December through March). Rainfall at Eniwetok was 1,219 mm. (48 in.) in 1945.

Atmospheric pressure is very uniform in the Marshalls. Over a period of four years the maximum was 761.6 mm. and the minimum 753.4 mm. Relative humidity is fairly high, and is only slightly lower in the northern atolls. Monthly means for different times of day at Jaluit ranged from 71 percent to 93 percent. In the southern Marshalls the degree of cloudiness is very high, but in the north cloudiness is less than 50 percent. The dominant winds are the northeast trade winds from December through March, and they are moderately strong. The calmest months are August and September. From May to November the wind comes more from the east and southeast, and during this period there may be sudden thunder storms or southwest gales. Hurricanes are uncommon.

**Gilbert Islands**

The climate of the Gilberts is tropical, but less uniform than in much of the rest of Micronesia. The southern Gilberts are even drier than the northern Marshalls. South of the equator, the rainfall averages about 995 mm. (39 in.), and in the northern atolls it may be about 3,500 mm. (136 in.). The average for Tarawa is 1,867 mm. (73.5 in.); but in 1950 the total was only 390 mm. Severe droughts sometimes occur in the south. On Onotoa Atoll the average rainfall is 980 mm. (38 in.) or a little less. Of recent years, 1950 was the driest, with only 167 mm. (all in the second half of the year) and 1946 was the wettest with only 2,162 mm. The driest month on Onotoa is October, with 33 mm.; the wettest is January, with 218 mm., average. The temperature ranges from 21.1° C. (70° F.) to 32.2° C. (90°F.). The southern islands lie between the west-flowing south equatorial current and the east-flowing equatorial counter current, and some have a local north-flowing current. The Gilberts are also at about the northern limit of the southeast trade winds. For most of the year there is a steady easterly trade wind, but from October to March occasional west and northwest gales blow.
Gressit—Introduction

Ocean Island has an annual rainfall of 1,905 mm. (75 in.). The winds are also easterly trades, with squalls from November to March.

Nauru Island has an annual rainfall of 2,057 mm. (81 in.). The winds and currents are from east to west, with westerly squalls from November to March.

FLORA

The relationship of most insects to vegetation is very close, as plants are the primary sources of food of a large proportion of the insect world and, indirectly, of all insects. The entomologist is concerned with the nature of the flora and its relationships for further insight into the distribution and sources of life in Micronesia. Although the seeds of some plants are more resistant to the elements than are many insects, and although some seeds may be more easily transported across the oceans, many of the same factors influence the distribution of plants and insects. The seeds of certain plants may be carried to islands by floating in water or attached to logs caught in the currents, by being blown great distances in storms, by being carried on the feet or bodies of birds, or by man.

The flora of Micronesia, partly for some of the above reasons, may be said to be richer than the insect fauna in terms of proportional representation. For instance, there appear to be almost three-fourths as many kinds of plants as insects on Guam. However, many of the plants were purposely introduced. In many continental areas there may be at least five times as many kinds of insects as higher plants. The environment of the high islands has provided greater diversity of ecological setting than that of atolls, permitting both the establishment of a greater variety of plant forms and the development of endemic ones through speciation. The Micronesian flora is characterized by numerous woody plants, jungle climbers, mangrove trees, palms, Pandanus, and ferns; but it has relatively few herbs, other than some common weeds and grasses of wide distribution.

According to Kanehira’s arrangement (1933) the flora of Micronesia included 1,085 species of higher plants. These were arranged in 594 genera of 137 families, and included 340 endemic species. This did not include the Bonin, Volcano, or Gilbert Islands; and it was far from complete for the areas treated as many additional species, including endemics, have been found since and as others may still remain uncollected. Furthermore, Safford’s numerous Guam records (1905) were ignored. Of the 594 genera listed, 8 were found in the Marianas but not the Carolines, 11 were found in the eastern Carolines (Truk, Ponape, and Kusaie) but not in the western Carolines or the Marianas, 33 were found in the western Carolines but not eastern Carolines or Marianas, 11 genera were common to both east and west Carolines and the...
Marianas (exclusive of generally distributed genera), 27 were found in both east and west Carolines but not in the Marianas, and 11 were found in the western Carolines and Marianas but not the eastern Carolines. In addition, 5 species were found to be endemic to the Marianas and the western Carolines; 3 species to be endemic to the Carolines as a whole; no species to be endemic to the Marianas and eastern Carolines; 8 species to be endemic to Saipan, Rota and Guam; 7 species to be endemic to Yap and Palau; 7 species to be endemic to at least two of the three east Caroline groups (Truk, Ponape, Kusai); and 2 species to be endemic to the Marianas and the east and west Carolines.

Kanehira records 31 species as endemic to Saipan, Tinian, and Rota together; 8 species as endemic to Yap; 65, as endemic to Palau; 12, as endemic to Truk; 35, as endemic to Ponape; and 14, as endemic to Kusai. In Glassman's "Flora of Ponape" (1952), 80 species are listed as endemic to Ponape. Kanehira, on the basis of his findings, concluded that the area he treated should be divided into four areas: (1) the Marianas; (2) the western Carolines; (3) the eastern Carolines; and (4) the Marshalls; and he concluded that the floras of the eastern and western Carolines were related, as were those of the Marianas and western Carolines, but that a barrier existed between the Marianas and the eastern Carolines. There are, however, no endemics in the Marshalls, and Kanehira did not indicate on his map of the floral areas the practical identity of the flora of the Marshalls with that of the Caroline atolls.

In a review of the flora of the Bonin Islands, Wilson (1915) mentions 107 species of native woody plants, of which 43 are trees (Juniperus, Pandanus, Cocos, Livistona, Cyphokentia, Celtis, Ficus, Morus, Cinnamomum, Machilis, Neolitsea, Hernandia, Boninia, Calophyllum, Scaevola, Lobelia, and others); 54 are shrubs (Rubus, Leucaena, Mimosa, Ilex, Sida, Eugenia, Callicarpa, Morinda, Oldenlandia, and others); and 15 are climbers (Freycinetia, Smilax, Piper, Clematis, Mucuna, Vigna, Cissus, Ipomoea, and others). The herbs are stated to be mostly cosmopolitan and a number of woody plants to have been introduced. The 107 species considered native include representatives of about 10 genera not listed by Kanehira for the Marianas, Carolines, and Marshalls.

Kanehira (1933) suggests five vegetation zones: (1) mangrove, (2) atoll growth, (3) strand vegetation, (4) mountain vegetation, and (5) cultivated areas and savanna. Glassman (1952) uses four categories for Ponape: (1) mangrove forest, (2) strand vegetation, (3) secondary growth of lowlands, and (4) rain forest and secondary growth of uplands. Hosokawa (1937) studied Truk vegetation. Fosberg (1946) goes into greater detail with the classification of the vegetation of Micronesia, and he presents the following categories:
1. Mangrove swamps (including *Nypa* and *Acrostichum* marshes and rock-bottomed mangrove depressions)

2. Strand vegetation
   (a) Extreme halophytic types on coasts of high islands and windward beaches of atolls
      (1) Rocky coasts
      (2) Beaches
   (b) Less halophytic types in the interior of atoll islets
      (1) Wet types, tending to be mesophytic
      (2) Dry types, tending to be xerophytic

3. Vegetation on raised coral limestone
   (a) On rough surface with little soil
      (1) Undisturbed forest
      (2) Secondary brush
   (b) On smooth surface with a layer of residual soil
      (1) Undisturbed forest
      (2) Secondary weeds and brush
      (3) Agricultural land

4. Vegetation on volcanic islands
   (a) Coastal plain
      (1) Cultivated or brushy dry land
      (2) Marshes
   (b) Lower primary forest
   (c) Secondary forest on slopes
      (1) Coconut—breadfruit
      (2) Mixed thickets and clearings
      (3) *Hibiscus tiliaceus*
   (d) Montane rain forest or cloud forest
   (e) Dwarf vegetation on exposed crests
   (f) “Savanna”

**Mangrove Swamps**

Mangrove swamps line much of the low shores of the volcanic islands, and may be found in shallow inlets of limestone islands (Fosberg, 1947). Ordinarily, mangrove grows on mudflats, in bays and in riverbeds, or on other low areas within the tidal zone. It may invade normal sand beaches, however, where the beaches are protected by fringing reefs. Mangrove consists of several groups of trees in Micronesia, and most types have either aerial roots or pneumatophores. *Rhizophora* has vertical or oblique prop roots from trunks and branches (fig. 25, b, c). *Sonneratia*, often the most seaward, has slender, pointed, erect root projections from the mud (fig. 3). *Bruguiera*, which grows more inland as a rule than do *Rhizophora* and *Sonneratia*, has somewhat erect knees on the roots. *Xylocarpus*, also growing more inland, has high thin buttresses extending along the tops of the roots. Other genera found in these swamps in Micronesia are *Lumnitzera*, *Excoecaria*, and *Barringtonia* (trees); *Nypa* (palm); *Clerodendrum* (shrub); *Derris* (liana); *Acrostichum*, *Davallia*, and *Nephelepis* (ferns); and orchids (epiphytes). Sometimes *Hibiscus*, *Pemphis*, or *Wedelia* may be mixed with mangrove. In num-
erous places the nipa palm (*Nypa*) grows in solid stands, which are often referred to as nipa swamps (fig. 25, a).

The mangrove flora is rich in Palau and becomes poorer northward and eastward. Of the trees, only *Rhizophora*, *Bruguiera*, *Xylocarpus*, and *Lumnitzeria* are found in Guam, and only *Bruguiera*, in Saipan. *Rhizophora* and *Bruguiera* are widespread in the Carolines, Marshalls, and Gilberts; *Lumnitzeria* occurs in the southern Marshalls; and *Xylocarpus* is found as far east as Kusaie. *Bruguiera* also occurs on Nauru.

![Figure 3](image)

**Figure 3.**—Ponape: Mangrove with *Sonneratia casolaris*, showing erect pneumatophores, and *Rhizophora mucronata*, showing prop roots (Glassman, 1949).

Mangrove is an important land builder and conserver, which is particularly significant on small islands. Mangrove or nipa swamps are somewhat unfavorable environments for insects, because the substrata are covered with water much of the time. However, a few were noted (see ecology), though this habitat was not sufficiently investigated for insects.
Strand Vegetation

Strand vegetation is that which lines the shores of high islands and covers most of the low islands. On raised islands, the strand zone may be very narrow. This vegetation is halophytic, or characterized by high saline tolerance. It tolerates not only salt spray but brackish ground water. The first plants that get a foothold on a new low island represent the strand vegetation. It persists and only rarely tends slightly toward a mesophytic forest. Where mangrove occurs, the strand vegetation may be found on narrow sand spits seaward from the swamps or where the land starts to rise landward of the swamps.

Strand flora is similar on rocky limestone and volcanic islands, except that *Pemphis* is dominant on limestone and lacking on volcanic coasts. On the limestone islands and low islands, according to Fosberg, *Scavola, Wedelia, Pandanus*, and *Terminalia* are found on both rocky and sandy shores. *Pemphis, Casuarina, Thespisa, Excoecaria, Clerodendrum, Barringtonia, Capparis, Heliotropium, Digitaria*, and *Fimbristylis* grow primarily on rocky shores; *Messerschmidia, Triumfetta, Cocos, Lepturus, Ipomoea pes-caprae*, and *Suria* grow on sand shores; *Cordia, Calophyllum, Hernandoa*, and, more rarely, *Pemphis* occur on the inner beach; coconut and breadfruit grow behind the beaches. *Morinda, Pandanus, Guettarda, Pisonia, Ochrosia, Hibiscus, Prenna, Eugenia, Polypodium, Nephrolepis, Wedelia, Taccia, Piper* (fig. 48, b), *Pteris*, and *Glochidion* grow in the interior of low islands; *Thuarea, Paspalum, Digitaria*, and *Lepturus* are found in grassy clearings; *Cyphes, Bleocharis, Jussiaea, Cyrtosperma*, and *Colocasia* are found in marshes; and various “weeds” grow around the villages.

Atoll vegetation is discussed further under the Marshall Islands, as more studies have been made on some of the Marshall atolls than in most other low islands of Micronesia.

Vegetation of Raised Coral Limestone

The flora on high coral islands represents an intermingling of strand vegetation and elements of the damp mesophytic forest. Some strand elements remain; but in general, the fleshy halophytic plants are lacking and the flora is much richer. Inland, this flora is characterized by *Elodocarpus, Ochrosia, Lantana, Pipturus, Artocarpus, Aglaia, Pandanus, Cysses, Fagraea, Claoxylon, Boerlagiodendron, Schefflera, Ficus, Premna, Guama, Eugenia, Hernandoa, Pouteria, Melanolepis, Cynometra, Pisonia, Erythrina, Randia*, and many other trees—festooned with *Canavalia, Mucuna, Ipomoea, Caesalpinia, Gymnosporium, Freycinetia*, and other vines—and by *Psychotria, Clerodendrum, Canthium, Tarenna, Wikstroemia*, and other shrubs and ferns. In Palau this flora
is even richer, with Guadubiopsis palms, Dracaena (figs. 21, b; 22, b), Casuarina, Pithecolobium, Pongamia, Meryta, and others. And in Palau most of the plants are limited to steep pitted slopes, with almost no soil, whereas in the Marianas most of them grow on flat plateaus with thin, though in places thick, red soil. Bikia (fig. 8, b), Capparis, Ficus, Jasminum, Clerodendrum, Barringtonia, and Elaeocarpus are common on steep slopes. Certain other genera are characteristic of limestone bluffs exposed to salt spray.

Where raised limestone covered with soil is cleared, “weeds” such as certain species of Cassia, Sida, Mallotus, Croton, Asclepias, Euphorbia, Paspalum, Eleusine, Cenchrus, Vernonia, Cleome, Portulaca, and Passiflora first appear. Later, brushy patches develop, with Leucaena, Psidium, Morinda, and papaya mixed with Ipomoea and Passiflora; and large areas may become covered with Melochia (as on Rota), Leucaena (as on Guam and Koror), Macaranga and papaya (as on Angaur), or Jatropha (as on Tinian). When rough coral surfaces are cleared, as on Angaur and Peleliu, a dense brush of Pipturus, Macaranga, Hibiscus, and other shrubs, mixed with Ipomoea develops. The native flora is apparently almost exterminated on these islands, whereas the above-mentioned invaders, along with Casuarina, have remained dominant.

Coastal Plain

The coastal plain zone is a narrow strip behind the strand and mangrove on high volcanic islands. As exemplified in Truk and, to a lesser extent, in Ponape, Kusaie, and Babelthuap, it consists of a raised fringing reef covered by rock debris. Originally, the vegetation was primary rain forest, but this persists only on Babelthuap, with some remnants on Ponape. This environment is primarily occupied by villages and cultivated areas. Dry ground is used for villages and for coconut groves, banana, breadfruit, Citrus, Annona, sweet potatoes, cassava, and other crops. It also supports mango, Ficus, Calophyllum, Terminalia, ivory nut palm (in Ponape and Truk), Pandanus, Macaranga, Morinda, Hibiscus, and other trees, with some undergrowth, Alocasia, grass, or “weeds.” Wet ground is cultivated to Cyrtosperma and Colocasia, or invaded by “weeds.”

Lower Primary Forest

The lower primary forest was originally rain forest, but it persists in only parts of Babelthuap (fig. 24, b-d), Ponape (figs. 4, 41, b, c), and Kusaie (fig. 49, a), with a few fragments higher up in Truk. It consists of large trees, including Parinari, Campnosperma, Couthovia, Cynometra, Dysoxylum, Ficus, Semecarpus, Randia, Fagraea, Pittosporum, Schefflera, Horsfieldia, and many others. Palms such as Pseudopinanga, Ezorrhiza, and Ponapea are
found. So are occasional slender, erect Pandanus; climbers such as Freycinetia, Canavalia, Piper, aroids, and Ipomoea; and ferns, orchids, and other epiphytes.

![Image](https://example.com/image.jpg)

**Figure 4.** Ponape rain forest, slope of Mount Nahmaland, at about 450 meters, with seedlings of *Exorrhiza ponapensis*, fallen fronds at left (Glassman, 1949).

**SECONDARY FORESTS ON SLOPES**

On most of the islands much of the rain forest has been destroyed up to altitudes of about 200 m. and replaced by mixed coconut and breadfruit groves, with bananas, Alocasia, and some shrubbery beneath; and with occasional thickets of native trees or dense growths of *Hibiscus*. War-time Japanese fields of sweet potato and cassava are heavily invaded by other *Ipomoea*, by *Merremia* and coarse grasses, or by *Macaranga, Acalypha*, or other “weed” shrubs. (See figures 37, b; 39, b.)

**MONTANE RAIN FOREST, OR CLOUD FOREST**

The montane rain forest (fig. 5, a, b) consists of scrubbly, dripping, mossy forest on steep slopes or ridges in the cloud zone, where soil is thin and the wind is strong. An association consisting of tree ferns, *Exorrhiza* and *Ponapea*
FIGURE 5.—Pompee, 1953: a, cloud forest ridge between two highest peaks (Nahnalaud and Ngilmeni) at about 800 meters, *Exorrhiza* palms at left; b, swampy slope just below summit of Mount Nahnalaud, with *Exorrhiza* palms, *Pandanus* (right), and *Thoracostachyum* (center); c, wind-blown ridge between Nahnalaud and Ngilmeni, with *Cyathus* tree fern.
palm, Freycinetia, and many stunted broad-leaved trees bearing epiphytes, ferns and mosses predominates. The moss-clad trunks or branches appear to have several times their actual diameter. This forest, common at high altitudes, may occur much lower when there is a cloud belt. It is well developed and preserved extensively only on Ponape and Kusaie, but some fragments remain in the Marianas. In the Palaus it is feebly developed because of the inferior elevation.

DWARF VEGETATION ON OPEN CRESTS

Dwarf vegetation on open crests develops where rainfall is high and winds strong. In general it can be said to be a modification of the montane rain forest. On Kusaie (fig. 49, b) it usually consists of tree ferns, ferns, and masses of moss and liverworts, and it is often dominated by Gleichenia. On Ponape (fig. 5, c) the high ridges are often heavily covered with dwarfed shrubs or trees, tree ferns, and dwarfed Exorrhiza; or open bogs or dense tangles of Pandanus patina may occur.

“SAVANNA” OR GRASSLAND VEGETATION

The grassland of Micronesia is not true savanna, as it is almost never on flat land. It occurs only on volcanic land, which probably was forested originally and converted into grassland by clearing and repeated burning. Yearly burning to improve grazing conditions prevents the natural forest from reappearing. This grassland (figs. 17, b; 23) is dominated in places by Miscanthus and other genera. Certain weeds and Casuarina appear where fire does not destroy them. Lycopodium, Nepenthes, Pandanus, and Gleichenia, together with a few shrubs, are characteristic in some places.

Where volcanic soil meets limestone, the former often supports grassland and the latter, forest. Regeneration of natural forest is more rapid on limestone, as grasses do not thrive on these soils. In Ponape and Kusaie, where rainfall is higher, forest regeneration is rapid on volcanic soil and grassland is rare. Truk, which is also volcanic, is intermediate in humidity and extent of grassland. The above information is largely after Fosberg (1946).

INTRODUCED PLANTS

Large numbers of plants were accidentally or purposely introduced during the migrations of early settlers, discoverers, colonists, and others. And with modern commerce, warfare, and aviation, they are being introduced at a more rapid rate. Many of these have been able to establish themselves, particularly on the larger high islands. Some of them have been mentioned above,
and others are noted under descriptions of islands or environments. Most of
the important agricultural plants—listed alphabetically in the section on
economic entomology—are introduced; but few came with the early in-
habits. Weeds are numerous and many are pantropical. Some which have
established themselves recently around airports or ports have come from
Hawaii. These include two species of Pluchea and one each of Trichachne and
Chloria. Species of Euphorbia, Ipomoea, Wedelia, Mimosa, Amaranthus, Mer-
remia, various grasses, and many others are important weeds.

DESCRIPTIO NS OF THE ISLANDS

INTRODUCTION

The geographical features of Micronesia are significant, not only because
of their interesting nature, but because of their effect on the insect fauna.
Insects are specialized animals requiring specific environments. Few of them
can survive in salt water, but require suitable land habitats, including par-
ticular plant and insect or vertebrate hosts. Small islands may have as many
kinds of plants as insects, because few insects can become established until after
the plants have arrived.

Micronesia, as the name suggests, is conspicuous for the small size of its
islands and for their abundance. Though the size of the insect fauna of an
island is correlated with the area of the island, other factors being equivalent,
the proximity of the island to similar islands, and to continental islands or
continents, has an important bearing on the richness of the insect fauna.

Table 2.—Highest islands in Micronesia (altitudes in meters)*

<table>
<thead>
<tr>
<th>Island</th>
<th>Altitude</th>
<th>Island</th>
<th>Altitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>†Minami Iwo Jima</td>
<td>970</td>
<td>Tonoas (Dublon), Truk</td>
<td>361</td>
</tr>
<tr>
<td>Agrihan</td>
<td>966</td>
<td>Chichi Jima</td>
<td>326</td>
</tr>
<tr>
<td>Asuncion</td>
<td>891</td>
<td>†Parallon de Pajeros</td>
<td>319</td>
</tr>
<tr>
<td>†Kita Iwo Jima</td>
<td>801</td>
<td>†Guguan</td>
<td>301</td>
</tr>
<tr>
<td>Ponape</td>
<td>791</td>
<td>Pefan, Truk</td>
<td>298</td>
</tr>
<tr>
<td>Anatahan</td>
<td>788</td>
<td>Uman, Truk</td>
<td>292</td>
</tr>
<tr>
<td>Alamanhan</td>
<td>745</td>
<td>Ulot, Truk</td>
<td>243</td>
</tr>
<tr>
<td>Kusaie</td>
<td>630</td>
<td>Babelthaup</td>
<td>242</td>
</tr>
<tr>
<td>†Pagan</td>
<td>573</td>
<td>Mang</td>
<td>228</td>
</tr>
<tr>
<td>Sarigan</td>
<td>549</td>
<td>Ngurlokabel, Palan</td>
<td>204</td>
</tr>
<tr>
<td>Roti</td>
<td>496</td>
<td>Ulelebele, Palan</td>
<td>186</td>
</tr>
<tr>
<td>Saipan</td>
<td>473</td>
<td>Yap</td>
<td>178</td>
</tr>
<tr>
<td>Haha Jima</td>
<td>457</td>
<td>Agigan</td>
<td>178</td>
</tr>
<tr>
<td>Ton (Toi), Truk</td>
<td>452</td>
<td>Tinian</td>
<td>172</td>
</tr>
<tr>
<td>Guam</td>
<td>406</td>
<td>Iwo Jima</td>
<td>169</td>
</tr>
<tr>
<td>Wena (Moen), Truk</td>
<td>370</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* After Bryan (1946a), National Geographic Society (1952), and U. S. Navy Hydrographic Office.
† Active volcanoes (Asuncion has been active during the twentieth century).
Other factors also affect the picture, including the direction from other land areas in relation to prevailing winds and sea currents, or possible wind directions during storms, and routes of human and bird migration. The richness and variety of the flora are of the greatest significance. Many factors affect the insect fauna directly, as well as through the dependent vegetation and other sources of food or habitat. Various categories of information pertaining to some of these factors are presented below, followed by discussion of the islands by groups.

High island groups, in order of decreasing height, are the Volcano Islands, the northern Marianas, Ponape, Kusaie, the southern Marianas, the Bonins, Truk, Palau, and Yap.

High island groups, in order of decreasing area, are the southern Marianas, Palau, Ponape, the northern Marianas, Kusaie, Yap, Truk, the Bonins, and the Volcano Islands.


ATOLLS AND LOW ISLANDS

An atoll ordinarily consists of an oval or irregular ring of small islets surrounding a lagoon. The islets are low, rarely over 3 meters in altitude, and generally consist of coral boulders, coral fragments and coral sand. Humus may have accumulated from decaying vegetation. Often there is some solidified beach sandstone on parts of the lagoon sides of islets. Fresh water is scarce. The lagoons are generally shallow and surrounded by reef if not by islands, and may or may not have entrances. Low islands are similar to atolls, but they do not have lagoons and are generally single islands or pairs of adjacent islets.

Gilbert Island atolls average 10 times as large in land area as do the Caroline atolls, and Marshall atolls average three times as large in area as do the Caroline atolls. In ratio of lagoon area to land area, the proportions are reversed, with Caroline atolls averaging 90 times as much lagoon as land, Marshall atolls averaging 66, and Gilbert atolls eight times as much lagoon area as land area. Table 3 lists figures for both atolls and isolated low islands in the Gilberts, Marshalls, and Carolines. Reef islets in high Caroline groups are excluded. There are no “low” islands in the Marianas, Volcano, or Bonin Islands. Barely exposed rocks of volcanic origin do not fall in this category.
Table 3.—Number and area (in square kilometers) of Micronesian atolls and isolated low islands*

<table>
<thead>
<tr>
<th></th>
<th>Carolines</th>
<th>Marshalls</th>
<th>Gilberts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atolls</td>
<td>31</td>
<td>29</td>
<td>11</td>
</tr>
<tr>
<td>Low islands other than atolls</td>
<td>11</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Total land area</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Both types</td>
<td>67</td>
<td>181</td>
<td>295</td>
</tr>
<tr>
<td>Atolls only</td>
<td>56</td>
<td>178</td>
<td>239</td>
</tr>
<tr>
<td>Average land areas</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Both types</td>
<td>2.2</td>
<td>5.3</td>
<td>18.4</td>
</tr>
<tr>
<td>Atolls only</td>
<td>1.8</td>
<td>6.1</td>
<td>21.7</td>
</tr>
<tr>
<td>Lagoon area of atolls</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total area</td>
<td>5,690</td>
<td>11,671</td>
<td>2,012</td>
</tr>
<tr>
<td>Average area</td>
<td>162</td>
<td>402</td>
<td>183</td>
</tr>
<tr>
<td>Ratio of land to lagoon area</td>
<td>1:90</td>
<td>1:66</td>
<td>1:8</td>
</tr>
</tbody>
</table>

* After Bryan (1946a) and Freeman (1951).

Bryan has published a check list of the world’s atolls with a few comparative notes (1953).

RAISED ATOLLS AND RAISED LOW ISLANDS

A few islands in Micronesia are, strictly speaking, neither low islands nor high islands. They have been called raised atolls because many are higher around some of the borders than in the center. Another characteristic which these islands have in common is their deposits of phosphate, which have presumably been formed by ancient accumulations of guano reacting with the coral limestone. It has been suggested that the formation of phosphoric acid with the seeping of rainwater through the guano deposits has acted upon the limestone to form calcium phosphate after the raising of the atoll lagoon above sea level.

Micronesian islands which are usually placed in the category of raised atolls are the following (followed by their altitudes in meters): Ocean Island (81), Nauru (65), Fais (20), Angaur (61), Marcus (formerly 21), and Peleliu (80). Ocean Island and Nauru are west of the Gilberts; the others, in the western Carolines, except Marcus which is east of the Volcano Islands. Angaur is part of the Palau Islands, but it is outside the main reef. It is not evenly raised, but has rough coral rock pushed higher in the northwest portion. Peleliu, just north of Angaur and at the south end of the Palau reef, has also been called a raised atoll, but it has distinct steep hills and ridges of different heights, suggesting more volcanic activity in connection with its uplift. Peleliu has limited phosphate deposits. Fais is poorer in phosphate than Angaur, Ocean, or Nauru; and Marcus is still poorer. The Daito Islands also...
belong to this category (Nugent, 1948), and so perhaps do Tobi, Merir, Pulo Anna, Sonsorol, and Gaferut.

The Ngemelis Islands, just northwest of Peleliu, are suggestive of slightly raised reef islets, but some of them are more strongly raised, resembling the high coral islands to their north.

**Bonin Islands**

The Bonin Islands (fig. 6) represent some peaks of the great submarine volcanic ridge extending from Tokyo Bay to Guam. The ocean bottom drops steeply on each side. The Ramapo Deep (10,373 meters in depth) lies just east of the chain. The Ryukyu Deep (7,335 meters) lies some distance to the west. The islands consist of a type of andesitic lava called boninite and sedimentary agglomerate tuffaceous rocks. There is coral limestone at the tops of some of the mountains, as well as fossil sea shells, and Eocene Nummulites (Hachisuka, 1930), indicating that the islands have been submerged and re-elevated since they were first formed. The islands stretch some 137 kilometers north and south and consist of three groups, Muko Jima Retto (Parry group), Chichi Jima Retto (Beechey group), and Haha Jima Retto (Bailey group). The islands are rough and irregular in outline, indicating considerable erosion and subsidence. The total area of the group is only 72 square kilometers (7,200 hectares). There are 97 islands and islets. There are many cliffs, but few beaches.

**Muko Jima Retto (Parry Group)**

Muko Jima group is the northernmost of the Bonins and includes four islands and a number of islets. The area is only 6.7 square kilometers. Kitano Shima, at the northwest, is steep and grassy and 51 meters high. To its east are three islets and some rocks. Muko Jima, the largest, is hilly in the north with an altitude of 91 meters, and with a plateau in the south. It lies three kilometers southeast of Kitano Shima. Harino Iwa, a series of sharp, jagged rocks, lies 1 kilometer southeast of Muko. Tamati Iwa is a rock between Harino and Nakado. Nakado (Nakadachi) Shima, the second largest of the Muko group, is 6 kilometers southeast of Muko. It is rough and rocky, with cliffs. The highest peak, Byobu-yama in the south, is 155 meters high, and Tsunagi-yama, in the northwest, is 121 meters high. Yome Shima, the southernmost island, is rough and rocky, with hills 51 and 67 meters high. There is a small island on each side.
Figure 6.—Map of Bonin and Volcano Islands.
CHICHI JIMA RETTO (BEECHEY GROUP)

Chichi Jima group is 34 kilometers south of the Muko Jima group. It consists of six islands and many small islets. The area of the group is 39 square kilometers. Ani Shima is rocky, with cliffs, and has hills 254 meters high on the south and 183 to 238 meters high in the northwest. Nishi Jima is west of Ani Shima, with small islets between. It is rocky, with precipitous cliffs, and is fringed with rocks or islets. The hill on the southwest peninsula is 100 meters high. Higashi Shima is east of Chichi Jima. Ototo Shima is north of Ani Shima and is hilly and barren, with some cliffs. Mago Shima, north of Ototo Shima, is small, with cliffs. Minami Shima, south of Chichi Jima, is narrow, with cliffs and offshore rocks or islets. There are two crater lakes and a larger sunken crater which forms a harbor. Chichi Jima, by far the largest of the group (25 sq. km.), is quite rugged. The highest altitude is 327 meters, near the center. Futami-ko (Port Lloyd), the largest and best harbor of the Bonins, is on the northwest (fig. 7). Nishino Shima is small, flat and grassy. It is 24 meters in altitude and is located about 129 kilometers west of Chichi Jima.

Figure 7.—Bonin Islands, Futami Harbor, looking north toward Omura (Port Lloyd), Chichi Jima (Paul Gantt, U. S. Commercial Co., 1946).
Haha Jima group is about 48 kilometers (30 miles) south of Chichi Jima and consists of the main island and five small islands. The total area is 26 square kilometers. Haha Jima is nearly as large as Chichi Jima. It is rough and mountainous, with the highest altitude of the Bonins (462 meters) near the middle. There are few beaches, and there is almost no level land. Of the small islands to the south, Muko (not the larger Muko to the north), 135 meters high, is southwest; Hira is 60 meters high, closer to Haha; Mei is 112 meters high, to the east-southeast; Imoto is 213 meters high and densely forested; and Ane Shima is 122 meters high and south of Hira and west of Imoto.

The original vegetation of the Bonin Islands was subtropical jungle. Being in a warm sea current, this more northern group is not very different in its environment from the rest of Micronesia, though its flora is somewhat distinct, and much poorer. With human exploitation, much native forest on some islands was supplanted by introduced pine, *Casuarina*, guava, *Acacia*, banyan, papaya, *Euphorbia*, *Hibiscus*, *Lagerstroemia*, and other trees or shrubs, as well as weeds. Herbs were originally rather few.

Volcano (Kazan) Islands

This group consists of three isolated islands (fig. 6) between the Bonin Islands and the northern Mariana Islands. These islands are also peaks of the great submarine ridge from Tokyo to Guam and include active volcanoes. The total land area is 30 square kilometers.

Kita Iwo Jima, the northern island, is 5 square kilometers in area and consists of an active volcanic cone 801 meters high on the south and 664 meters high on the north. The slopes are steep, with some cliffs.

Iwo Jima (area 20.5 sq. km.) is largely a somewhat plateau-like, flat-topped dome with some small cones and with Suribachi-yama (169 meters), an extinct volcano, at the end of the southern peninsula (fig. 8, a). Steam and sulphur vapors are emitted from cones in the north.

Minami Iwo Jima is smaller (3.8 sq. km.), circular, and 969 meters high. The slopes are steep, with cliffs and a few rocky beaches. This active volcano is the highest peak of Micronesia, in the broad sense.

Iwo Jima has had its natural vegetation destroyed and has only a partly replaced secondary growth. Kita Iwo Jima and Minami Iwo Jima are steep and have never been inhabited. Their natural growth, largely scrubby, persists; but nothing has been published on their vegetation. The flora is not rich in species.
Mariana Islands

Northern Marianas

The northern Marianas are small or of intermediate size, and mostly rather high, including several of the highest islands of Micronesia (fig. 9). They are strictly volcanic, with no raised coral, if Medinilla is grouped with the southern Marianas; and there are no atolls or low islands. They include the only active
Figure 9.—Map of Mariana Islands.
volcanoes of Micronesia proper. Vegetation is somewhat limited in extent and variety.

Farallon de Pajaros, or Urucas Island (lat. 20° 32' N.), is the northernmost of the northern Marianas. It is an active volcano 319 meters in altitude and only 2 square kilometers in area. The slopes are steep, there are no beaches, and the island has not been inhabited. Grass and a few trees grow only on the south side.

The Maug Islands (lat. 20° 01'/2' N.) are a group of three steep peaks surrounding a lagoon, which represents a sunken crater. North Island has an altitude of 228 meters and an area of 0.5 square kilometer. There are no beaches, no water, and only a few shrubs. Sea birds nest there. West Island is 180 meters high and 0.7 square kilometer in area. There is a group of small pandanus and papaya plants, and grass and vines on the more gentle slopes. East Island has an altitude of 216 meters and an area of 0.93 square kilometer. It had a weather station during the Japanese period. At that time there were vegetables and a few coconut palms, and dense low bushes and trees on the northwest side.

Asuncion Island (lat. 19° 40' N.) is an almost perfect volcanic cone 891 meters high. The area is 7.3 square kilometers. There are several coconut groves; and banana, taro, pineapple, breadfruit, squash, limes, and mangoes grow on the lower slopes of the west and south sides. There were two villages during the war.

Agrihan Island (lat. 18° 46' N.) is a volcanic cone 966 meters high and 47 square kilometers in area, last active in 1917. The highest peak in Micronesia proper, its slopes are covered by sword grass and have deep ravines and sharp ridges, with dense vegetation, partly of introduced plants. These formerly included coconut, papaya, breadfruit, mango, lime, orange, taro, yam, sugar cane, and pineapple. Many native plants are still found. The monitor lizard, colonies of sea birds, and goats, are present.

Pagan Island (lat. 18° 07' N.) consists of two volcanic peaks with a low connection. The total area is 48 square kilometers. The northeastern part is Mount Pagan, 570 meters high and an active volcano; and the southwestern part is 518 meters high and has several craters, some of them periodically active. Peaks on the isthmus are of 543, 449, and 316 meters in altitude. There was formerly a village and coconut groves, banana, *Casuarina*, sword grass, *Pandanus*, and many other plants.

Alamagan Island (lat. 17° 36' N.) is a volcanic cone 745 meters high and is at present inactive. The area is 11 square kilometers. There are trees, undergrowth, coconuts, bananas, papayas, *Pandanus*, ferns, and other plants in the ravines and on the lava flows; and brush and sword grass grow on the upper slopes. Formerly, there were two villages.
Guguan Island (lat. 17° 19' N.) has two volcanic peaks, the northern one 248 meters high and active, the southern one 301 meters high. The area is 4.2 square kilometers. Low grass grows on the volcanic ash; and breadfruit and certain trees and shrubs grow in the southern ravines, but no coconut palms. The island is uninhabited. There are two small rocks between Guguan and Sarigan.

Sarigan (Sariguan) Island (lat. 16° 43' N.) is a volcanic cone with twin summits, 548 and 549 meters in altitude. The area is 5 square kilometers. The island was inhabited under the Japanese, who grew coconut palms, papaya, taro, yams, pineapple, and squash. Monitor lizards, nesting sea birds, feral fowls, and bats are present.

Anatahan Island (lat. 16° 21' N.) is oblong, with a large volcanic crater 788 meters high toward the west end. The area is 32 square kilometers. Three small beaches and the formerly inhabited portion of the island are on the west end. Most of this part of the island is covered with native vegetation or coconut palms; but banana, papaya, ferns, vines, shrubs, and trees are present. The rest of the island is largely precipitous, and almost without vegetation. The floor of the crater is covered with tall grass. Monitor lizards and numerous rats and land crabs are present. There are small pools of water in some of the ravines. This island is warmer and damper than Saipan. Rainfall is heavy and the peaks are often covered with clouds.

SOUTHERN MARIANAS

The southern Marianas Islands are comprised of several of the larger islands of Micronesia, including the largest, Guam. These are volcanic islands which have, at several levels, great amounts of coral limestone raised up from beneath the sea. In some places, such as the northern half of Guam, coral limestone forms terraces, or a huge block in the form of a plateau, several cubic kilometers in volume. Coral limestone also occurs on the tops of the highest peaks of some of the more volcanic and hilly portions. Farallon de Medinilla is sometimes classed with the northern, and sometimes with the southern, Marianas. Geologically, it is more like the southern Marianas, having raised coral limestone.

Four principal types of vegetation are found. Mangrove is of minor importance. Strand vegetation is normal, except where it merges with the raised limestone forest. The latter was formerly extensive, but much of it has been cleared in recent years. “Savanna” grassland dominates much of the volcanic areas.

Farallon de Medinilla (lat. 16° 01' N.) is a narrow, precipitous ridge of raised coral limestone, 80 meters in altitude. The area is 0.9 square kilometer.
Figure 10.—Map of Saipan: inset shows areas of limestone and of volcanic rock, including small areas of alluvium or other mixtures of volcanic and limestone rock or soil. (Inset adapted from manuscript map by P. J. Cloud, R. G. Schmidt, and H. W. Burke.)
The ridge is somewhat flat-topped and covered with shrubs. There are deposits of guano, and the island has probably not been inhabited. This island is 72 km. (45 miles) north-northeast of Saipan. Geologically, it probably belongs to the southern Marianas, though it is a little closer to Anatahan than to Saipan.

**Saipan**

Saipan (fig. 10) is the second largest (area 121 sq. km.) of the Mariana Islands, and northernmost of the southern Marianas, except for Farallon de Medinilla. Topographically, Saipan is more diverse than the other Mariana Islands, and its geology is more complex. The outline of the island is irregular, with bays on both sides. Coral reef is extensive on the west, but very limited on the east. A rough range extends down the northern two-thirds of the island. The highest peak is Mount Tagpochan, 473 meters high, just south of the center, and the lesser peaks—Mount Atchugan, Mount Putosuka, and Magpi Peak—are in the northern third. Much of this higher land consists of irregularly raised coral limestone pushed up by volcanic action, but there is also a considerable area of volcanic land distributed irregularly. The southern part of the island consists of a plateau largely covered by lateritic clay soil of mixed volcanic-coraline origin. The eastern edge of Saipan consists mainly of cliffs (fig. 11). The western border is low, forming a broad coastal plain from 1 to 4 meters in altitude. It is mainly sandy and even has some sand dunes near the southwest end. Most of the southern plateau and of the western coastal plain are cultivated, principally to sugar cane. The principal villages are Garapan at the middle of the west coast and Chalan Kanoa on the southwest coast. There is a small lake, Susupe, near Chalan Kanoa. The Hagman Peninsula, on the middle of the east coast, is partly flat and fairly low. There is a hill at the southeastern corner of the island, on the southern plateau.

Strand flora is well developed on Saipan. Most of the coastal plain on the west side is cultivated. Lake Susupe is nearly fresh and is surrounded by marshes, or swamps, where grow *Paspalum, Phragmites, Acrostichum*, and *Clerodendrum*. Volcanic areas are grassland or have secondary forest with *Acacia, Albizia*, and other trees. The upland limestone originally was covered with rain forest, but this was largely destroyed during the war and has been invaded by *Acacia* and *Albizia*.

**Tinian**

Tinian (101 sq. km.) is a fairly low island of plateaus consisting primarily of terraces of raised reef limestone of four or more levels, divided by lines of cliffs or bluffs (figs. 8, b; 12). Some of the terraces have tilted, causing irregularities. Most of the level surfaces of the terraces are covered with soil
Figure 11.—Saipan: a, Hagman Point, showing scrub at top of limestone cliff, forest in small valley on limestone, Casuarina and sword grass on volcanic slope in background; b, forested Magpi cliffs (limestone), abandoned sugar plantation in foreground; c, Fangu-chuluyan Bay, showing sword grass on conspicuous outcrop of gray volcanic rock, broken secondary forest in background, and forest on limestone cliffs. (Fosberg, 1946.)
Figure 12.—Map of Tinian.
of varying thickness. There are some limestone sinks, one of which contains a small lake. The highest altitudes are Mount Lasso (172 meters) in the north central part of the island and lower hills in the north, east, and south. There are a few very small basalt outcrops, and some of the soil is said to be volcanic. Tinian was used by the Spanish for grazing cattle, which were hunted for meat. The island has lost most of the natural vegetation of its flat limestone terraces to cultivation. Eighty percent of the area is arable. Under the Japanese, this was mostly planted to sugar cane, but much of it has grown up to brush since the war. However, cattle grazing and vegetable growing are being developed. The sea cliffs have limited vegetation, comprised chiefly of Bikkia, Hedyotis, and Myoporum, with Barringtonia near the base of the cliffs. Pemphis and Messorchidia grow closer to the water.

Agigan

Agigan (Aguijan) is 7.2 square kilometers in area and is 24 kilometers from the southern end of Tinian (fig. 12). This island is similar to Tinian, but it has less level land and more variation in terrace levels. In fact, as many as eight levels of limestone terraces can be counted. The highest altitude (178 meters) is near the center of the island. The coastline is rough and without beaches. Fresh water is very scarce. Agigan’s vegetation is similar to that of Tinian, but more native scrub remains.

Agigan is the site of an experiment started in 1949 to test the effectiveness of the predaceous African snail, *Gonaxis kibwistensis*, for the control of the giant African snail, *Achatina fulica*. Goats, rats, monitor lizards, and coconut crabs are present.

Rota

Rota (fig. 13), with an area of 85 square kilometers, lies between Saipan and Guam. It is the highest of the southern Marianas, rising to 496 meters, just southwest of the center. The island consists of a series of five or more elevated coral limestone terraces, largely sloping seaward. The highest point consists of volcanic rock projecting through the limestone, and more volcanic rock and soil is exposed on the south side near As Malete, but it is capped in the center with limestone. In general, the soil is fairly thin; and the island is not very productive agriculturally. Rota has had its vegetation less disturbed than have the other southern Marianas. At higher altitudes on the rough limestone the forest becomes more mesophytic and richer in species. *Prenia netia*, ferns, and orchids are common. There is a poorly developed grassland on the volcanic summit, as well as a grove of *Acacia*. Former cultivated fields and cane plantations were largely grown up to weeds and brush in 1946, but now some vegetables are being raised.
Guam (fig. 14) is the largest island of Micronesia, with an area of 558 square kilometers, and is the third highest of the southern Mariana Islands (406 meters). The northern half of the island consists of a great raised plateau of coral limestone. It is more or less flat but slopes gradually to the south, from 175 meters at the north end down to about 60 meters or less between Agana and Barrigada, with some higher terraces behind Agana (fig. 15). On this large coral plateau there are a few low, eroded volcanic hills, including Mount Santa Rosa in the northeast, Mount Machanào in the north, and Mount Barrigada in the east. This northern plateau is edged almost entirely with cliffs, with just a few narrow beaches. Sometimes narrow beaches border bottoms of cliffs. Just northeast of Agana there is a marsh (Agana Swamp) which is just barely above sea level.

The southern half of the island is irregular and consists largely of volcanic rock or soil. A line of peaks, all higher than the northern plateau, extends southward parallel to the west coast. These peaks include Mount Chachao, Mount Alutom, Mount Alifan, Mount Lamlam (highest), Mount Junujong Manglo, Mount Bolanos, and Mount Sasalaguan, ranging from 265 to 406
Figure 14.—Map of Guam, inset shows areas of limestone, volcanic rocks, and mixed limestone and volcanics consisting of alluvial deposits or argillaceous (clay) limestone contaminated with volcanic material. (Inset adapted from manuscript map by Tracey, Schlanger, Dean, Stark, and May, U. S. Geological Survey.)
meters high. There is some coral limestone rock here and there in the southern half, at all altitudes, including the extreme summits of Mount Lamiam and Mount Alifan. And there is quite a bit of coral rock near the eastern coast south of the middle of the island. East of the ridge of peaks near the west coast, the land slopes to an irregular plateau of about 100 to 150 meters in altitude, with lower valleys and basins. Much of the area drains into the Talofofo River; but to its north, quite an area drains into the Ylig River. The east coast of the southern half is partly of low cliffs and partly with beaches behind coral reef. The west coast is rugged, but with few cliffs, and in some parts with a narrow coastal strip. Caves are found in the center of the island and in some of the cliffs. There are no rivers on the northern plateau, as the water sinks into the porous coral rock.

Point Oca, where much collecting was done, is on a fairly low part of the coralline plateau between the beaches of Tumon Bay and Agana Bay. Part of the plateau here, south of the coastal cliffs, slopes almost continuously to the narrow Agana beach. Natural vegetation has been largely eliminated since 1945 (fig. 16, a).

Guam formerly had extensive jungles on the limestone plateau on the northern half (fig. 16, b, c), but since 1945 these have been eliminated for airfields or buildings on a considerable portion of the area. The volcanic
Figure 16.—Guam: a, Point Oca, scrub and weeds at top of limestone cliffs, 1951; b, north-central limestone plateau, mixed forest, with breadfruit, Pandanus, and papaya, 1945; c, north-central plateau, natural forest with Pandanus and Cycad, 1945.
Figure 17.—Guam: a, rice field just northwest of Inarajan, showing Usinger and Swezey collecting in 1936; b, southeast side of hill south of Mount Alifan, showing sharp line of demarcation between forest growing on raised reef coral (summit shaded by cloud) and Miscanthus sword grass on soil of volcanic origin below. (Bryan, 1936.)
Caroline Islands

The Carolines (figs. 18, 19) stretch over a great expanse of ocean, some 3,860 kilometers east and west, from about 1° to 10° north of the equator. There is great diversity in the geology and geography of the Carolines. The archipelago includes three assemblages of high islands (Palau, Yap, Truk), two or less single high islands (Ponape, Kusaie), 31 atolls, and 11 isolated low islands or raised low islands. In addition, there are coral islands associated with the high islands, such as the islands of considerably raised coral rock in Palau and low islands of the Palau and Truk barrier reefs and on the Ponape and Kusaie fringing reefs. There is a total of 963 islands or islets in the Carolines, and the total land area is 1,200 square kilometers. Thus the Carolines represent the largest subdivision of Micronesia, with the greatest area, greatest geographical extent, largest number of both high islands and atolls—though the Marshalls have a larger number of individual islands—and the greatest geological and geographical diversity. The Carolines, however, lack active volcanoes, do not include the highest islands of Micronesia, and do not extend far from the equator.

None of the high islands of the Carolines are particularly young, and some of them are severely eroded, and some are somewhat sunken. The older islands, Palau and Yap, are the westernmost; and the youngest is Kusaie, the easternmost, with Ponape next youngest. Thus from east to west, the islands are older, except that Yap may be older than Palau. The highest is Ponape (787 meters), with Kusaie, Truk, Palau, and Yap in order of decreasing altitude. Thus, the altitudes of the high Carolines decrease more or less as the ages of the groups increase. Limestone raised more than a few meters is found only in the western Carolines; and metamorphic rock is found only in Yap and Palau, though there are some traces in Truk. Yap and Palau are west of the sial (andesite) line, and the other high islands are east of it.
The Carolines have vegetation of extreme diversity, including all categories discussed above. Grassland is well-developed only in Palau and Yap, and montane forest and its open dwarfed ridge-top type are highly developed in only Ponape and Kusaie. Palau and Yap have much richer floras than do the rest of the Carolines. The vegetation has been very seriously disturbed on Truk and Yap, and it is the least disturbed on Kusaie and Ponape. Lowland jungle other than mangrove is extensively preserved only in Palau, where it occurs on both limestone and volcanic islands, though with very different composition in the two environments. Babelthuap is perhaps the only island with any remaining continuity between mangrove swamp, nipa palm swamp, lowland swampy jungle and upland jungle, as most other islands have a fringe of coconut palms between mangrove and natural forest, if the latter persists. The steep narrow coral islands, also found only in the Palaus, do not have the fringe of coconut palms and rarely have mangrove.

**PALAU ISLANDS**

The Palaus (fig. 20) are the westernmost high island group of Micronesia, the largest group of the Carolines, and the most diverse topographically and in terms of types of islands. They include volcanic islands, high coral islands, low coral islands, raised atoll (phosphate) islands, an atoll and incipient
atolls, as well as barrier reefs, fringing reefs, and shoal reefs. The Palau s, however, are probably not as old geologically as Yap and do not have the variety of ancient rocks that Yap has. Botanically, this is the richest and most diverse group of Micronesia.

A large barrier reef which surrounds much of the Palau s is wider and more distant from the islands on the west (see Semper, 1873, 1881). Angaur is completely outside the reef to the south; and Ngaiangl Atoll, Ngaruangl Atoll, and Kossol reef are outside to the north. On the northern half of the east coast of Babelthuap, the barrier reef approaches the coast and becomes a fringing reef. The only islands on the barrier reef are Peleliu, the Ngemelis Islands, Ngeregang, and a few other low islands, all in the south.

Ngaiangl (Kayangel) Atoll is the northernmost land of the Palau s, except for Ngaruangl, an incipient atoll just north of it which has a single islet without vegetation. Ngaiangl is a small atoll with four islets, all on the east. From north to south and also in order of decreasing size, they are Ngaiangl, Ngariungs, Ngarapalas, and Gorak islets. There are extensive coconut groves, partly damaged by Oryctes, and some dense semi-natural vegetation of both scrub and large trees. Ngaiangl, though a small atoll, is humid and close to Babelthuap, and thus has a relatively rich flora and dense vegetation (Gressitt, 1952, 1953a). Kossol reef, a largely enclosed triangle south of Ngaiangl, is a potential atoll. To its west, the barrier reef extends some distance

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**Figure 19.—Map of eastern Caroline Islands.**
Figure 20.—Map of Palau. (Note: On inset, latitude lower left should read 8° 2' 30".)
north of Babelthuap. Just north of Babelthuap are two narrow volcanic islets, Ngaregur and Ngarekela. They are not very high, but have a little scrub as well as coconut palms.

Babelthuap is the largest island of the Carolines (397 sq. km.) and the second largest island of Micronesia. It is the largest island which is preponderantly of volcanic rock, though it is relatively low (242 meters). There are 23 higher Micronesian islands, and some raised coral islands to the south of Babelthuap are almost as high. This, in itself, is an indication of great age, together with the obviously great erosion of its low hills and

Figure 21.—North-central Babelthuap, 1951: a, low hilltop with almost no soil, possibly low-quality bauxite, with stunted Gleichenia ferns; b, andesite peak north of center of island, possibly second highest in Palau, Dracena left center.
the extent of the bauxite, which develops from andesite with infiltration of acids from decaying vegetation under tropical conditions. Since much of the andesite occurs on open ridges, it must have developed under conditions of different topography, preceding a long period of erosion. Babelthuap is about 16 kilometers wide and 43 kilometers long, north and south, being broad in the south and tapering to a narrow peninsula in the north. It is more mountainous in the western half, which is slightly rugged in parts, with a few peaks or dome-like hills (fig. 21). Between areas of this rough land on the west is Ngaremedu Bay, with a small opening; and draining into the bay are several sunken streams, including the Ngaremkeskang, lined with mangrove and dense tropical jungle. Many of the hills around the area are also densely forested. There are only four or five villages on the west coast, most of them near Ngaremedu Bay and in Ngaremengu to its north. Almost the entire west coast is lined with mangrove, which in some parts forms quite a wide belt (fig. 30, b). The mangrove belt also extends along part of the north peninsula, and is broad at its extreme north tip.

The east coast of Babelthuap is fringed with mangrove in most of the southern half and with sand beaches, which are somewhat interrupted by mangrove, in the north. Along parts of the northeast coast coconut palms (fig. 24, a) grow on low slopes immediately behind the mangrove, which is spreading on the beaches. At Namai Bay, near the middle of the east coast, is the opening of the drainage for much of the northeast part of the island. Extensive mangrove forest grows in or near the bay, and behind the mangrove is much lowland rain forest. Ngardok Lake, south of Namai Bay, and the country to its south, drains out well south of Ngchesar. Another large system of streams drains into Irrai Bay. On quite a bit of the interior upland there have been clearings for Japanese agriculture or bauxite excavations; but much forest persists. In the south and along much of the east coast lie many of the villages, with coconut groves, taro patches, and cassava fields. In the south many of the low ridges and hill tops are grassy, or even show bare red earth. In the center and north many of these situations are covered with *Gleichenia* (fig. 21, a). The northern peninsula is densely populated and largely covered with coconut, grass, or *Pandanus*. This area is partly hilly and partly low. There is only a little raised coral limestone on Babelthuap, most of it at the extreme south and southeast, where several "islands" of raised coral (fig. 27, b) are separated from it only by mangrove swamp, or are actually connected. The vegetation on the steep slopes of these coral portions is extremely dense, including fewer large trees, and a flora somewhat different from that of the volcanic portion.

The lower portions of the major streams on Babelthuap have rich mesophytic jungle (fig. 24, c, d) merging with mangrove forest (fig. 25) or
swamps of large erect Pandanus (figs. 23, c, 24, b). On some of the lower hill slopes are many dense stands of tall Alpinia, but generally these grow in the shade of tall jungle trees. The hill vegetation is highly varied, consisting primarily of woody plants, with large pure or mixed stands of Pseudopinanga palm (fig. 24, c) and with Freycinetia (fig. 24, d) and other climbers abundant. In the numerous clearings in the interior—mostly originating from bauxite excavation, Japanese agricultural projects (fig. 23, a) or ancient civilization (fig. 23, b)—grassland, grass and Pandanus, or Gleichenia

Figure 22.—North-central Babelthuap, 1951: a, Saccharum spontaneum and old Japanese marker (with termite nest) on former road from Ngaremiskang to Ngardma; b, looking down from clearing across native forest to coast between Ngardma and Ngarard.
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Figure 23.—Babelthup: a, former Japanese agricultural area in Irrai, overgrown with grass in 1951; b, ancient Palauan terracing, near Ngaremeskang River, Ngaremengai District, showing grass and Pandanus, 1952; c, Pandanus swamp and grass near road from Irrai to Ngatpang, in Imelik District, 1951.
Figure 24.—Babelthuap: a, coconut palms damaged by Oryctes, one bearing large nest of Nasutitermes brevitarsis, Ulungu, 1951; b, Pandanus mangrove swamp, lower Ngaremkeskang River near Ngarembe Bay; c, upper tidal area in Ngaremkeskang River, with Pseudophinanga palms; d, Freycinetia hanging from jungle trees on upper Ngaremkeskang River, 1952.
Figure 25.—Mangrove on Babelthuap, 1952: a, nipa swamp in lower Ngaremeskang River; b, Rhizophora in channel leading to Ngatpang; c, Rhizophora, near Ngatpang.
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persist, with some Dracaena, Nepenthes, and various shrubs intermixed. Much of the Glociehia grows in dense pure growths on ridges or summits, and it often indicates bauxite (fig. 21, a). Of the tall grasses, Saccharum spontaneum (fig. 22, a) has formed dense stands difficult to penetrate, often on the abandoned Japanese roads through former sugar cane fields. Many coconut palms have been destroyed, particularly in the south, by the coconut rhinoceros beetle (Oryctes; fig. 67, b).

The western half of Koror [Oreor], south of Babelthuap, is low, eroded volcanic rock (fig. 26, b, foreground; 30, b, upper center), like Babelthuap. This is true of all of Ngerkabesang and part of Malalak, both of which are close to Koror and connected to it by causeways. Koror is the principal town of Palau; Malalak is its sea port; and Ngerkabesang is well populated and (like Koror) partly agricultural. Coconut palms have been exterminated from the three islands. Western Koror and much of Ngerkabesang have been considerably disturbed by man and have many introduced plants. Some areas are of mixed grassland, with Pandanus and miscellaneous shrubs or weeds. A sizeable area of virgin forest remains on the north side of Ngerkabesang. Mangrove is also present. Eastern Koror is of high limestone, like the islands just to the northeast, and belongs with the next group.

High limestone islands (figs. 26, b; background; 27; 30, b, background) of greatly raised coral form the rest of the central and south-central Palau, and they thus resemble the northern half of Guam. However, except for the few mentioned above, they are entirely coralline and consist of very narrow steep ridges, in straight or sinuous lines; have steep forested slopes and have few bare cliffs. Except for Mecherchar (Ei Mark), the southernmost large high coral island, none of them is more than 2 kilometers wide though some have coastlines of many kilometers. The lower slopes are generally deeply undercut at the water level (fig. 27, b, c). As this tidal-zone indentation is continuous and fairly even, with the exception of the very rare beaches, the undercutting is apparently caused by solution of limestone by carbonic acid, not by wave action. Ulebebel (Auptagel, Aapapushkaru) is 185 meters high. It is just southwest of Koror and, with it, forms an inland sea studded with raised coral islands (fig. 26, b). Ngwikabel (fig. 27, a) the largest and also the largest purely limestone island in Micronesia, in terms of volume of coral, is 204 meters high. It is 19 square kilometers in area and the second largest island of Palau. Toward the south, the altitude gradually declines. Ngarmalk (“northwestern Auptagel”), separated from Ulebebel by a partly artificial cut and very close to the volcanic part of Koror, is also artificially connected with Malalak. It has an interior brackish lake which is surrounded by forested ridges (fig. 26, a) of limestone, the lowest about 15 meters high. The lake has some mangrove and fish; and it has tide changes of
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Figure 26.—Central Palau: a, forest on Ngarmalk ("northwest Auluptagel"), Krauss, 1952; b, parts of Ulebsehel (Auluptagel), east Koror and smaller limestone islets, from volcanic portion of Koror, 1951; c, mangrove on small inlet of Ngurukdabel Island, 1952.
Figure 27.—Limestone islands, central Palau, 1952: a, view from Ngaremee light-house, northeast Ngurudabel, to northwest, with another part of Ngurudabel at left and Ngerikabasang, Malakal, Ngarmalk, Ulebsebel (hiding Koror), and southern Babelthup, in background; b, island just off southeastern Babelthup; c, Garreru Island, near Babelthup.
at least 50 cm., presumably through hidden cracks in the limestone. According to maps, Mecherchar (Eil Malk), which is 9 square kilometers in area, has a similar large lake and several small ones, and the limestone part of Koror has two. There are many nearly enclosed indentations on Ulebschel and Ngurukdabel (fig. 26, c). It is difficult to gain access to most parts of these islands because of the undercut edges and dense vegetation. There are several groups of smaller high limestone islands west of Ngurukdabel and Mecherchar. Such islands total more than 200. Ngaiargas, between Ngurukdabel and Mecherchar, has a large, flat, sandy central area between raised coral at each end. Ngereneyans, which also has a beach, is not far north of Ngaiargas.

![Figure 28](http://example.com/figure28.jpg)

**Figure 28.**—Southern Palau, 1951: a, northern Peleliu, from northeast, Mount Amingal at left; b, central Angaur, with tidal lake in old phosphate diggings, from high portion in northwest.

The vegetation on these numerous high limestone islands, including eastern Koror, is rich, dense, and practically undisturbed. *Gulubiopsis* palms are conspicuous on the higher portions, as are *Pandanus, Ficus, Dracaena, Guettarda, Premna, Wikstroemia*, and many others. *Bikka* is conspicuous on the lower cliffs.
Peleliu (figs. 28, a; 29) is the largest of a group of islands on the southern end of the barrier reef. Some of these islands are low reef islets, but most are somewhat raised coral islands. Peleliu, on the southern tip of the reef, is the third largest island (12 sq. km.) of Palau. It has been called a raised atoll, though it is quite irregular and has long ridges on the west side and peaks up to 80 meters high near the north end. It has had some phosphate which has been mined. The central portion is largely mangrove (fig. 29) which grows around the large bay. The east coast is low, and some of the islets on the northeast, such as Ngabad, are also low. Peleliu was extensively forested before the war, but most of the forest has been destroyed and little native vegetation remains. The present growth is a tangled secondary jungle of Macaranga, Hibiscus, Pemphis, Pandanus, Casuarina, and many weed plants. Coconut palms have been almost exterminated by Oryctes.

The few reef islets in Palau are like atoll islets, in that they are at least partly planted to coconut palms and have introduced plants. However, at least one, Ngabad close to Peleliu, has a richer flora than most atolls. Just north of Peleliu, Ngesebus, Ongewaol, and Ngergoi are irregularly raised. Ngergoi (Garakayo), the highest, is under 70 meters. To its northwest are the Ngemelis Islands (fig. 30, a), consisting of a string of narrow islands.
which range in height from very low to 20 meters or a little more. The low areas still have coconuts, despite the fact that the palms are practically gone from Peleliu and its nearby islets. To the northwest, the islets are higher; and beyond these are higher, raised coral islands both on and within the barrier reef. Northeastward from Peleliu, including Ngeregong, which is just south of Mecherchar, they are all low.

Figure 30.—a, raised limestone islands at right, from Admasah Island, Ngemelis Islands (slightly raised reef islands), 1951; b, air view of central Palau with southwestern Babelthup in foreground, Koror and Ulebschel in center, part of Nguruklabel in right background, 1952.
Angaur [Ngaur] (fig. 28, b) is 10 kilometers southwest of Peleliu and the barrier reef. It is a raised atoll and a rich phosphate island 4 kilometers long and 8.3 square kilometers in area, with an altitude of nearly 65 meters in the northwest. Its coconut palms have been exterminated by Oryctes. Angaur had much of its native vegetation destroyed by the war, with the consequent weed jungle invasion, though a little more native vegetation remains than on Peleliu. Eugenia, Randia, Casuarina, Ficus, Barringtonia, Pisonia, Messerschmidia, Guettarda, Pandanus, and other trees are conspicuous in the native forest; and Macaranga, Hibiscus, Morinda, Abrona, Ipomoea, and papaya are dominant in the weed growth.

The Palauan population, now about 6,500, is said to have been about 50,000 in 1800. During late Japanese times there were 10,000 Japanese in Palau.

**YAP ISLANDS**

Yap (fig. 31) consists of a close group with an area of 100 square kilometers. There were formerly three principal islands, but the Germans created a fourth when they cut the Tageren Canal which separated Gagil and Tomil districts from the rest of the main island of Yap (or Ruul). This separated northeast portion is sometimes called Gagil-Tomil (or Gagil) Island (figs. 32, a; 33, b). Just to the north of Gagil and Tomil, and almost touching it at several points, is Map Island; and just to the north of Map, also nearly touching, is Kumu Island. The group is surrounded by a fringing reef from 1 to 4 kilometers wide. Besides the main islands, there are a few tiny islets in the bays or between the large islands.

Yap represents the aged, eroded top of an old volcanic peak based on metamorphic rock. The surface rocks are largely metamorphic, but in the eastern portion there is weathered lava. Yap is just west of the sial line, demarking the edge of a possible ancient continental shelf. The islands have been termed continental, although their insect fauna would hardly seem to bear this out. The presence here of the only mayfly in Micronesia, of three kinds of caddisflies, and of certain other insects does seem suggestive; but the lack of so many others which are abundant in the Philippines and New Guinea, coupled with the fact that many of the types of insects found in Yap are also found as far east as Ponape or Kusaie, seems to argue against that thesis. At any rate, Yap has the most ancient rocks of Micronesia, the greatest amount of metamorphic rock, and the greatest variety of minerals, including bauxite, manganese, iron, copper, zinc, and asbestos. It has few beaches, and only a few narrow strips of coral sand behind beaches on northwestern Yap and northern Map. The coasts are mostly bordered with mangrove forests.
Not only are the Yap Islands greatly eroded, but there has been much subsidence. The divisions between the islands and other indentations represent sunken river valleys (fig. 32, b). The routes of the former streams can be distinctly traced on a map showing the reef areas and can be seen clearly from the air as dark, sinuous depressions with coral growth on the sides. The hills of Yap, gradually sloped and with some limited steeper slopes, are greatly worn down (figs. 32, a, b; 33). The highest summit, Mount Tabi-
Figure 32.—a, looking northeast from lower slope of Mount Madaade, Yap Island, with parts of Gagil and Tomil Districts and Map Island in background, 1952; b, air view of part of Yap, showing sunken river valley and pale grassland on slopes, 1952; c, air view of Pakin Atoll, west of Ponape, from southeast, 1953.
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wol (178 meters), is in north-central Yap Island; and just south and north of it are some ridges nearly as high. Mount Madaade, to the south of Tabiwol and just northwest of Kolonia (Yaptown), is also nearly as high as Tabiwol. There are some similar hills on Runung Island, and one lesser one on northern Map Island. Those on southern Yap Island and in Gagil and Tomil are lower.

Most of the lower hills or slopes of Yap are open and grassy, with scattered Pandanus or mixed shrubbery, which includes Pandanus, Gleichenia, Nepenthes (fig. 41, d), Lygodium, and other plants. The steeper slopes and ravines are mostly forested (fig. 33, a), but this forest has been much

Figure 33.—a, panorama north from Mount Madaade, Yap Island, mainly secondary forest; b, view to east from Mount Madaade, across to Gagil and Tomil. (Fosberg, 1946.)
disturbed by the agricultural practices of the Yapese. War damage was minor in Yap. Some of the steeper slopes are more or less natural in their vegetation, and here the forest is mesophytic. However, it is probable that many plants and insects have become extinct.

The Yapese population in 1948 was 2,744, but in 1783 it was estimated to be about 40,000.

 **TRUK**

Truk (fig. 34) consists of a very interesting group of old volcanic islands which are much sunken or eroded. Surrounding these islands, in places at some distance, is a great barrier reef, which has often been called Truk Atoll or an “almost atoll.” However, the presence of high islands within a reef lagoon does not agree with the definition of, or theories on, atolls. In comparing Truk and Ponape, it can be imagined that Truk might have been developed from an island like Ponape which had more or less gradually subsided a few hundred meters at a slow enough rate for the coral on the edge of the fringing reef to keep growing close to the surface of the sea. Thus the fringing reef would be transformed to a barrier reef, at some distance from higher peaks remaining above sea level. There is evidence, including sunken river valleys, of recent subsidence in Truk, though there are also some coral flats a meter or so above sea level. In addition, there is older evidence of great subsidence and re-elevation, in the form of two old wave-cut terraces, one about 100 meters, and the other 30 to 50 meters, above present sea level. There is also evidence of erosion over a long period.

The Truk barrier reef ranges from 45 to 65 kilometers in diameter and is about 225 kilometers in circumference. It has about 40 small reef islets, like those of an atoll, with a total area of 4.1 square kilometers. The lagoon has an area of 2,129 square kilometers, in addition to the 96 square kilometers of land area of the islands within the lagoon. It is thus slightly larger than Kwajalein, the world’s largest non-sunken atoll. The lagoon ranges in depth to about 75 meters (41 fathoms), and much of it is 35 to 65 meters deep. There are also numerous shallow areas, with some reefs awash in isolated spots and around islands.

Within the lagoon are about 40 islands, six of them moderately large and most of them very small. Only about 12 are more than 50 meters in altitude. The highest and largest is Ton (Tol) Island. Its highest peak, Mount Unibot (Unipot or Tumital), is 452 meters high. Next in height is Wena (Moen) Island (fig. 39), 370 meters high, and Tonoas (Dublon), 361 meters high. Next in height come Fefan (298 meters), Uman (292 meters), and Utot (243 meters). Ton and Wena, the two highest, are almost at opposite ends of the east-west grouping of major islands. Caves are found in the volcanic rock on several of these islands.
Figure 34.—Map of Truk.
The rocks of Truk consist largely of basaltic lava, and there is no high raised coral limestone. There is much evidence of erosion, as well as subsidence. Subsidence is more evident on Ton (figs. 35, 36), which seems to consist of five sunken peaks connected principally by mangrove swamps growing on coral, with the bays filling up with coral growth. The northwest portion of

![Image of Ton Island, Truk; panorama to north, from near summit of north slope of Mount Unibot, with Pata in left background, 1953.](image)

**Figure 35.**—Ton Island, Truk; panorama to north, from near summit of north slope of Mount Unibot, with Pata in left background, 1953.

![Image of views from near summit of Mount Unibot, 1953: a, northwest, with Pole in center and end of Pata in right background, to left of view shown in figure 35; b, northeast, with Clunkien village in lower foreground, to right of view shown in figure 35.](image)

**Figure 36.**—Views from near summit of Mount Unibot, 1953: a, northwest, with Pole in center and end of Pata in right background, to left of view shown in figure 35; b, northeast, with Clunkien village in lower foreground, to right of view shown in figure 35.

Ton is Pata (sometimes called Pata Island), and the southwest is Pole (or Pole Island). Mount Unibot is on the southeast portion. The north-central and northeast portions are a little lower than Pata and Pole, but each is more than 160 meters high.

The high islands of Truk once had a rich and varied vegetation, but it has been greatly disturbed by the activities of man (fig. 39). In fact, almost no
undisturbed vegetation remains. The nearest approach to it is mangrove and the steep forest on the east slope of Mount Unibot on Ton Island (figs. 37, 38), and even here it is indented with some trails and cultivation. On the tops of most of the higher peaks some native plants, such as the tall palm *Exorrhiza carolinensis*, *Cynometra*, and *Ficus* remain, but with admixture of second growth of weeds, grasses, *Hibiscus*, and *Ipomoea* and *Merremia* vines. Many *Exorrhiza* remain on the summit of Mount Chukumong on Wena Island, and a fair number on Tonoas; but few grow on the summit and east side of Mount

![Figure 37.—Truk, Ton Island, Mount Unibot, 1953: a, partial secondary forest on summit, Nephrolepis and Cordyline in foreground; b, upper level of cultivation (dry taro, banana) on north ridge; c, secondary growth on summit; d, summit from north side.](image)
Unibot on Ton. A very few may be seen on Utot. Ivory nut palms (*Cocloccerus*) are more widespread, being at low or medium altitudes in clearings or forest. The raised reef coastal plains on Wena, Tonoas, and other islands are largely cultivated or overgrown with *Miscanthus, Phragmites*, and other tall grasses. Many of the former areas of mixed coconut palms and breadfruit trees were replaced by fields of sweet potatoes and cassava by the Japanese during the war. These are now abandoned and largely covered with weeds, particularly *Merremia peltata*.

![Image](image.jpg)

**Figure 38.**—Large millipedes (*Polyconocerus*) around aroid on trunk of tree 12 cm. in diameter, in forest shown in figure 37, a, 1953.

The vegetation of reef islets is similar to that of atolls, consisting of coconut, breadfruit, shrubs, grasses, and ferns and including *Pandanus, Mesera-schmidia*, and *Scaevola*, especially, along the beaches.

The Trukese population was 9,510 in 1948, but in 1827 it was said to be about 35,000.

**Ponape**

Ponape (fig. 40) is the third largest single island of Micronesia (334 sq. km.) and the highest island of the Carolines (791 meters). It is higher than any of the southern Mariana Islands. Besides the main island of Ponape, there are several small volcanic islands close to or nearly touching it and several very small islets on parts of the reef, which is partly fringing and partly a barrier reef separated by deeper water. There are about 25 small islands, half of them volcanic. Ponape and the nearby atolls of Ant and Pakin are sometimes called the Senyavin Islands.
Figure 39.—Truk: a, air view of much of Wena (Moen) Island, with Mount Tonachau in foreground, Mount Chukumong (Teroen) at upper right center, Nantaku (Civil Administration Area) in center, and part of Tonos (Dublon) Island in background; b, cultivated area on Wena, with taro, banana, coconut, and cassava. (U. S. Commercial Co., 1946.)
Most of Ponape, except for some limited coastal plains or gentle lower slopes, consists of rather steep mountains. In the central portion, extending from northwest to southeast, is a series of mountains (fig. 44), most of them connected by high ridges, and some ranges which extend northeast from the center, with lower mountains in the east and south. There are several peaks and some long ridges, which are more than 600 meters in altitude. The highest peak is Mount Ngihnepi (fig. 5, a, c), just south of the center of the island. In the same range is Mount Nahimalau (figs. 43-45), practically as high (788 meters), and Dolen Walk, Dolokatar, Dolotomw, and Poaipoi. To the northeast of Nahimalau are Dolen Pipilap, Dolen Rahkiet, and others; and to the
Figure 41.—a-c, Ponape: a, clearing in native forest, side of Mount Temwetemwene-sekir at 250 meters, *Exorrhiza ponapensis* palm, *Alpinia* in foreground, 1953; b, lowland rain forest between Nanipil and Nanpohnmal, with *Ponapea* palms and *Cyathaea* tree fern, 1953; c, overgrown road from Nanipil to Nanpohnmal with ferns, *Pandanus*, *Ponapea*, etc., 1953. d, Yap, near Maki, Gagil, with *Nepenthes mirabilis* and *Gletchroida linearis* on savanna (Fosberg, 1946).
Figure 42.—Ponape, 1953: a, light trap (operating as Berlese funnel in daytime) in partly overgrown clearing on side of Mount Temuwatemwenskir, at 280 meters; b, young mangrove (*Rhizophora*) growing on coral dredgings along passage between Sokehs and Ponape; c, Sokehs Island from west of Colonia.
northwest are Dolemire, Nahmalek, Pairot, Dolen Kiepw, and Temwetemwensekir (figs. 41, a; 42, a). Most of the peaks named are more than 600 meters in altitude, and others are nearly as high.

Geologically, Ponape appears to be younger than Truk, and it is less sunken. It is richer in insects and has more endemics, but this may be related to the much lesser destruction of the forests and the much greater variety of natural environments persisting. Ponape consists primarily of basalt, some of which is in columnar form, particularly on Sokelia (Jokaj) Island (fig. 42, c) in the north.

The towns are near the coast, and houses are scattered along some coasts. Colonia (Colony, Ponape) is on the north coast, with houses and farms scattered on the plain or low table land to the south. Rohnkiti is in the southwest, and Madolenihm is in the southeast.

Ponape has the most extensive native forests remaining in Micronesia; and together with Kusaie, it has the most highly developed rain forest. Wet jungles cover most of the interior, even reaching to the coast in some places. Mangrove is extensive and includes Sonneratia (fig. 3), Rhizophora (fig. 42, b), Bruguiera, Luminitzera, Xylocarpus, and Heritiera, as well as the Nypae...
palm. Since there are few beaches, strand vegetation is extensive only on the reef islands. In disturbed areas *Hibiscus, Macaranga, Lantana, Leucaena,* several grasses, and other plants form a distinct secondary growth in the lowlands (fig. 44; 46, a) and on certain steep slopes where sweet potatoes were planted during the war.

The rain forest (figs. 4, 5, 43, 45) is very rich and includes most of the native plants. It covers most of the steep slopes and summits and some lowlands. At lower altitudes it includes *Cyathea, Pandanus, Alpinia, Preyecinetia, Ponaapea, Campnosperma, Elaeocarpus, Terminalia,* and some *Exorrhiza.* At medium altitudes, *Exorrhiza* is dominant (figs. 4, 41, a) and continues up to some of the higher summits. *Cyathea, Pandanus, Gynotroches,* and *Thoracostachyum* are dominant at the highest altitudes (fig. 5). Mosses, ferns and other epiphytes are conspicuous on the high, wet ridges and are almost constantly dripping with water from rain or fog. A pure forest of *Pandanus patina* covers much of the top of Mount Ngihneni.

Dominant insects at the highest altitudes are large tettigoniids, gryllids, and weevils, all of which are found particularly in the centers of *Pandanus* and
Thoracostachyum plants (fig. 5, b). Small weevils are found in some of the shrubs. The giant toad (*Bufo marinus*) is common and is found on the tops of the highest mountains, whither it has recently spread. The giant African snail is present in the lowlands, but it is said to have diminished since the introduction of the toad.

The Ponapean population is about 6,000. In 1820 it was estimated at about 15,000, but in 1891 it had fallen to 1,705.

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**Figure 45.—Ponape rain forest on slope of Mount Naualand, at about 500 meters, showing Freycinetia ponapensis (right), Cyathoe nigricans (left foreground), and Erythrina ponapensis (upper center). (Glassman, 1940.)**
Figure 46.—Eastern Carolines: a, mixed secondary forest at foot of Mount Temwet-emwensekir, Ponape, 1953; b, taro swamp on Ringutoru Islet, Kapingamarangi Atoll (K. P. Emory, 1950).
Kusaie (Ualan) is the easternmost and southernmost high island of Micronesia, and the farthest east of the Carolines. (See figures 19, 47.) It is probably the youngest of the high islands of the Carolines. It has the steepest slopes, in general, and the narrowest ridges. It is somewhat similar to Ponape, but smaller (109 sq. km.) and not as high. The highest peak, Mount Puinkol (Fenkol, Crozer), is 630 meters high and near the center of the island (fig. 48, a). Mount Matante (Buache), in the north (fig. 51, b), is 593 meters high and less precipitous and more volcano-like in appearance. In the central and southern parts are many other peaks, including Tafeayat (fig. 51, a), and sharp ridges, in part connected with Mount Puinkol. Many of the steep slopes are still forested, partly with second growth.

Kusaie is surrounded by a fringing reef which is quite narrow and close to the island in places. On the south and part of the east coasts are long narrow islets near the edge of the reef, with narrow stretches of water between them and the main island, and often with mangrove on both sides of the water (figs. 49, a; 50, a). Mangrove borders most of the shores. Lele Island (fig. 50, b),
on the northeast, possesses a hill, the principal town, and ancient ruins (fig. 48, b).

Kusaie consists largely of basalt, which is partly columnar; and there is some bauxite and clay on the island. Cave deposits of guano of the small bats (*Emballonura*) were reported by Christian (1899), but it appears to be swiftlet guano, according to Clarke (1953).

The vegetation of Kusaie is similar in many ways to that of Ponape. It is essentially dominated by rain forest and mangrove (fig. 49, a). The coastal

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*Figure 48.*—a, central portion of Kusaie from Lele Island, Mount Fuinkol in center, Fuinwukat at right, 1953; b, ancient ruins, Lele Island, Kusaie, *Nephrolepis* above, *Piper* in upper center, *Procis pedunculata* (slender leaves) at right center, and *Phymatodes scolopendria* at lower left, 1953.
Figure 49.—Kusaie Island: a, mangrove area, east coast, with *Nephrolepis* in center and *Sonneratia* at right; b, *Cyathaea* tree ferns on ridge of Mount Matante. (Clarke, 1953.)
Figure 50.—a, light trap in mangrove swamp, Pukusrik; b, Lele (left) and Mutunlile (right) from "Hill 1010." (Clarke, 1953.)
Figure 51.—a, Mount Tafeayat, Kusaie, from west side, taken from trail at about 120 meters altitude (Townes, 1946); b, Mount Matante, on Kusaie, with part of Lele Islet in foreground (Townes, 1946); c, Pingelap Islet, Pingelap Atoll, showing breadfruit, coconut, and banana, 1953.
plain is primarily planted to coconut palms and taro and the lower slopes near it are planted to breadfruit, citrus, and banana. *Premna* and *Wedelia* are common weeds in the coconut groves.

Secondary forest covering many of the slopes includes *Hibiscus*, *Ficus*, *Boehmeria*, *Laportea*, *Pandanus*, and *Elaeocarpus*. The lower primary forest includes a number of large trees, two genera of tree ferns, and many vines and ferns. *Ponapea* palms are present, but these are less abundant than the *Exorrhiza* palms on Ponape. *Frecycinetia* is common. On the high sharp ridges a specialized flora dominated by *Gleichenia* is conspicuous, and there are some small shrubs and *Cyathaea*, just below or on the ridges (fig. 49, b).

The monitor lizard and the giant toad are present, but the giant African snail has not been introduced.

The population of Kusaie is about 1,700. In 1824 it was estimated at about 3,000; and in 1874 it had dropped to 379.

**CAROLINE ATOLLS AND LOW ISLANDS**

Atolls are characteristic of tropical seas where there are submarine plateaus. The Marshalls and Gilberts consist entirely of atolls or single isolated low islands; but in the Carolines, the numerous atolls or other low islands follow, in general, the path of the high islands from west to east. In the far west they extend southwest toward Waigiu, just west of New Guinea. Kapingamarangi, south of Nukuro, is far to the south, between Truk and Ponape and close to the equator. To the east there are only two—Mokil and Pingelap, between Ponape and Kusaie—and no more to the eastward until the Marshalls and Gilberts. The greatest concentrations of Caroline atolls are in the east-central and west-central portions of the archipelago, near Truk and west of Truk.

The atolls or low islands are merely listed with a few statistics, since they are fairly uniform in their low altitude (rarely over 2 meters high), in their make-up of fragmented coral, in the form of gravel and sand, often with a little cemented "beach sandstone" of solidified coral sand. The islets, or those with available names, are listed in clockwise order, starting at the middle of the north side of the atoll reef. The atolls are listed from west to east. (See figures 18, 19.) The most heavily populated Caroline atolls are Pingelap, Woleai, Losap, Lukumor, and Ulithi.

Tobi (Tokobei) is the westernmost island of Micronesia (fig. 52, a). It is 3° north of the equator and 131° E. It is closer to Morotai, Halmahera, Waigiu, and New Guinea than to the Palaus. Tobi is a single low island, 0.6 square kilometer in area, with a fringing reef (Tayama, 1935a). Tobi, as well as Merir, Pulo Anna, and Sonsorol, is a low island with fairly luxuriant vegetation of limited atoll flora. Conspicuous plants are coconut, *Pandanus*, bread-
Figure 52.—Western Caroline low islands: a, center of Tobi Island, taro swamp in old lagoon of raised atoll; b, beach on lagoon side of Halik Islet, Halik Atoll; c, taro swamp in center of Merir Island. (Krauss, 1952.)
fruit, papaya, lime, *Calophyllum*, *Terminalia*, *Cerbera*, *Morinda*, *Scaevola*, *Meeserschmidtia*, taro, pineapple, squash, chili, tobacco, spider lily, *Miriabilis*, grasses, ferns, and others (Krauss, 1953). Some of these islands are suggestive of slightly raised atolls, having depressed interiors and even a little phosphate. In some, it may be difficult to distinguish between natural depressions and artificial ones made for taro pits. The population of Tobi was 141 in 1948, whereas it was about 400 in 1832. (See Motoda, 1939.)

Helen Reef, about 80 kilometers east-southeast of Tobi, is an atoll with only two very small uninhabited islets and with a large area of sand, exposed at low tide, around one islet.

Merir is a single low island with an area of 0.9 square kilometer (fig. 52, c). It is 170 kilometers northeast of Tobi, and is inhabited.

Pulo Anna is another single low island, said to be a slightly raised atoll. It has small deposits of phosphate. This island is some 65 kilometers northwest of Merir, and like Merir, it has a narrow fringing reef and is inhabited.

Sonsorol, 100 kilometers north of Pulo Anna, consists of two separate single low islands, each with its own narrow, fringing reef. Their combined area is 1.9 square kilometers, and they are less than 2 kilometers apart. The northern island is Fana and the southern one is Sonsorol. Sonsorol is said to be a raised atoll and has phosphate deposits. It is inhabited. Sonsorol is about 280 kilometers southwest of Angaur, southernmost of the Palau group.

Ngaiangl (Kayangel) Atoll (figs. 20; 56, a, c) is considered part of the Palau Islands, being situated just north of Babelthuap. It is a small atoll with four islets, Ngaiangl, Ngariungs, Ngarapalas, and Gorak, all on the east side. Because of its humid climate and its proximity to the Palaus, it has a relatively rich flora (Gressitt, 1952, 1953a) and an unusually rich insect fauna for an atoll. (See insect fauna.)

Ngaruangl, an atoll reef with a single barren islet, is just northwest of Ngaiangl. There are no plants, but marine craneflies are present (Gressitt, 1953a).

Ngulu is an atoll some 300 kilometers east of Ngaiangl and 200 kilometers south-southwest of Yap. The lagoon has an area of 380 square kilometers, but the reef is somewhat sunken and the land area is only 0.43 square kilometer. The islets are Taapuyap, North, Meseran, Donugantamu, Uatschuluk, Yanenchiki, Pigaras, Ngulu, Rattogoru, Jalangaschel, Letjegol, and Perifukumazo, mostly in the southeast. The atoll is inhabited.

Ulithi (fig. 53) is the largest atoll of the Carolines, in terms of land area (4.6 sq. km.), though just barely larger than Satawan, Woleai, and Namonuito. It is about 175 kilometers east-northeast of Yap and is the northernmost group of the Carolines. It is a somewhat complex assemblage. The main atoll is partly sunken, with wide openings in the reef. To the east is another sunken
Figure 53—Ulithi Atoll, air views: a, an islet showing seaward side at left and in foreground and lagoon side at right, with two very small islets on reef in distance; b, view across an islet from lagoon side, showing another islet beyond indentation on seaward side of reef. (U. S. Navy.)
atoll with two islets, Jar and Gielap. Between the two atolls lies a straight stretch of reef with four islets, including Losip, Pau, and Bululub. The islets of the main atoll include (from north, clockwise) Potangeras, Horaizon, Malotel, Mogmog, Sorlen, Yagoroporapu, Ewachi, Asor, Palalop, Mangejang, Lolang, Passarai, Lossau, Feilab, Furaza, Pugelug, Pig, Ealil, Eau, Songeti-gech, Elipig, Pigelele, Song, Pogel, Sorenlen, Lam, Piras, Elemat, Eleute, Delesag, and Yareruwachichi. The population is several hundred.

Fais is a raised atoll, just east of Ulithi and 2.8 square kilometers in area. Its altitude is about 19 meters. There are deposits of phosphate, and only a partial narrow fringing reef. The island is inhabited.

Sorol, some distance south of Fais and east of Ngulu, is an elongated atoll with a narrow lagoon involving only part of the reef. The land area is 0.9 square kilometer. The islets, from northwest to southeast are Bigelimol, Bige-
liwol, Falesaidid, Birara, Sorol (the largest), and Bigelor. Sorol is inhabited.

Eauripik Atoll (fig. 54) is about 275 kilometers east-southeast of Sorol and is the westernmost of the large group of west-central Caroline atolls and low islands. It is a narrow atoll, and extends east and west, like Sorol, but it is less attenuated at each end. It is about 10 kilometers long and has a land area of only 0.23 square kilometer. The islets are Siteng, Eauripik (the largest), Bekefas, Elangkilek, and Ono.

Woleai is northeast of Eauripik and is the third largest Caroline atoll, in terms of land area (4.5 sq. km.), and the fourth largest in human population (about 500). It is one of the few which has had an airfield, which was operated by the Japanese. The islets are Jalangigerei, Tagaulap, Mariaon, Woleai (largest), Paliau, Raur, Sand, Falalis, Luisaga, Pial, Falu lemariete, Farlap, Falu cegalao, Elingarik, Utagal, Peregaregar, Saliap, Falamalok, Taramat, and Farailes. There are some wide openings in the reef.

Ifaluk (Ifalik, Furukku) Atoll (figs. 52, b; 55) lies east of Woleai some 80 kilometers. The area is 1.47 square kilometers and the human population about 350. The islets are Ifaluk, Flalap, Ella, and Eragarap (very small). Ifaluk and Flalap are largest, and subequal in size. The lagoon is round, with a shallow sandy entrance between Ella and Flalap; and Flalap extends outward from the main circle of the reef.
Faraulep (Furaaarappu) Atoll, some distance north of Halik, has an area of 0.4 square kilometer. The islets are Fuasubukuru, Pigue, Faraulep (largest), and Eate. The reef is somewhat angular, but the lagoon is round and has openings at the southwest. The population was about 300 in 1935.

Gaferut (Grimes or Gurimesu) Island is a single island on a small reef well to the northeast of Faraulep and has an area of 0.1 square kilometer. It is the nearest of the Caroline Islands to the Marianas. The island is uninhabited, though trees are present.

Olimarao (Onomara) Atoll is southeast of Faraulep and northeast of Halik. The area is 0.2 square kilometer; and there are only two islets, Olimarao (the larger) and Falifil. The reef is subcircular, with openings in the south. The atoll is uninhabited, though palms grow there.

Elato (Erato) Islands, southeast of Olimarao, consist of two atolls separated by less than their lengths. The northern one is slender with the lagoon divided by reef in the center and with only four islets: Elato, Oletel, Kari, and Falipi. The southern atoll, called Lamolior, has only two islets, Toas and Ulor. The total area of the group is 0.5 square kilometer. The population is about 50.

Lamotrek (Lamochuk) Atoll is just east of Elato and separated from it by less than its own length, and its area is 0.98 square kilometer. The islets are Palue, Lamotrek (largest), Falaitae, and some tiny islets. The atoll is triangular, with several openings in the reef. The population is about 200.

Satawai (Tucker, Sasaon), a single island on a small reef east of Lamotrek, has an area of 1.3 square kilometers. The population was nearly 300 before the war, but is much smaller now.

West Fayu (Faui, Fuiyao) Atoll is an extensive oval reef with an opening and a branch, but with only a single island. It is 0.06 square kilometer in area and is uninhabited, but it is planted with coconut palms.

Pikelot (Pikelo, Coquille, Pigerotto) Island is a single small islet (0.09 sq. km. in area) not far east of West Fayu. It is uninhabited, but has coconut palms.

Puluwuk (Shukku) Island is the southwesternmost of the east-central Caroline assemblage, and is well over 200 kilometers east of Satawai of the west-central Carolines. Puluwuk consists of a single island with a narrow fringing reef. It has a shallow swamp or lagoon near the north end, and might be a very slightly raised atoll. The area is 2.8 square kilometers, and the population is over 200, whereas in 1819 it was about 900.

Puluwat (Enderby, Endabi) Atoll is north of Puluwuk and well east of Satawai. The area of 3.2 square kilometers takes in the islets of Puluwat, Sau, Alet, To, and Elangelab. Puluwat and Alet (east and west) are large and
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subequal in size. The lagoon is small, with openings on the south. The population is well over 200.

Pulap (Tamaram, Pourapau) Atoll is northeast of Puluwat. It is narrow and longest north and south, and the reef is partly sunken and incomplete. The islets are Pulap, Tamaram, and Fanadik, with a total area of 0.99 square kilometer. The population is about 300.

Namomuito (Onon, Ororu), the world’s second largest atoll, is triangular. Most of the reef is somewhat sunken, with islets near the corners and near the middle of the east side. The lagoon is 1,875 square kilometers in area and ranges from 10 to 80 meters in depth. The islands are Magererik and Magur on the north; Ono, Amurtride, Behilper, Biho, and Onari on the east; Weltot and Pisaris on the southeast; and Ulit on the southwest. The total land area is 4.4 square kilometers, and the population is about 300.

East Fayu (Lutuke, Rukute) is a single island east of Namomuito. It is slender and somewhat irregular, with a small swamp or lagoon in the narrow center, and the fringing reef is fairly wide. The area is 0.37 square kilometer, and the island is uninhabited, but has coconut palms.

Nomwin (Namolipiafan, Nomuun) and Murilo Atolls are very close together and not far east of East Fayu Island. Together, the three (or at least Nomwin and Murilo) are known as the Hall Islands (Horn Shoto). Nomwin is about 80 kilometers north of Truk and has a large lagoon with a narrow reef, which has several openings. The islets are Pisira, Icup, and Fanamu on the east; Setoaneris, Setoanelap, Elin, Pissisin, Nomwin, Pisief, and Pielau on the south; and Pisilemo, Oinian, Ulape, and Eate on the west. Icup, Fanamu, and Nomwin are the largest. The total land area is 1.8 square kilometers, and the population is about 300.

Murilo (Muriro) Atoll, just east of Nomwin, is a large atoll with a partly sunken reef. Some of the islets are Eor and Murilo on the east; Ruo (the largest), Fanano, Numurus, and Pisanius on the west; and Eliniff, Eliluk, Eliniies, Besela, and Sol to the northwest. The total land area is 1.28 kilometers, and the population is about 300.

Knop (Royalist Islands) is a slender oblong atoll just 3 kilometers south of Truk. (See figure 34.) The reef has several narrow entrances. The islets are Givry (Tachibana) on the north and Hacq (Fararu, Fuji), Lauvergne (Fanek, Taira), and South Island (Epis, Minamoto). The total land area is 0.49 square kilometer; and the group is uninhabited.

Nama is a single low island surrounded by a narrow reef. It is southeast of Truk, east of Knop, and just northwest of Losap. The area is 0.74 square kilometer, and the population is over 500.

Losap Atoll is just southeast of Nama. Modestly small, it has a narrow reef with a few openings. The islets are Oite, Laoi, and Losap on the east; Pis,
Talap, Famanwin, and Aluanubu on the south; and Alaminwassel on the northwest. Laol, Pis, and Talap are largest. The land area is 0.72 square kilometer, and the population is about 700.

Namoluk (Namorukku) Atoll is well to the southeast of Losap and nearly 200 kilometers southeast of Truk. It is triangular, with an opening on the southwest. The islets are Toinom and Umpan on the northeast; Amas on the southeast; and Namoluk and Lukan on the northwest. Toinom, Amas, and Namoluk are about equal in size. The total land area is 0.83 square kilometer, and the population is about 300.

Etal, Lukunor, and Satawan Atolls are just southeast of Namoluk and together are called the Mortlock (Nomoi) Islands. Etal Atoll, the smallest and northernmost, is triangular and entirely enclosed. The islets are Parang on the north, Etal on the south, and Unon on the west, with smaller islets on the east. The land area is 1.9 square kilometers and the population is about 250.

Lukunor Atoll is southeast of Etal and just northeast of Satawan. The reef is oval, with one opening in the south. The islets are Kurum, Piesum, and Lukunor on the east; Saponoch (Sopunur), Fanofa, Piesin, Pien, and Oneop on the southwest. Lukunor is the largest. The total land area is 2.82 square kilometers; and the population is about 1,500.

Satawan is much larger than Etal and Lukunor and just south of them. The reef is suboblong and narrow and has a north and south opening. The islets are Moch (More), Lalan, Farafor, and Fuausan on the northeast; Ratau, Fatikat, Satawan, Ta, Lipiapa, and Aliare on the southeast; and Ompulan, Kutu, Orin, Pien, Pike, Mariung, Lipos, Lenasul, Aelangrik, and Afarene on the northwest. The total land area is 4.5 square kilometers, and the population is about 1,500 (1,000 in 1935).

Nukuoro (Nugoro) one of the more isolated Micronesian atolls, is 200 kilometers southeast of Satawan and the Mortlock Islands. Though much closer to these east central Carolines than to any of the other eastern Carolines, it is closer to Ponape than to Truk and is practically in the eastern quarter of the Carolines. Nukuoro is nearly round, with a completely enclosed reef and about 40 islets on the north, east, and south, including Tongakerikeri, Kapinivere, Namutuotoa, Motumui, Arukanui, Tahangatabu, Tahangaroro, Motu Ituo, Sapinimatok, Motu Wei, Ahurooa, Tuila, Shugnaurohu, Takonran, Nukuoro, Shemukdei, Kaujene, Motu Itoto, Deahma, and Oromange. The land area is 1.67 square kilometers, and the population consists of about 250 Polynesians.

Kapingamarangi (Greenwich) Atoll (figs. 46, b; 57) is nearly 300 kilometers south of Nukuoro and is the most isolated group in Micronesia, except for Marcus and Wake. It is one degree north of the equator and is almost as close to atolls north of New Ireland as to Nukuoro. It has about
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31 islets, all on the east side. They include Ringutoru and Nunakita on the northeast; Werua (Ueru), Touthou, Taringa, Matiro, Hukuhenua, Tetau, and Hare on the east; and Pumatahati on the southeast. The land area is 1.84 square kilometers, and the population is about 500. This is the westernmost island inhabited by Polynesians.

Oroluk Atoll (lat. 7° 38' N.) is only slightly east of Kapingamarangi and Nukuro in longitude, but it is the northernmost of the eastern Caroline Islands. It is the third largest atoll of the Carolines in lagoon area and is the second most isolated. The islets are extremely small and uninhabitable, except Oroluk, at the northwest corner. The land area is only 0.45 square kilometer, and the population is very small.

Ngatik (Natikku) Atoll is southwest of Ponape and a long distance southeast of Oroluk. The reef is elongate-oval, with one opening, and has some coral heads in the lagoon. The islets are Peina on the north; Bigenkarakar, Jirup, Bigenkelang, Pikenmategan, Wat, and Uataluk on the southeast; and Ngatik on the west. The land area is 1.74 square kilometers; and the population is about 250.

Pakin (Pagenema) Atoll is just northwest of Ponape. It is elliptical (fig. 32, c) and has no true opening. The islets are Peilepwil, Uyetik, Wolomwin, and Mant on the southeast; Nikalap (northwest and largest) and Tomwena. The land area is 1.1 square kilometers and the population is very small, if the atoll is inhabited at all now.

Ant (Anto, Andema) Atoll is just west of Ponape and separated from it by less than its own diameter. The reef is slender, irregular in outline, and has a southern opening; and there are coral heads inside the lagoon. The islets are Patja on the east; Nikalap Aru (Karap), Imansappu, Wachikichi, Panshanki, Nakappu, Naron, Remba, Shikaro, Chinbareku, Toronmurui, and Pamuk Inwintiati on the south; and Wolauna on the northwest. The land area is 1.85 square kilometers. The population was 40 in 1935, but the atoll may be uninhabited at present.

Senyavin Islands is a name for Pakin and Ant Atolls, together with Ponape.

Mokil Atoll (fig. 56, b) is about 170 kilometers east-southeast of Ponape. It is small and has a very narrow lagoon without an entrance. The islets are Mokil on the northeast; Urak on the south; and Manton on the northwest. Only Mokil is inhabited. The land area is 1.24 square kilometers, and the population is about 450.

Pingelap Atoll (fig. 51, c) is nearly 100 kilometers east-southeast of Mokil and 240 kilometers west-northwest of Kusaie. It is small, like Mokil, with a high ratio of land to lagoon area. Both are more like Gilbert atolls than like most other Caroline atolls. The lagoon is entirely enclosed and contains coral heads and inward extensions of the outer reef. The islets are
Figure 56.—Caroline low islands: a, north end of Ngariungs Islet, Ngaiangl Atoll, Palau, showing solidified beach sandstone (limestone), with Pandanus at right, 1951; b, lagoon side of Manton Islet, Mokil Atoll, drifted coconuts on beach, 1953; c, village near lagoon beach, Ngaiangl Islet, Ngaiangl Atoll, large Calophyllum tree at left, 1951.
Pingelap on the southeast and Takai and Tugulu on the northwest, with only Pingelap inhabited. The land area is 1.75 square kilometers. The population of approximately 1,500 is about the densest in Micronesia, and it has one of the highest incidences of Hansen's disease in the world.

Vegetation of some Caroline Atolls

Nguiangl, the westernmost true atoll of the Carolines, is just outside the Palau barrier reef and thus is fairly rich in flora. I collected 67 species of plants in a very short period of time (Gressitt, 1953a). Dominant plants are coconut, breadfruit, papaya, banana, citrus, Calophyllum (figs. 56, c; 65, d), Barringtonia, Pisonia, Pandanus (fig. 56, a) and various ornamentals. Scaevola and Messerschmidtia are common along the beach. The main island has many coconut palms on the lagoon half, except at the north end; taro swamps just north of the center; and dense seminatural vegetation farther north. Ngariungs is densely covered with tall jungle and scrubby second growth, with some Rhizophora. The coconut palms have been badly damaged by the coconut beetle. Ngarapalas Islet has some dense scrub and some coconut palms, and Gorak islet has mostly coconut palms and a few bushes.

Figure 57.—Map of Kapingamarangi Atoll; drawn by E. H. Bryan, Jr.
Ulithi, (fig. 53) one of the largest Caroline atolls, is, like Ngaiangl, a rich, wet atoll, presumably with a very similar flora. Some islets are dominated by coconuts, *Cyrtosperma*, and *Colocasia*; and some, cleared during the war, have secondary weed and shrub growth.

Woleai is largely planted to coconuts, except Utagal which is dominated by breadfruit, papaya, *Pipturus*, taro, *Hibiscus*, other introduced plants, and some forest of *Guettarda*, *Barringtonia*, *Eugenia*, and *Pandanus*.

Nomwin Islet of the Hall Islands is dominated by breadfruit, in part mixed with coconuts, *Guettarda*, *Morinda*, *Pandanus*, *Cordia*, *Messerschmidia*, *Scaevola*, *Aiocasia*, and other plants. The island is very wet and densely forested.

Nukuoro has many coconuts and large breadfruit trees, as well as the typical atoll plants. It is a wet atoll.

Kapingamarangi (fig. 57), the southernmost of the Carolines, lacks a number of common atoll plants and has an impoverished flora. It is slightly drier than Nukuoro, but coconut and breadfruit trees are abundant and *Morinda*, *Premna*, *Hibiscus*, *Calophyllum*, *Messerschmidia*, *Guettarda*, *Scaevola*, and taro (fig. 46, b) are present.

Mokil and Pingelap are wet atolls and are fairly rich in vegetation. They are similar, but Pingelap has a moderately extensive mangrove swamp of *Rhizophora* and *Sonneratia* on the lagoon side of the indentation near the north end of the southern islet. Coconut, breadfruit, banana, *Cyrtosperma*, and *Tace* are abundant on both atolls, with *Scaevola* and *Messerschmidia* forming a distinct fringe on both sides of some of the uninhabited portions of the islets. St. John (1948) lists 57 species of plants for Pingelap, and Glassman (1953) adds a few to that number.

The vegetation of the Marshall Island atolls has been studied in much greater detail than has that of the Caroline atolls. A more detailed discussion of atoll vegetation is presented under the vegetation of the Marshall Islands. However, most Caroline atolls are richer in flora than are Marshall atolls.

**Marcus and Wake**

Marcus (Minami Tori Shima) Island is extremely isolated, being 1,000 kilometers east-northeast of Farallon de Pajaros (the northernmost Mariana island), 1,300 kilometers east of Iwo Jima, and a little farther west-northwest of Wake. It is a slightly raised atoll, or table reef, with the lagoon obliterated except for some small dry areas of alluvial soil northwest of the center. The island is triangular with blunt and slightly broadened angles. The altitude was reported as 22 meters in 1903, but the island was leveled during World War II (Kuroda, 1954). The area is 3 square kilometers. The island is dry and is not normally inhabited. It formerly possessed considerable vegetation, but
Marcus was studied by W. A. Bryan (1903), who collected 12 species of insects. These, however, were lost. Forty species of insects were collected by Sakagami (1953).

Wake Atoll, or Wake Island (Otori Shima), is extremely isolated, being about 600 kilometers north-northwest of Pokak (Taongi) in the Marshalls, 1,450 kilometers from Marcus, and 1,800 from Kure (near Midway). Wake is a slightly raised atoll, with the lagoon intact. There are three islands, Peale (north), Wake (east and south), and Wilkes (southwest), the west side consisting of reef only. The highest altitude is about 6 meters, and the area is about 11 square kilometers. The group, not normally inhabited earlier, has been an important air base since 1935.

**Figure 58.—Map of Marshall Islands.**

The Marshall Islands (fig. 58), which consist of 29 atolls and five isolated low islands, represent one of the greatest concentrations of such islands. Though they have fewer of both atolls and isolated low islands than do the
Carolines, those of the Marshalls are larger, on the average, both in lagoon and land area than those of the Carolines and have greater populations. The Marshalls have larger average lagoon areas and smaller land areas than do the Gilberts. The northern Marshalls are dry and the southern groups are wet atolls. The groups are classed in two chains, Ralik and Ratak, both extending more or less from northwest to southeast. Ralik, the western chain, is treated first.

**RALIK CHAIN**

Ujelang (Ujlang, Arecifos, Providence) Atoll (fig. 59, d) is the westernmost of the Marshalls and one of the most isolated. It is also the Marshall group nearest to the Carolines (nearest to Mokil). Ujelang is narrow, with a narrow reef with two openings on the southwest. The 27 islets are scattered and include Bikom, Bokonenellap, Jerko, Pokon, Kiloken, Morina, and Raej on the northeast side; Ujelang, Bieto, Nelle, Enellap, Enemanet, Kirene, and Kalo on the southwest side. The land area is 1.73 square kilometers and the population is about 150.

Eniwetok (Eniwetok), Brown) Atoll is also rather isolated, being the northwesternmost of the Marshalls and over 200 kilometers from both Ujelang and Bikini. The lagoon is very large and subrounded, and the 40 islets are scattered and include Bokelu, Bokanhako, Runo, Bokaidik, Boken, Enjebi (Engebi), Aej, Lajor, Amnon, Bijle, Lojowa, and Billa on the north; Runit, Ananij, and Jobtan on the east; Medren (Parry), and Eniwetok (Eniwetok) on the southeast; Ikudon (Igurin), Mot, Boken, and Bikin on the southwest. The land area is 5.85 square kilometers. The population was 128 in 1946, and the people were moved to Ujelang in 1947.

Bikini (Eschscholtz) Atoll is well east of Eniwetok and northwestern Ailinginae. It is large, with wide openings on the south side. The 36 islets are widely spaced and include Aen on the north; Bikini and Eneo on the east; Aerkol, Bikdren, Eneman, and Erebot on the south; and Nam on the northwest. The land area is 6.0 square kilometers. The population was 159 in 1937. This island has been a nuclear bomb testing site and the inhabitants were moved to Kili, via Rongerik.

Ailinginae [Aelinginae] Atoll is east-southeast of Bikini and just southwest of Rongelap. It is narrow, with openings on the south side. The 25 islets are almost entirely on the south side and include Majkorel, Joreia, Wijjune, Rubonwot, Enebuk, Makil, and Karwe. The land area is 2.8 square kilometers, and the island has been long uninhabited.

Rongelap (Ronglap, Pescadora) Atoll, between Ailinginae and Rongerik, is large and irregular in outline, with several openings. The 55 islets are mostly
on the east, though some are on the south and north. They include Namen, Kobale, Melut, and Eneaetak on the east; Rongelap, Arbar, Keroka, and Burok on the south, and Jokdik, Aidik (Airikku), Ekoj, and Lomulol on the north. The land area is 7.95 square kilometers, and the population is about 100.

Rongerik (Rongrik, Rimski-Korsakoûf) Atoll is just east of Rongelap and is the northeasternmost of the Ralik Chain. It is roughly rounded, with wide openings. The 13 islets are on the north and east sides and include Betbet, Motlap, Bikenaren, and Rongerik on the northeast; Keroka and Enewetak on the southeast; and Bok on the northwest. The land area is 1.68 square kilometers, and the population has been extremely small, except when the Bikini Islanders were temporarily there.

Wotto ([Wotto], Schanz) Atoll is half way between Ailinginae and Ujae and is northwest of Kwajalein. It is relatively small and is irregular, with several openings on the west. The 14 islets are mostly on the north and southeast and include Mejurwon, Enebnak and Wotto (Wotto) on the north; Bokommetok, a long sand spit on the east; and Wutie, Enjejto, and Kaben on the south. The land area is 4.3 square kilometers, and the population is about 35.

Ujae (Katherine) Atoll (fig. 62, a) is southwest of Wotto and west of Lae and Kwajalein. It is elongate, with a northwest extension and openings on the west. The 13 islets are mostly on the east side and include Enelamoj and Alle on the northwest; Ebaju, Ruot, and Wojak on the east; Ujae on the southeast, and Bokerok and Bok on the west. The land area is 1.86 square kilometers, and the population is about 250.

Lae (Brown) Atoll (fig. 59, c) is between Ujae and Kwajalein. It is small, is subtriangular, and has an opening on the west. The 18 islets are mostly on the northeast and include Kibung on the north; Lwejap, Enemonmon, and Lae on the east; and Loj on the southwest. The land area is 1.45 square kilometers, and the population is about 150.

Kwajalein (Menschikov) Atoll (fig. 59, a, b), the largest atoll in the world, is the center of the Ralik Chain. It is elongate and irregular, with many openings and with part of the reef sunken. The lagoon area is 2,174 square kilometers, and the length is about 130 kilometers. The 90 islets are scattered on all sides and include Errop and Roi-Namur on the north; Kauetb, Enewetak, Meik, Bikej, Kongojokenen (Gugegwe, including Bweje), Lojjaion (Loi), Lojjaero; Ebeje (Ebeje), Kwajalein, Enluoj, and Enlapkan on the southeast; Ellep, Onnak, Nel, Enmat, Ero, Ele on the southwest; and Ebaten on the northwest. The land area is 16.4 square kilometers, and the native population is about 1,000. There has been much opportunity for introduction of insects from distant regions by air and sea transport.
Figure 59.—Northern Marshalls: a, *Pisonia* forest, Enewetak Islet, Kwajalein Atoll; b, *Pisonia* forest, Enewetak Islet, Kwajalein, leeward lagoon side; c, opening in mixed forest occupied by a blanket of *Wedgesia biflora*, Lae Islet, Lae Atoll; d, *Pomphix* forest on slightly emerged reef limestone, Enetlap Islet, Ujelang Atoll. (Fosberg, 1952.)
Lib (Princessa, Lip) is a small single island with a narrow fringing reef. It is south of Kwajalein and northwest of Namu Atoll. The land area is 0.93 square kilometer, and the population is about 80.

Namu ([Nanou], Musquillo) Atoll is between Kwajalein and Ailinglapalap. It is long and narrow, and somewhat irregular, and it has three openings on the west. The 50 islets are mostly very small and scattered on the east and south. They include Majkon (Kaginen) and Ebonun on the northeast; Jeluk, Rowo, Enejeij, Enenak, and Mae on the southeast; Nienon, Lwoen, Lukoj, and Andel on the southwest; and Namo (Namu) on the northwest. The land area is 6.26 square kilometers, and the population is about 350.

Ailinglapalap (Ailinglaplap, Elmore, Odia) Atoll is just southeast of Namu and some distance north-northeast of Jaluit. It is large and subtriangular, with several openings. The 51 islets are well scattered, and some in the northeast and southwest are quite long. They include Je (Jih), Mejil, and Ja on the northeast; Airok, Ailinglapalap, Bikajeh, Tolen, and Koto-Eniak on the south; Wojja, Katteij, Mejejok, and Biker on the west. The land area is 14.7 square kilometers, and the population is about 750.

Jabwot is a single isolated low island with a narrow fringing reef, located east of Namu and northeast of Ailinglapalap. The land area is 0.57 square kilometer, and the islet is uninhabited. Coconut palms are present.

Jaluit (Bonham) Atoll is well south of Jabwot and Ailinglapalap and between Namorik and Majuro. It is large and irregular in outline, with a few openings. The 83 islets are on all sides; but most of them are on the east, where some are quite long. They include Ren, Kijen, Mejae, Mejetto, and Imroj on the northeast; Ajijen, Arrween, Imej (Emidj), Amnon, Enejet, Jobwar, and Jaluit on the southeast; Mange, Majurirok (Elizabeth), Ae, and Pinlep on the southwest; and Boknake on the northwest. The land area is 11.34 square kilometers and the population is about 1,000.

Kili (Hunter) is a single low island between Jaluit and Namorik and closer to Jaluit. It is narrow and surrounded by a narrow fringing reef. The land area is 0.93 square kilometer, and the population was about 150 before World War II. The Bikini Islanders are now settled with them on Kili.

Namorik (Baring) Atoll, west of Kili and Jaluit, is a small atoll with an enclosed angular reef. The two islets are Ajalto-Namorik, curving around the northeast and southwest corners, and Marmar, at the northwest. The land area is 2.77 square kilometers, and the population is about 480.

Ebon (Boston) Atoll, southeast of Namorik, is the last of the Ralik Chain and the southernmost of the Marshalls. It is of moderate size and circular and has an opening on the southwest. The 22 islets are on all sides, but the best developed ones are to the south. They include Enenaitok and Ebon (Jittaken,
Jittoen) on the southeast; Enilook, Toka, and Enekoion on the west. The land area is 5.74 square kilometers, and the population is about 750.

**Ratak Chain**

Pokak (Taongi, Poknakku, Gasper Rico) Atoll (fig. 61, b) is the northernmost of the Marshalls and one of the most isolated groups of Micronesia. It is arcuate, being convex on the east and concave on the west. The reef is complete, with some coral heads in the lagoon. The 12 islets are in the southeast and include Kanome, Breje, Sibylla, Pokak, and South. The land area is 3.23 square kilometers, and the group is uninhabited.

Bikar (Dawson) Atoll is southeast of Pokak and northeast of Utirik. It is subrhomboid and has a very narrow entrance on the west. The five islets are Jalikik, Almeni, Jaboero, and Bikar on the southeast and a very small one on the northeast. The land area is 0.49 square kilometer, and the group is uninhabited.

Utirik ([Wutrok], Kutusov, Utirik) Atoll (fig. 62, b) is south of Bikar and just northeast of Taka. It is triangular and fairly small and has an opening on the west. The six islets are in the south and include Bike, Elluk, Bekrak, Wutrok (Utirik), and Aon. The land area is 2.4 square kilometers, and the population is about 170.

Taka ([Toke], Suvarov) Atoll is just southwest of Utirik. It is similar to Utirik and is subtriangular, with two openings in the west and with six islets; all in the southeast, including Lojiron, Toke (Taka), and Watuerok (Elluk). The land area is 0.57 square kilometer, and the group is uninhabited.

Ailuk (Tindal, Watts) Atoll, south of Utirik and Taka and between Jemo and Mejit, is elongated north and south, with openings on the west. The 56 islets are on the east side, except for two, and include Kapen, Enejelar, Bikon, Aliej, Enejomaren, Baojen, Bwerorkan, Ulika, Marib, Jabbwi, and Ailuk on the east. Akuwe is on the west. The land area is 5.36 square kilometers, and the population is about 325.

Mejit (New Year, Mejij) is a single island east of Ailuk. It is irregular in shape with a small open lagoon on the west, suggesting a small, slightly raised atoll. The land area is 1.80 square kilometers, and the population is about 330.

Jemo ([Tyemo, Temo) Island (fig. 61, a) is a single oval islet with a narrow fringing reef on the west end of a long submerged bank. The land area is 0.15 square kilometer, and the islet is uninhabited.

Likiep (Count Heiden) Atoll is not far southwest of Jemo and is northeast of Kwajalein. It is subelliptical with openings on the southwest. The 72 islets are on all sides, but mostly on the straight northeast side. They include Mat,
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Emijwa, and Jetonijev on the north; Melang, Jebal, Kole, Loto, Likiep, Ae­
kone, and Lukonwor on the southeast; and Kabinwood on the west. The land
area is 10.25 square kilometers, and the population about 600.

Wotje (Romanzov) is a large atoll southeast of Likiep, northwest of Maloe­
lap, and just north of Erikuh. It is about in the center of the Ratak Chain, and
is suboblong, east to west, with southern openings. Some of the 72 islets are
very small, and they are mostly on the north and southeast. They include
Ormej, Enibing, and Wotje on the northeast; Kimejo, Enjejtak, and Ukon
on the southeast; and Kajien and Nihung on the northwest. The land area is
8.18 square kilometers, and the population is about 350.

Erikub ([Erkup], Bishop, Junction) Atoll is moderately large and just
south of Wotje. It is oblong, lying northwest-southeast, and has openings on
both sides. The 15 islets are on all sides but the northwest, most of them on the
southeast side. They include Aretojeong, Aretojeirok, Bokullu, and Boken on
the east; Dru and Erkup ([Erikuh]) on the south; and Eneko on the west. The
land area is 1.53 square kilometers, and the group has been uninhabited in
the past, though it now has 14 people.

Maloelap (Kaven, Calbert) Atoll is southeast of Wotje and Erikub and just
north of Aur. It is large and subelliptical, lying northwest-southeast, and has
several openings on the west. The 71 islets are well distributed, but more of
them are on the northeast side. They include Kapen, Erbar, Wonmak, Enea,
Jang, and Tar on the north; Tarwa, Kimar, and Aerok on the southeast; and
Enenion and Bwibwi on the southwest. The land area is 9.8 square kilometers,
and the population is about 480.

Aur (Ibbetson) Atoll is just south of Maloelap and well north of Majuro.
It is moderately large and subrhomboid, with openings on the west. The 42
islets are mostly on the east side and include Biken on the northwest; Tabal on
the northeast; Enoq, Ejej, and Aur on the southeast; and Mumot on the
southwest. The land area is 5.6 square kilometers, and the population about
430.

Majuro (Arrowsmith) Atoll is well south of Aur and just west of Arno. It
is of moderate size and transversely elongate, with openings on the north.
There are many islets on the north, and land with only a few breaks on the
south. Among the 60 islets are Kolalen, Eneko, Enemanet, Jaroj (Rita), and
Uliga on the northeast; Telap (Dalap), Rairok, Enenelip, and Ajeltak-Woja­
Arrak-Majuro on the south; and Jeluklap and Rongrong (Roguron) on the
northwest. The land area is 9.16 square kilometers, and the population is about
1,600. Spoehr (1949) studied the village in 1947.

Arno (Daniel, Peddlar) Atoll (fig. 60) is just east of Majuro and north
of Mili. It is fairly large and of unusual shape, with long eastward and north­
ward projections forming a large northeastern crescent with reef openings near
its middle. There is a separate narrow lagoon at the end of each of the two projections. The northern lagoon is closed and the eastern one has an opening on the inside of the crescent. There are about 130 islets; but the number is variable, as storms have broken some and united others. In general, the northern islets, or those inside the crescent, are small, and few of them are much longer than broad. Most of the southern islets are long and narrow, some extremely so. The islets include the following: Namwi and Bikarej, respectively on the north and south sides of the north lagoon; Tutu, Kijbwe, Jilong, and Takleb (Tagalip) near the middle of the crescent; Longar-Tinak and Kilange on the outer and south sides of the east lagoon; Ijoen, and Aljaltuon-Matolen, Ine, Arno, Kemman, Ulen, and Kilomon on the south and southwest portions. Arno, on the southwest, is the widest islet and Ine, on the south, is by far the longest, being some 20 kilometers long and including the subdivisions Matolen, Ine, Jabu, Kinajong, and Lukwoj (east to west). Most of Ine is less than 200 meters wide, and it is about 100 times as long as broad. The best study of atoll insect ecology was done at Arno, primarily on Ine, by Usinger and La Rivers (1953). (See also Anderson, 1951; Hatheway, 1953; Marshall, 1951; and Stone, 1951a, 1951b for vegetation and other aspects.) The total land area is 12.95 square kilometers and the population was estimated at 1,155 in 1950.
Mili ([Mille], Mulgrave) Atoll is south of Arno and east of Jaluit and, except for Narik, is the southernmost of the Ratak Chain. Narik might be considered part of Mili, which is large, transversely oblong, and irregular, with openings on the north and with small enclosed lagoons at the northeast and southeast corners. It is about 52 kilometers long. There are about 90 islets, but some are either barely separated or connected by sand strips. They are shorter on the north and east and longer on the south and west, and they include Buruwon and Namakke on the east; Enewa, Enejet, Arbar, Mille (Mili), and Melka on the south; and Nar, Naieto (Aln), Tokawa, and Jobonwor on the northwest. The land area is 14.9 square kilometers, and the population is about 300.

Narik (Knox, Narikrik) Atoll is just southeast of Mili and is the southeasternmost of the Marshalls. As it is separated from the protruding southeast corner of Mili by only 4 kilometers of water which is no more than 10 meters deep in places, Narik might be considered a former part of Mili, like one of the protruding accessory lagoons of Arno which had the connection torn away by storms. Narik is very narrow with one or two narrow openings at the ends. There are about 18 islets, including Narikrik on the south, Enenlukap on the west, and Jiktok on the north. The land area is 0.98 square kilometer, and the group is uninhabited.

**VEGETATION OF MARSHALL ISLANDS**

Vegetation in the Marshalls varies with the climate, being poorer in the northern, dry atolls and richer in the southern, wet atolls. The vegetation is strand formation, with coconut palms dominating. The dense human population over a long period has restricted the flora considerably, reducing some plant species to very small populations or to extinction on certain atolls. Marshall atolls are richer in flora than are many central Pacific atolls or the Tuamotus, but poorer than Caroline atolls. Fosberg (1946) believes this due to the fact that the Marshalls, and even more so the Carolines, are closer to high islands and particularly to continental sources. According to St. John (1953), 18 weeds were introduced to the Marshalls before 1941, five of them—belonging to the genera *Jussiaea*, *Eragrostis*, *Phyllanthus*, *Conchris*, and *Centella*—having been brought by Micronesians before the nineteenth century.

Eniwetok, a dry atoll, has conspicuous brushy, scrubby forest of *Scaevola*, with *Guettarda*, *Messerschmidia*, and *Pisonia* mixed in, and vines of *Ipomoea*. This scrub is low where the islets are narrow. Such grasses as *Lepturus* and *Eragrostis* grow in open places. *Digitaria*, *Triumfetta*, *Boehravia*, and *Portulaca* are found on open sand. Fosberg found that weeds and *Lepturus* invaded first on sandy surfaces of disturbed land and that such native plants as *Scaevola*, *Messerschmidia*, and *Guettarda* recovered first on gravel and rock. In
1946 cultivated plants included cucurbits, *Ricinus*, tomato, sorghum, and *Brassica*. Breadfruit is rare.

Likiep is intermediate between a dry and a wet atoll. Breadfruit is common; and *Morinda*, *Guettarda*, *Premna*, *Pandanus*, *Lepturus*, *Boerhavia*, *Polypodium*, *Cyrto sperma*, *Terminalia* (fig. 66, b), *Calophyllum*, and *Hernandia* are present.

Kwajalein is moderately dry and somewhat similar to Likiep in its vegetation. A brush of *Scaevola* and *Pisonia* (fig. 59, a, b) is common and includes *Messerschmidia* (*Tournefortia*), *Ipomoea*, *Vigna*, *Euphorbia*, and *Chloris*.

Ailinglapalap is a large, wet atoll with luxuriant vegetation, the wide islets permitting somewhat mesophytic conditions. Some parts are rocky and seem to have fairly undisturbed vegetation. Coconut and breadfruit are dominant, with undergrowth of *Wedelia*, *Premna*, *Pipturus*, and *Hibiscus*. *Pisonia*, *Calophyllum*, *Pemphis*, *Messerschmidia*, *Soulamea*, *Hernandia*, *Ochnasia*, *Saravana*, *Thuarea*, *Vigna*, *Polypodium*, *Intsia*, *Guettarda*, *Pandanus*, and *Morinda* are present. Mangrove of *Sonneratia* and *Rhizophora* is found on Airik Islet. Bananas and many cultivated plants grow there.

Majuro has the same rainfall as Ailinglapalap; but because its islets are narrower, the vegetation is less mesophytic. Coconut and breadfruit are dominant, and *Premna*, *Morinda*, *Guettarda*, *Scaevola*, *Messerschmidia*, *Pemphis*, *Pleurya*, *Fimbrystis*, *Cynodon*, *Cenchus*, *Eleusine*, *Pandanus*, *Ochnasia*, and others are present. Mangrove is represented by *Bruguiera*. *Tacca*, *papaya*, *taro*, and some other cultivated plants are common.

Arno (fig. 60) has had its vegetation studied in detail by Hatheway (1953). There are 129 species of vascular plants according to Anderson (1951) and Stone (1953). In 1952, 78 percent of the land surface was in coconut and breadfruit forests, maintained by the weeding of invaders. The original vegetation consists of *Scaevola*, *Messerschmidia*, *Pandanus*, *Terminalia*, and *Guettarda* on the boulder ramparts and extending inland up to 30 meters on windward sides of islets. This merges on stony soils with a forest six to 18 meters high of *Barringtonia*, *Hernandia*, *Ochnasia*, *Intsia*, *Pandanus*, *Guettarda*, *Pisonia*, and *Cordia*. Some of these, with *Allophylus* and *Pipturus*, grow on sandy interiors. *Pemphis* dominates on eroding lagoon shorelines and saline flats; and mangrove dominates saline swamps. *Pandanus* grew originally in fresh-water swamps now used for taro. The ground layer in the coconut and breadfruit groves include *Lepturus*, *Fimbrystis*, *Cassytha*, *Triumfetta*, *Vigna*, *Wedelia*, *Tacca*, *Nephrolepis*, *Asplenium*, and other herbs, ferns, or shrubs.

Jaluit is, in general, similar to Majuro and Arno; and as on those islands, coconut and breadfruit are dominant. Mangrove includes *Bruguiera*, *Intsia*, and *Lumnitzeria*, with *Barringtonia* around the edges of inland swamps and *Sonneratia* on the reef flat. *Alocasia* is common and *Luncaena* and *Vigna* (fig. 65, b) are present.
After a new atoll islet is formed by coral boulders and smaller fragments washing up on the reef and sand has accumulated, colonization by 12 or so common strand plants commences. These take root on newly exposed coral sand or gravel just above the high tide level. Accompanying these higher plants is a crust of blue-green algae. The first plants to arrive—Messerschmidia—

Figure 61.—Northern Marshall Islands: a, Messerschmidia forest with Scaevola and Cocos, Jemó Island; b, top of lagoon beach, Shylla Islet, Polake Atoll, showing Lepturus, Portulaca, Messerschmidia, and Scaevola. (Fosberg, 1952.)
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dia, Scaevola (figs. 61, a; 65, a, c), Lepturus (fig. 61, b), and Guettarda—readily establish themselves as drift seedlings. Next come Pandanus, Portulaca (it is slightly questionable as to whether Portulaca drifted from elsewhere), Triumfetta, and Vigna. Less often seen as seedlings from drifted seeds are Cocos, Ipomoea, Hernandia, Calophyllum, Intsia, Morinda, Barringtonia, Suriana, Terminalia, and Wedelia, according to Fosberg (in press). Edmondson (1941) showed by experiments that coconut can seed itself by drift; and I have seen examples of it, as well as an abundance of Barringtonia seeding itself on a new portion of Ngarapalas Islet of Ngaingl Atoll in the Carolines. Fosberg noticed that in the Marshalls some seeds, such as those of Entada and Mucuna, drift ashore; but these were not seen to germinate. However, he felt certain that genera other than those mentioned above arrived by drifting as seeds. Some of them need to be carried farther inland than the beach rampart in order to establish themselves. Pisonia is carried by birds, its sticky seeds adhering to feathers. Bauhinia, Peperomia, and Adenostemma also have sticky seeds and may be carried by birds. Cassytha and Pipturus are probably carried in the stomachs of birds. So, probably, is Scaevola, in addition to floating as seeds. Some seeds not used as food may possibly be taken as gizzard stones by predaceous sea birds (Marshall, 1951). Some native plants other than weeds are transported by man; for example, mangrove to landlocked pools. Luomala (1953) notes that the Gilbertese plant any seeds that drift to beaches.

Fosberg (1953a) states that Pacific atolls may have three to 150 species of plants. Salinity is a great limiting factor, in addition to isolation, limited soil, and paucity of environments.

Coconuts are dominant on most Marshall and other Micronesian atolls. Well-tended plantations have undergrowth restricted to grasses, Fimbristylis, Euphorbia, and introduced herbs; but if untended, underbrush of Wedelia (fig. 59, c), Clerodendrum, Ipomora and various shrubs develop. On the wetter atolls, breadfruit trees are mixed with coconuts, or dominate, producing a dense, shady, canopy forest with ferns and Piper. Scrub forest is dominant where coconuts have not been planted. Guettarda, Pandanus, Messerschmidia, Pisonia, Ochrosia, Intsia, Pipturus, Souamica, Terminalia, Allophylus, Cordia, and Barringtonia are characteristic. Pisonia forest (fig. 59, a, b) may become stable and permit development of phosphate (see soils), but under some conditions it may be invaded by Ochrosia and eventually eliminated. There is a rough concentric arrangement of the vegetation (Fosberg, in press), with Messerschmidia and Guettarda, fringed at the top of the beach on the windward side with Scaevola (figs. 61, 62). Scaevola also lines the leeward border of the islet. These may be the dominant plants on dry atolls. Mangrove develops on leeward beaches or inlets. Rhizophora requires continuous tidal interchange, but Bruguiera, Lumnitzera, and Pemphis (fig. 59, d) do not. The concentric
arrangement depends upon the width of the islets. The mesophytic breadfruit, fern, and taro environments, as well as those for banana and other introduced plants, are possible only in broader portions, and *Pisonia* in moderately broad areas. Sandy portions, particularly on dry atolls, may be dominated by *Lep­turus* (fig. 61, b); rocky portions, by *Boerhavia* and *Portulaca*. *Sida* and *Heliotropium* are also characteristic on dry atolls. All atoll plants must be somewhat salt tolerant because of the occasional storms. Most temperate vege-

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**Figure 62.**—a, forest edge, Bokerok Islet, Ujae Atoll, with *Pisonia*, *Scaevola* and *Pemphis*; drift log in foreground; b, windbeaten *Scaevola* scrub, Bekrak Islet, Utirik Atoll. (Fosberg, 1952.)
tables cannot survive on atolls, and agriculture may be limited to the food plants of long standing: coconut, *Pandanus*, taro, and *Tecoma*; with banana, papaya, squash and limes holding a limited place on damper atolls.

**Gilbert Islands**

The Gilbert Islands (fig. 63) are an integral part of Micronesia, forming its southeastern corner, but they are almost as close to the Ellice Islands as they are to the Marshall Islands, and thus form a connecting link between Polynesia and the rest of Micronesia. The Gilberts consist of 11 atolls and five reef, or low, islands. They are much larger in land area and much smaller in lagoon area than are those of the Marshalls and Carolines, thus having a high ratio of land area to lagoon area. The Gilberts stretch from northwest to southeast between 3° 20' N. latitude to 2° 42' S. and are thus divided almost in half by the equator. They lie between 172° 35' and 176° 50' E. longitude. The islets of most of the atolls of the Gilberts are on the east or southeast because of the prevailing winds and currents, but those of Butaritari are more on the southwest because of the different local current.

![Map of Gilbert Islands](image)

*Figure 63.—Map of Gilbert Islands.*

The highest islets are less than 4 meters above sea level. The soil is largely sand, low in humus and poor in water retention. The vegetation is limited in extent and variety, particularly in the southern islands, where rainfall is low and where severe droughts occur about one year in seven. Thus a rich insect
fauna cannot be supported. This paucity of fauna in the southern Gilberts might suggest a partial barrier and a more distinct boundary to Micronesia; but if most insect immigrants to Micronesia from Polynesia are carried in air currents at high altitudes, this aridity would primarily affect the local fauna only.

The total land area of the Gilberts is 295.5 square kilometers. The population in 1947 was 29,414. The people are Micronesians, though most of them are darker than other Micronesians.

In the Gilberts, the longer individual atoll islets are rarely given names. The names used are generally those of villages or parts of the islands.

Makin Meang (Little Makin), the northernmost, is a reef island and consists of three small islets in a row and covers an area of 7.25 square kilometers. The southern end is three kilometers north of Butaritari. Rainfall is heavy and vegetation luxuriant. The population is about 1,000.

Butaritari ("Makin") Atoll has a lagoon which is relatively large for the Gilberts. The land area is 11.6 square kilometers. There are two long islands on the southeast side of the triangle, including Butaritari, and about 20 small islets. The islets include (clockwise, from north) Ubrantakoto, Namoka, Natata, Kuma, Butaritari, Kotabu, Tukerere, Nabuni, Oteariki, and Bikati. The population was 1,829 in 1947.

Marakei (Mathew) Atoll is more than one degree distant from Butaritari. The lagoon is very small, and the two islands, north and south, almost completely enclose the lagoon, leaving only a boat entrance. The land area is 10.2 square kilometers. The population was 1,805 in 1947.

Abaiang (Apaiang, Charlotte) Atoll is not far southwest of Marakei. The land area is 28.6 square kilometers, making it the second largest atoll of the Gilberts. There is one very long island along the northeast side to the south end, and there are about six small islands (including Iku, Teirio, Nuotecu, Nankirata, Twin Tree, and Ribono) and several very small ones on the southwest and north. The lagoon is free of reefs in the southeast and also affords entrances for ships. The population was 2,813 in 1947.

Tarawa (Cook, Knox) Atoll, just south of Abaiang, is the present political center of the Gilberts and has the densest population. The land area is 20 square kilometers, and the lagoon is large. There are nine long islands—including Taritai, Buota, Eita, Bairiki, and Betio (Bititu)—and about six very small ones, all on the east and south side of the triangular reef. Tarawa suffered much destruction of coconut palms and other vegetation during World War II. The population was 3,528 in 1947.

Maiana (Gilbert, Hall) Atoll is some 40 kilometers south of Tarawa. The land area is about 25.9 square kilometers, making it the third largest of the Gilberts. The lagoon is proportionately small. There is a single long island extending the full length of the northeast and southeast sides of the oblong reef.
with a few very small islets on the lower southwest. The population was 1,484 in 1947.

Abemama (Hopper, Roger) Atoll, about one degree southeast of Maiana, has a land area of 17 square kilometers and a fair-sized lagoon with ship entrances. There is one long island (Tabian-Binoiman) along the north and northeast sides and five smaller ones, including Tabonua, Kabangaki, Bike, and Abatiku, on the southeast and southwest. The population was 1,184 in 1947.

Kuria (Woodle) is of the reef type, with two islands, Oneaka and Kuria, close together; and there is no lagoon. The land area is 12.92 square kilometers. The population density is low, with 313 in 1947.

Aranuka (Henderville) Atoll is just east of Kuria and southwest of Abemama, and it is just north of the equator. There are an eastern and a western island on the triangular reef, with some tiny islets between on the north. The land area is 15.5 square kilometers and the lagoon is small and shallow. The population is sparse, totalling 366 in 1947.

Nonouti (Sydenham) Atoll is south of the equator and one degree southeast of Aranuka. There is one long island on the east side, several narrowly separated ones on the northeast, and two separate small islands—Tetabakia at the south end and Numatong on the northwest. The land area is 25.5 square kilometers, and the lagoon is large. The population was 2,233 in 1947.

Tabiteuea (Tapiteuea, Drummond) Atoll, southeast of Nonouti, is the largest of the Gilberts. Most of the lagoon is narrow and incompletely enclosed. The land area is 49 square kilometers or less. There are two larger islands, Anikai-Utira on the northeast side of the north end and Buariki-Taku (Nuguti) at the southeast end, with many small islets along the sinuous northeast side between them. The population was 4,131 in 1947. This atoll and the next three to be discussed form the Kingsmill group.

Beru (Francis) Atoll, one degree east of Tabiteuea, consists of a single long island of 21 square kilometers. It encloses the small, narrow lagoon, except for the open central half of the west side. The population was 2,433 in 1947.

Nikunau (Nukunau, Byron) is a narrow reef island lying one-half degree east of Beru. The land area is 18 square kilometers, and there is a small landlocked lagoon in the north. The population was 1,724 in 1947.

Onotoa (Clerk) Atoll (fig. 64) lies southeast of Tabiteuea and has a land area of 13.5 square kilometers. The lagoon is small and partly open. There are two long islands on the east side. Tanyah or North Island ("Buiarton") including Buariki, in the north, and Otoeie on the southeast. There are several small islets between and two islands at the southern end, the larger and southwesternmost being Tabuaroarae. A small islet, Temuah, at the northwest, is the westernmost. This dry atoll was the site of the Pacific Science Board's 1951
atoll expedition. Insects were collected by the botanist E. T. Moul (1954) of Rutgers University. The population in 1947 was 1,821.

Tamana (Rotcher) is a single narrow reef island nearly 65 kilometers southeast of Onotoa. The land area is 5.2 square kilometers. The population was 1,032 in 1947.

Arorae (Hope, Hurd) is also a single reef island, 80 kilometers to the east of Tamana and slightly south of it. This is the southeastern tip of Micronesia. The land area is 13 square kilometers. The population was 1,749 in 1947.

![Map of Onotoa Atoll](image)

**Figure 64.—Map of Onotoa Atoll.**

**VEGETATION OF GILBERT ISLANDS**

The Gilbert Islands have a limited flora, as the development of vegetation on the islands is controlled by rainfall. The northern Gilbrels have a fairly well-developed atoll vegetation, not very different from that of the southern Marshalls, but the southern Gilberts have a much more poorly developed vegetation. Among the conspicuous plants are such typical atoll species as members of *Calophyllum*, *Cordia*, *Scaevola*, *Hernandia*, *Barringtonia*, *Messerschmidia*, *Pemphis*, *Morinda*, *Ochrosia*, *Alocasia*, *Colocasia*, *Cyrtosperma*, *Guetarda*, *Cocos*, *Pandanus*, *Musa*, and *Artocarpus*. In the southern groups, *Calophyllum* and *Barringtonia* and some of the others are rare, with most of the brush consisting of coconuts, *Pandanus*, *Scaevola*, and *Guetarda*. Breadfruit trees are rare in most of the southern Gilberts (Luomala, 1953).

During World War II there was very serious destruction of vegetation on Butaritari ("Makin"), Tarawa, and Abemama atolls. In fact, 150,000 coconut palms are said to have been destroyed (Luomala, 1953). In 1947 there were
2,277,062 bearing coconut palms in the entire Gilbert group, or about 70 bearing palms per Gilbertese.

**Ocean and Nauru**

Ocean (Banaba) Island is a single raised coral island, generally called a raised atoll, lying some 375 kilometers west of the Gilbert Islands and just south of the equator. The area is 5.9 square kilometers, and the highest altitude is 81 meters. There are no streams, and little soil. The island is rich in phosphate deposits, which are exploited. Vegetation, both natural and cultivated, has long been encroached on or destroyed. What remains is dense in only some areas. It includes coconuts, mango, guava, banana, *Terminalia*, and papaya, but no taro.

Nauru (Pleasant) Island is similar to, and about 320 kilometers west of, Ocean Island; but it is larger, being 21.3 square kilometers in area, and is a little closer to the equator. The fringing reef is narrow. Nauru’s highest altitude is 65 meters. Like Ocean, this island is rich in phosphate deposits, which have only been partly exploited. Vegetation is extensive but not dense. It includes *Euphorbia*, *Capparis*, *Calophyllum*, *Thespesia*, *Pandanus*, *Bruguiera*, *Terminalia*, and *Scaevola*. Ocean and Nauru are described by Ellis (1936).

**Fauna**

**Isolation in Micronesia**

An important factor in the development of specialized faunas on oceanic islands is the isolation of the islands. Starting with, say, a small group of colonists, the fauna of an island is the result of isolation, plus time, plus ecological opportunity. The latter involves the size, topographic and vegetational diversity, and suitability of climate of the island. Thus a tropical high island offers much greater ecological opportunity and greater chance of initial survival than does a low island. Degree of isolation, again, determines to a considerable extent the numbers of potentially successful colonists and thus determines the degree of competition, which is important. Well-isolated islands which receive few immigrants may have successful colonists which develop great divergence from the ancestors, to the extent of new genera developing and filling empty ecological niches.

The genic makeup of the original colonists is important, as it affects the extent of variability and mutations and thus affects adaptability. Extreme isolation gives full play to the potentialities of the genic complement of the colonizing ancestors. However, with occasional reintroduction of individuals from parent populations, as happens in less isolated islands, genic divergence and consequent diversification would be retarded. Thus speciation is more active on
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the more isolated islands, or at least on those which receive less frequent immigrants, given sufficient time and ecological opportunity. Less endemism is to be expected on newer and less isolated islands.

For instance, natural isolation in Micronesia is not so extreme as it is for the Hawaiian Islands, for the Marquesas, or for southeastern Polynesia. Micronesia is relatively near two major continental areas—eastern Asia and New Guinea—representing the eastern Palearctic, Indo-Chinese, Philippine, Malayan, Wallacean, and Melanesian zoogeographical areas. It is also close to central Polynesia.

The relative degrees of isolation for Micronesia as a unit and for its major subdivisions are compared with certain other Pacific island groups in table 4.

Table 4.—Isolation in Micronesia and other Pacific island groups; distances (in kilometers) for closest part of respective groups or areas

<table>
<thead>
<tr>
<th>ISLANDS</th>
<th>HOT</th>
<th>HAWAII</th>
<th>JAPAN</th>
<th>PHILIPPINES</th>
<th>MOLUCCAS</th>
<th>NEW GUINEA</th>
<th>OKINAWA</th>
<th>MICRONESIA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bonins</td>
<td>6,100</td>
<td>6,100</td>
<td>980</td>
<td>2,800</td>
<td>3,400</td>
<td>3,700</td>
<td>1,290</td>
<td>(750)</td>
</tr>
<tr>
<td>Volcano Is</td>
<td>5,900</td>
<td>6,200</td>
<td>1,350</td>
<td>2,400</td>
<td>3,100</td>
<td>3,300</td>
<td>1,320</td>
<td>(550)</td>
</tr>
<tr>
<td>Marianas</td>
<td>5,000</td>
<td>5,900</td>
<td>2,000</td>
<td>2,250</td>
<td>2,350</td>
<td>2,100</td>
<td>1,820</td>
<td></td>
</tr>
<tr>
<td>Carolines</td>
<td>2,900</td>
<td>4,400</td>
<td>2,600</td>
<td>600</td>
<td>290</td>
<td>370</td>
<td>2,050</td>
<td></td>
</tr>
<tr>
<td>Marcus</td>
<td>5,100</td>
<td>4,600</td>
<td>1,770</td>
<td>3,430</td>
<td>3,900</td>
<td>3,420</td>
<td>2,630</td>
<td></td>
</tr>
<tr>
<td>Wake</td>
<td>4,050</td>
<td>3,700</td>
<td>3,100</td>
<td>4,400</td>
<td>4,700</td>
<td>3,700</td>
<td>4,000</td>
<td></td>
</tr>
<tr>
<td>Marshalls</td>
<td>2,600</td>
<td>3,640</td>
<td>3,300</td>
<td>3,900</td>
<td>3,700</td>
<td>2,250</td>
<td>3,800</td>
<td></td>
</tr>
<tr>
<td>Gilberts</td>
<td>1,450</td>
<td>3,700</td>
<td>4,800</td>
<td>5,200</td>
<td>4,800</td>
<td>2,400</td>
<td>5,000</td>
<td></td>
</tr>
<tr>
<td>Ocean</td>
<td>1,900</td>
<td>4,250</td>
<td>4,600</td>
<td>4,800</td>
<td>4,400</td>
<td>2,000</td>
<td>4,900</td>
<td></td>
</tr>
<tr>
<td>Nauru</td>
<td>2,220</td>
<td>4,500</td>
<td>4,400</td>
<td>4,400</td>
<td>4,000</td>
<td>1,700</td>
<td>4,600</td>
<td></td>
</tr>
<tr>
<td>Johnston</td>
<td>3,800</td>
<td>1,400</td>
<td>5,500</td>
<td>7,400</td>
<td>7,600</td>
<td>5,400</td>
<td>6,400</td>
<td>2,150</td>
</tr>
<tr>
<td>Hawaii</td>
<td>4,250</td>
<td>6,000</td>
<td></td>
<td>8,300</td>
<td>8,500</td>
<td>6,800</td>
<td>7,300</td>
<td>3,600</td>
</tr>
<tr>
<td>Marquesas</td>
<td>5,000</td>
<td>3,300</td>
<td>9,800</td>
<td>10,300</td>
<td>9,800</td>
<td>7,400</td>
<td>10,200</td>
<td>4,600</td>
</tr>
<tr>
<td>Society</td>
<td>3,000</td>
<td>4,000</td>
<td>9,400</td>
<td>9,600</td>
<td>8,100</td>
<td>6,700</td>
<td>9,600</td>
<td>3,500</td>
</tr>
<tr>
<td>Samoa</td>
<td>1,000</td>
<td>4,100</td>
<td>7,400</td>
<td>7,200</td>
<td>6,700</td>
<td>4,000</td>
<td>7,400</td>
<td>1,750</td>
</tr>
</tbody>
</table>

The Mariana Islands form a fairly consistent north-south chain, with only moderate breaks of less than 120 kilometers each; but the high island groups of the Carolines are widely separated: 450 kilometers between Palau and Yap, 1,600 between Yap and Truk, 700 between Truk and Ponape, and 560 between Ponape and Kusaie. Kusaie is the most isolated high island of Micronesia in the sense that it is farthest from an actual continent, but the Marianas are farther from continental islands than is Kusaie. Kusaie is 1,500 kilometers from Bougainville, whereas Guam is 2,250 kilometers from Mindanao. Guam is slightly closer to Australia than is Kusaie, and quite a bit nearer to New Guinea. The Gilbert Islands, though almost as distant from the Solomons as
are the Marshalls, are much nearer to the New Hebrides and Fiji and are about as close to the Ellice Islands as to the Marshalls. Wake Island is the most isolated Micronesian low island, in the sense of distance from the nearest high island, although Marcus Island is farther from the nearest land. Wake is only about 600 kilometers from Pokak (Taongi), the northernmost Marshall atoll; and Marcus is about 1,000 kilometers from Farallon de Pajaros, the northernmost Mariana island.

The atolls of Micronesia are, for the most part, separated by less than 300 kilometers from the nearest atoll or high island. The break between the Gilberts and the Marshalls is just over 320 kilometers (Makin to Mili), and the break between the Marshalls and Carolines is just a little greater (Ujelang to Mokil). Ocean Island is 300 kilometers from the central Gilberts, and Nauru is about 300 kilometers from Ocean. Within the Carolines, the breaks between Kusaie and Pingelap; Nukuoro, and Kapingamarangi; Eauripik and Sorol; Ngulu and Ngaingl; and Angaur and Sonsorol are each in the neighborhood of 300 kilometers. The break between the Caroline and Mariana islands is about 450 kilometers (Gaferut to Guam). The northern Marianas are separated from the Volcano Islands by 600 kilometers (Farallon de Pajaros to Minami Iwo). The break between the Volcano Islands and the Bonin Islands is about 180 kilometers (Kita Iwo to Haha Jima).

The nearest approaches of Micronesia to other areas are the following: the northern Bonin Islands, just over 300 kilometers from Sofu Gan (Lot's wife), southernmost of the immediate chain extending south from Tokyo Bay; the Marshall Islands, 2,200 kilometers from Johnston Island, which is 1,000 kilometers from Hawaii; Tobi Island, westernmost of the Carolines, which is 220 kilometers from the Asia Islands, north of Waigiou Island off New Guinea, and less than 300 kilometers from Morotai in the Moluccas; Kapingamarangi, southernmost of the Carolines, about 500 kilometers from the Tabar Islands, just off New Ireland of the Bismarck Archipelago; Nauru, about 1,000 kilometers from the Nukumanu Islands, northeast of the Solomons; and Arorae, southeastern Gilberts, about 360 kilometers from Nanumea, nearest of the Ellice Islands and 800 kilometers from Baker Island, near Canton Island and the Phoenix Islands. The small island of Parece Vela, about halfway between Guam and Okinawa might be considered part of Micronesia, but no insects are at hand from there.

As to major islands, Guam is 2,250 kilometers from Samar and Mindanao. Palau is 830 kilometers from New Guinea, 870 from Morotai in the Moluccas, and under 930 each from Mindanao, the Talaud Islands, Halmahera, and Waigiou. Truk is nearer to New Guinea than it is to Palau or Yap, and nearer to the Bismarck Archipelago than to Guam. Ponape is closer to Manus, New Britain, Bougainville, Choiseul, and Santa Isabel than it is to Guam. Kusaie is
closer to Australia than it is to the Bonins, and closer to New Guinea than to Guam. Arorae, in southeasternmost Micronesia, is more than three times as far from the Bonins and Tobi as it is from Fiji. Arno is closer to the Hawaiian Islands than to Palau, Yap, or the Bonins. Palau is nearly five times as far from Arno as from Mindanao. The broad expanse of Micronesia, 5,100 kilometers east and west and 3,000 north and south, indicates that its extent is much greater than its separation from neighboring areas, thus making it difficult to speak of isolation of the area as a unit, or of its endemicity. In other words, we must consider the isolation of groups of islands or single islands within the area, both in terms of separation from other parts of Micronesia and from neighboring areas. However, in spite of the fact that Micronesia neighbors on various zoogeographical regions, the insect fauna is not as diverse as might be assumed from this situation. This, again, suggests that the insect fauna is highly selected and that its ancestry consists largely of types of insects prone to be transported by air or water and originating from certain sources in particular. It also suggests that the insects brought by pre-European man came from limited sources.

Though we may point out that Truk, Ponape and Kusaie are closer to the Bismarcks than to Guam, we must mention that there is a very great deal more in common between the insect faunas of the eastern Carolines and Guam than between any of the Micronesian islands and any of the major Melanesian islands. The striking difference is in the lack in Micronesia of many groups of insects, even up to families or orders, which are conspicuous in the faunas of the continental islands. Many of these conspicuous groups include large insects of many sorts, including beetles, butterflies, and moths.

**SPREAD OF INSECTS BY THE ELEMENTS**

Possibly most of the natural infiltration of insects to oceanic islands is to be attributed to movements in the atmosphere. It has been assumed that pre-human insect populating of such islands has taken place largely by means of the insects being blown across wide areas of ocean in storms, or by floating to the islands in logs or natural rafts from the mouths of rivers on continents or continental islands, or by being carried by birds. Since ocean currents are largely caused and controlled by the prevailing winds in a given season, the direction of transport of both air-borne and surface-floating insects is principally controlled by air currents. It might be assumed, then, that the populating of a group of islands by insects would take place from the direction of prevailing winds and sea currents, though Zimmerman (1948) stresses the importance of storms. However, it has been shown by Palmer (1951) that typhoons and tropical storms of the western north Pacific are merely extreme, strong examples of a relatively common type of equatorial atmospheric vortex. Many of
the vortices, which form in the vicinity of the Marshall Islands and move westward toward Asia never reach storm intensity; nevertheless, since they are cyclones, west winds prevail south of their centers (say between 0° and 5° N.) during their passage toward the continent. Thus, during the so-called wet season, west winds may extend for several weeks at a time along the equator from Asia across the Carolines to the southern Marshalls, and may attain speeds as high as 28 km./hr. (15 knots), even in the absence of typhoons. Frequent temporary changes, therefore, must not be overlooked in assessing transport of insects by air currents in terms of average wind directions, or in terms of sources and directions of storms. Above the surface winds, are high air currents (jet streams) of great velocity and of different directions from surface winds. Though largely above probable survival levels for most insects, they may have some role in dissemination. The proximity of the Mariana and western Caroline islands to Formosa, the Philippines, the Moluccas and New Guinea would suggest possibilities of transfer of insects in the winds circulating around vortices; that is, in directions opposite to the trade winds.

The migration routes of birds also must be taken into consideration, both from the standpoint of carriage of insects or their eggs on the bodies of birds and from the standpoint of possible seasonal variations in wind currents at certain altitudes which are taken advantage of by migrating birds and which might also influence insect dispersal. Some primary bird migration routes in Micronesia are along the Mariana-Iwo-Bonin chains to Palau and Japan, and perhaps sometimes along these chains all the way from New Zealand to eastern Siberia. Another route is from the Philippines direct to Palau, and perhaps to a lesser extent, eastward from there across the Carolines. Sea birds are particularly abundant in the above-mentioned dry area in the central Pacific because the converging winds direct plankton floating in the wind-induced ocean currents to an area of high concentration. This increases the fish population both by directly providing food to the plankton-feeding fish, and therefore also the fish preying upon such plankton feeders, and by the greater coral growth around islands in that area, which provides additional favorable environments for fish or other animals serving as food for birds. This dry area lies just south-east of the Gilbert and Ellice Islands.

Many of the predominating groups of insects in Micronesia may be somewhat arbitrarily assigned to two categories relating to the possible method of their introduction to the islands. First, buoyant insects are apt to be borne by the atmosphere. These include the adults of the plentiful small moths and the dragonflies and damselflies. Secondary in this category are the less well-represented caddisflies and a single mayfly species. Since these two latter groups are largely temperate in distribution, as are the absent stoneflies, it might be assumed that they would be better represented in Micronesia if the
nearer continental areas were not largely tropical. The second category comprises the more compact or heavy-bodied insects, such as weevils and other beetles, certain true bugs, and other groups, many of which are found in logs or other dead vegetation and which might have been brought in floating logs.

Insects in neither of these categories and those not likely to be carried by birds might be assumed to have arrived with the aid of pre- or post-European man, though the above categories are not rigid and do not necessarily exclude many types of insects. They are, rather, two extremes between which lie most other insects. Many insects carried in air currents are small species, and may be even wingless, the highest altitude records (9,140 m.) being for spiders (Glick, 1939). The scarcity of butterfly species in Micronesia is interesting, as they are relatively stronger fliers than most small moths. Several of the larger lepidopterous insects in Micronesia—the sphinx moths and certain nymphaid butterflies like Hypolimnas and Precis—are very strong fliers and probably arrived partially under their own flight power, rather than by being carried passively in air currents as was probably the case for a large proportion of the small winged or non-winged species of insects and arachnids.

Possibly some Micronesian insects came from tops of high mountains in New Guinea, whence they were lifted by rising air currents. The latter process is a well-known phenomenon (Müller, 1871).

**Spread of Insects by Ocean Currents**

Ocean currents are caused primarily by prevailing winds and by differences in water temperatures, by rotation of the earth, and by the shape of continents or other large land masses. In Micronesia, the prevailing currents are a north equatorial current in the northern portion and a south equatorial current reaching part of the southern portion, both westward in direction and both turning and converging in an eastward equatorial counter current in the southern Carolines and Gilberts. In the Palau Islands, for instance, logs are washed ashore which may come from New Guinea, but by a very indirect route which may take them toward the central Pacific, then westward through the Carolines. (See figure 62, a.)

**Insect Fauna of Micronesia, a Provisional Statement**

As Micronesia is an assemblage of oceanic islands divided into a number of groups, many of them somewhat isolated from one another, the insect fauna is not something homogeneous, but rather, a collection of many divided populations. On the other hand, though much endemcity has developed, there appears to be a great deal in common between the insect faunas of the different island groups. In other words, the ancestors of species in the same taxonomic groups in different islands may have been the same to a considerable extent, or at
least very closely related species. Again, certain families or orders are represented on some islands and not on others. Because of the little-known and apparently complex origin of the Micronesian insect fauna, a general statement of its makeup and relationships is difficult.

Essentially, Micronesia has an insect fauna of small species, the ancestors of many of which might have been brought by the air or by objects floating on the sea, plus a considerable number brought by man. Possible sources include all the neighboring areas, such as Japan, the Ryukyu Islands, Formosa, the Philippines, the Moluccas, New Guinea, the Bismarck Archipelago, and islands of eastern Melanesia and central and southeastern Polynesia. The fact that there is much in common with central and southern Polynesia does not, perhaps, any more mean migration from that direction than a more or less common origin relating to the type of insects transported, or than a more or less common source of origin, which probably centered in eastern Melanesia. On the other hand, there is much evidence, particularly in western Micronesia, of Asian origins of insect types scarce or lacking in Polynesia. This even includes continental Asian types on all of the high islands of the Carolines and southern Marianas. The Melanesian influence is also strong in the west.

Furthermore, it is difficult to compare the Micronesian insect fauna with that of other areas in terms of numbers of species, because the area is divided into so many units of different sizes of islands or island groups. Similar populations on different islands are often very slightly different. In other words, genic variability is progressing in different directions. Very roughly, the insect fauna of Micronesia may be somewhat equivalent in number of species to that of Hawaii or Samoa, but none of these faunas are as yet known well enough to make this a definite statement. Zimmerman (1948) states that over 5,000 species have been recorded from Hawaii and that many more have not been collected or named. Only about 1,700 species are included in “Insects of Samoa,” but it is obvious that this must be a small percentage of the actual fauna. Townes (1946) estimates that the insect fauna of Micronesia would total about 7,000 species. However, the indications from the collections now assembled, though many groups have not yet been sorted, are that the total fauna may number 10,000 species or more. It is tentatively assumed that about one-half of the species are represented in the material at hand, and it is estimated that these collections total about 5,000 species, including the other groups of terrestrial arthropods to be covered in this series.

It seems clear that the insect fauna of Hawaii is much older than that of Samoa or Micronesia and that the majority of the native insects have evolved over a great length of time from a very small number of introductions. If the Hawaiian Islands were nearer a continental area, undoubtedly many more introductions would have taken place and there would have been less opportunity
for the amazing evolution that has taken place there, involving new adaptations
to ecologic niches, amplification of certain groups of insects from possible single
ancestors, and total lack of other major groups of insects. Samoa represents still
a different picture, with a much more evenly rounded insect fauna suggesting
numerous introductions, as its proximity to a "continental" fauna (that of
Fiji) would indicate. The situation with Micronesia is more comparable to that
of Samoa, but the origins of the Micronesian insects are probably more diverse.
The land area of the Hawaiian Islands is about six times that of Micronesia,
and Samoa is only slightly larger in land area than Micronesia. However,
Hawaii is more temperate and more isolated from sources of introductions
than are Samoa or Micronesia. Micronesia differs markedly from Hawaii and
Samoa in the number of islands involved, being much more divided into small
scattered units, a large percentage of them atolls. In this respect, it is more
comparable to southeastern Polynesia, which also has groups of both high
and low islands (Society, Cook, Austral, and Tuamotu Islands), but the
high islands of Micronesia are nearer to continental areas than are those of
southeastern Polynesia. The Marquesas are somewhat intermediate, in re­
spect to form and isolation, between Hawaii and Samoa. Though they are
farther from actual continents than Hawaii, the Marquesas are nearer to other
high islands, as well as to low islands, and a little nearer to continental islands.

Townes (1946) estimates that of a supposed fauna of 7,000 species of in­
sects in Micronesia, 15 percent were introduced by man, 45 percent were
widely distributed Polynesian or East Indian species, and 40 percent were
endemic.

Table 5 presents figures comparing the number of insects in Micronesia,
Hawaii (Zimmerman, 1948), Samoa (Buxton et al., 1927-1935; Buxton,
1938), the Society Islands (P. E. S., 1935), the Marquesas (Adamson, 1936,
1939; Mumford, Adamson, et al., 1932-1939), and Fiji. Many figures are
rough estimates. Others are those found in the literature. Fiji is added to give
comparison for an isolated Pacific continental island group.

Table 6 presents figures for the approximate number of species for each
order of insects from three atolls and one high island (Guam), together with
very rough estimates for the numbers of species collected to date in Micronesia
as a whole. Also given, for comparison, are the numbers recorded in “Insects
of Samoa” (Buxton, Hopkins, et al., 1927-1935) and Sabrosky’s figures for
the world to the end of 1948 (1952).

The three atolls represent three different categories: Ngaiaangl, a small
humid atoll close (30 km.) to a major high island (Babelthup); Arno, a fair­
sized, humid atoll in the southern Marshalls; and Onotoa, a fairly large, dry
atoll in the southern Gilberts. The figures do not represent equivalent collect­

Table 5.—Comparisons of Pacific island insect faunas

<table>
<thead>
<tr>
<th></th>
<th>Micronesia</th>
<th>Hawaii</th>
<th>Samoa</th>
<th>Marquesas</th>
<th>Society Is.</th>
<th>Fiji</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total land area (sq. km.)</td>
<td>2,976</td>
<td>16,685</td>
<td>3,136</td>
<td>1,059</td>
<td>1,535</td>
<td>18,272</td>
</tr>
<tr>
<td>Number of major high islands (roughly over 8 km. long)</td>
<td>20</td>
<td>8</td>
<td>4</td>
<td>9</td>
<td>6</td>
<td>22</td>
</tr>
<tr>
<td>Total number of high islands</td>
<td>110</td>
<td>13</td>
<td>12</td>
<td>11</td>
<td>9</td>
<td>250</td>
</tr>
<tr>
<td>Number of atolls or isolated low islands</td>
<td>84</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Number of low islets</td>
<td>2,300</td>
<td>25</td>
<td>2</td>
<td>1</td>
<td>40</td>
<td>10</td>
</tr>
<tr>
<td>Estimate of total number of species of insects</td>
<td>10,000</td>
<td>12,000</td>
<td>7,000</td>
<td>2,000</td>
<td>1,000</td>
<td>25,000</td>
</tr>
<tr>
<td>Number of species recorded</td>
<td>4,000*</td>
<td>5,000</td>
<td>1,800</td>
<td>850</td>
<td>250</td>
<td>3,000</td>
</tr>
<tr>
<td>Percentage of endemicity of known native spp</td>
<td>45</td>
<td>98</td>
<td>49</td>
<td>50</td>
<td>25</td>
<td>90</td>
</tr>
</tbody>
</table>

Number of native species of certain groups:
- Fulgoroidea
- Cicadidae
- Cicadelloidea
- Psyllidae
- Trichoptera
- Cerambycidae
- Cercosporidaceae
- Elateridae
- Tipulidae
- Aculeate Hymenoptera

* Estimate of present collections, excluding arthropods other than insects.

Gressitt—Introduction

Insect collecting, though on short visits in different months (Gressitt, 1952, 1953a). The collection from Arno (Uisinger and La Rivers, 1953) represents thorough searching for a few months and, presumably, close to the total actual fauna. The collection from Onotoa represents a season’s part-time work by the botanist, Mou (1954). Townes (1946) estimates that a large, humid atoll like Ulithi, relatively close to high islands and continental areas, might possess an insect fauna of 1,200 species, whereas a rich, isolated, large atoll might have 800 species and a large, dry atoll like Eniwetok and others in the northern Marshalls might have 500 species. Roughly, the atolls of Ngaiangl, Arno, and Onotoa fall into these three categories. However, Ngaiangl is small, but closer to a high island, and Onotoa is in a more southern area on the “invasion route” from central Polynesia. Fair estimates may be 1,100 species for Ngaiangl, 500 for Arno, and 170 for Onotoa. Townes’ estimates may be in part a little high. Cole (1951) listed 55 species of insects for Bikini Atoll in 1947, following the first atom bomb tests held there.

In some insect groups in Micronesia, there appear to be rather small numbers of genera, often concentrated in a few tribes or subfamilies, with other subfamilies entirely lacking or represented only by an occasional, recently
introduced species. Then, within the few genera represented, there are often a limited number of species-groups with wide geographical representation within Micronesia. In some groups the populations on different high island groups appear to be only slightly distinct, suggesting not very ancient genetic separation. The original colonists may have descended from the same parent species, that is from the same origin, at the same or at different periods. Or they may have been transported from one high island group to the next. Thus each of these species-groups forms a Rassenkreis or Artenkreis. The relative differences between the different populations may not be equivalent, and some may be termed species and others subspecies. It appears difficult to avoid the use of the subspecies category, for though the populations may be functionally non-interbreeding because of isolation, their period of isolation and consequent ecologic and genetic differentiation may not yet have rendered them appreciably or completely potentially inter-sterile. Some of such genera, or species-groups, may be of New Guinean origin; or they may be endemic and of Melanesian origin.

Table 6.—Representation of insects on high and low Islands

<table>
<thead>
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| Total                  | 1,191| 273         | 296        | 96                     | 4,001              | 1,649     | 685,900*  |

* After Saborosky. Orders of insects absent from Micronesia are: Protura, Plecoptera, Mecoptera, and Megaloptera; and the suborder Symphyta of the Hymenoptera is also lacking. Figures for other terrestrial arthropods are omitted, as the material has not been well enough sorted.
relationship. Others may have more western, or more rarely, southeastern relationships.

In some groups, it appears that much of the endemic fauna may be of New Guinean origin, or of other Melanesian or Polynesian relationship; whereas many of the non-endemic forms or isolated, apparently endemic species may be of Malayan or Philippine origin.

Some elements in Micronesia are proving to be closely related to some in the Malagasy Subregion. This is particularly true in connection with small islands such as the Seychelles, Bourbon, and Mauritius; also, to a lesser extent, with Madagascar. Some representatives of the groups concerned are found also in various Melanesian islands, or even more widely distributed in the Pacific; but not in Asia, or at least not in continental Asia. In a few cases, representatives appear to be known only from Micronesia and the Mascarene Islands, near Madagascar. Some groups are known from Madagascar to Micronesia and Polynesia, but they are not known from the Asian continent or the continental Asiatic islands. Others are found in these extremes and also in New Guinea, the Philippines, and the Ryukyus. Though it is too early to draw conclusions from these suggested distribution patterns, they may be in part the result of primitive groups having survived in these small islands while becoming extinct on larger islands through competition. Thus, on small islands like those in Micronesia, we may find forms which could not survive the competition with more specialized forms on continental islands. Whether such primitive elements are more easily transported to, or established on, small islands than other insects is a question for further thought. Obviously they could not have come from continental islands recently, if they are actually extinct there. A better knowledge of the fauna of New Guinea is needed to help clarify these points, and it should be emphasized that the above suggestions are tentative. Individual workers may find great deviations from these suggested affinities of the Micronesian fauna. (See Mayr, 1940.)

Faunas of the Island Groups

The insect fauna of the Bonin Islands is heterogeneous, with some endemic elements both of Oriental and Micropolynesian relationships, and species of obvious Palearctic (Japanese) origin, many probably recently introduced forms. Though they represent an overlapping of Oceanic and Asian elements, the Bonins are more properly placed with Micronesia than with the Palearctic Region or the Indo-Chinese or Malayan Subregions of the Oriental Region.

The Volcano (Kazan, Iwo) Islands have been so inadequately collected that it may be difficult to judge their relationships. However, the endemic
fauna may be insignificant; and many of the species present may be introduced from Japan, the Bonins, or the Marianas, and may consist primarily of widespread species.

Marcus Island has a small fauna, but some indications of endemity.

The Marianas have a complex fauna of multiple origin. Oriental forms are well in evidence, and many species have obviously been introduced from the Philippines at different periods. Others have been introduced from Japan, Okinawa, Formosa, Palau, or elsewhere. The endemic species are both of Oriental and Oceanic relationships. Direct relationships with New Guinea are probably few. The number of genera represented may be higher than in other island groups of Micronesia except for Palau. Yap and Ponape may approach the Marianas in general representation, and have some higher groups not found in the Marianas. The Marianas have rather few endemic genera. These remarks refer primarily to the southern Marianas, as the northern Marianas appear to have a younger, as well as a poorer, fauna, with few endemics. Guam may have more than 2,000 species. Esaki (1930, 1950) states that the Bonins and Marianas are Oriental, but neither Indo-Chinese nor Melanesian, being intermediate. However, Philippine and Malayan relationships must be emphasized also.

Palau has the richest fauna of Micronesia, both in numbers of species and in numbers of higher categories. Palau may have up to 5,000 species. The origin of the Palau fauna is undoubtedly diverse, but there are a number of striking New Guinea-Wallacean relationships, as well as Philippine or Malayan affinities. At least some of the latter two may represent introductions related to the travels of man. Among groups known only from Palau in Micronesia are Mantidae, Phyllinae, Rutelinae, Dynastinae, Glaucytini, Mutiliidae, Scoillidae, and Crabronidae, excluding a few species known to be introduced in other islands. These include mantids in Guam, Saipan, and Truk and a Philippine rutelid and scoliid, in the Marianas. Papilionidae are found only in Palau and Yap, except for a Japanese Papilio introduced to the Marianas. Proportionately, there may not be as many endemic genera in Palau as in Ponape.

Yap presents a puzzling picture. Although, in general, it appears to represent an attenuation of the Palau fauna, with fewer genera and species, it appears to be richer in the water insects than is Palau. Yap has the only representative of Ephemeroptera in Micronesia and also has at least three species of three different genera of Trichoptera. To compare the other island groups, there is one trichopteran on Guam, one in Palau, two in Truk, at least two on Ponape, and one or two on Kusaie. Yap appears to have fewer weevils than such island groups as Palau and Ponape. This may be partly the result of extermination through depletion of the flora. It is estimated
that Yap has 1,700 species. Esaki (1950) states that Yap and Palau are continental islands and belong to the Melanesian Subregion, that the Bonins and Marianas are Oriental, and that the rest of Micronesia is western Polynesian. However, other interpretations may develop.

Truk is also puzzling in its representation and affinities. It appears to be exceedingly depauperate in some groups, whereas in others it has peculiar endemic forms, seemingly without close relationships. Truk's affinities appear mixed, but undoubtedly New Guinea has exercised a strong influence. Relationships appear closer to Ponape than to Palau or Yap. Truk may have over 1,200 species.

Ponape is a rich center of endemism, with many interesting forms, some without precisely known affinities. The altitude and ecological diversity, as well as isolation, have contributed to the endemism, though the age is not very great. Ponape, Palau and the southern Marianas may be said to be the principal centers of endemism and faunal development in Micronesia. Probably Ponape possesses the greatest number of endemic genera. It may have over 2,000 species.

Kusaie represents an attenuation of the Ponape fauna, with some local endemism, often to the extent of subspecies, or species very closely related to those on Ponape. Kusaie may have over 1,500 species.

The atolls and reef islands of the Marshalls, Gilberts, and Carolines present a poor and rather uniform fauna. Endemism appears to be limited and is often general; that is, with a species being common to many atolls, rather than peculiar to a single atoll. Perhaps most of these supposed endemics will be found on the nearest high islands. An interesting case in point is that of a cicindelid beetle of presumed Philippine origin on Nukuoro Atoll. It is the only cicindelid known from Micronesia, and how it reached Nukuoro is a subject for speculation. The total fauna of these low islands is probably under 2,000 species.

To briefly summarize the faunal relationships of the areas neighboring on Micronesia, Japan is Palearctic, with Oriental influence in the south; the Ryukyus are Indo-Chinese, with the mixture of Palearctic elements in the north; and Formosa is Indo-Chinese, with Palearctic elements in the high mountains and Malayan influence in the southern lowlands. The Philippines, exclusive of Palawan, are more or less of a subregion of their own, with Melanesian-Wallacean relationships (Dickerson, et al., 1928), as well as Malayan. The Philippine fauna extends northward to Botel-Tobago Island off Formosa, with some fragments as far north as the southern Ryukyus. The Wallacean, or Celebes-Moluccan, area is again rich in peculiar forms, with strong New Guinean and Philippine, and lesser, Malayan relationships. New Guinea with the Bismarcks, Solomons, and north Queensland repre-
sents the center of importance of the Melanesian Subregion. Fiji represents an
extreme attenuation and divergence of the Melanesian fauna, but an important
source for central Polynesia. New Caledonia and the Loyalty Islands have
a fauna which is highly peculiar and which constitutes a strong subsection of
Melanesia. The New Hebrides fauna is somewhat related to those of the
Solomons, Fiji, and New Caledonia. Australia, exclusive of north Queensland,
and New Zealand represent quite different faunas; in fact they comprise a
different zoogeographical region and may have had little influence on Micronesia,
though there is Australian influence in New Guinea and Wallace.

It may not be possible to assign Micronesia to a single zoogeographic
subregion. But it may prove to be referable to a general Oceanic or Micropolynesian area (excluding New Zealand) representing an extenuation of the
Oriental Region in the broad sense, with mixed elements of several subregions,
particularly Melanesian, and with strong Philippine, Malayan, and Wallacean
influence in western Micronesia.

These statements are tentative and preliminary, and a more adequate
discussion of the insect fauna of Micronesia must await the careful study of
the collections by the many collaborators. A synthesis of results and opinions
will be made in a late issue of this series.

TERRESTRIAL VERTEBRATE FAUNA

As the terrestrial vertebrate fauna of Micronesia is limited, each member
has a potentially greater role in relation to insects, either as a predator or
as a competitor, though most are predators. The extinction of a single species
of terrestrial vertebrate has a potentially great effect upon the balance of
insect populations. Thus conservation is of the greatest importance in Micronesia (Coolidge, 1948).

MAMMALS

There are few native mammals. The large fruit bats of the genus Pteropus
are the most widespread of the native mammals, unless one of the rats is
considered native. The small insectivorous bats of the genus Emballonura are
scarce or absent on many islands, and their abundance may be correlated with
availability of insect food. They are absent from the Marshall Islands (Marshall, 1951; Schnee, 1904). Rats of several species, including the familiar
northern Rattus rattus, are abundant on many islands, particularly the Marshalls. The Polynesian rat, R. exulans, or a close relative, is widely distributed
and probably has been present the longest. In Guam R. mindanensis, or a
near relative, is common; and there are probably four or more species in
Palau, including relatives of R. nitidus and R. flavipectus from China. A
Japanese rat occurs in the eastern Carolines. Rats feed mainly on drying copra on most islands, but they also feed on young coconuts, on other fruit, including melons, and on insects. The mouse, *Mus musculus*, is found on Guam, and probably elsewhere. A small shrew (*Sorex*) has become established on Guam since 1952. Other introduced mammals include dogs, cats, cattle, water buffalo, goats (feral only on a few Mariana Islands), horses (Marianas), pigs (wild on Babelthuap, Kusaie, and perhaps a few other islands), deer (Bonins, Guam, Ponape), a monkey (Palau), and few if any others. Schnee (1904) states that goats and cattle could not survive in the Marshalls without imported food. Cattle became feral on Tinian during Spanish times and were hunted. Keate states (1788) that in 1783 there were no "quadrupeds," no dogs, and only rats and a few cats in Palau. This suggests the absence of feral pigs, though Keate's party hardly visited Babelthuap. Krämer states (1917) that Palau had pigs, dogs, monkeys, and goats in 1910, and that cattle were introduced in 1791. A dugong is known from Palau, but is now rare.

**Birds**

Baker (1951)—excluding the Bonins, Iwo, the Gilberts, Ocean Island, Nauru Island, Marcus Island, and Wake Island—records 206 birds representing 150 species which belong to 91 genera of 37 families which belong to 13 orders. Of the 206, eight are introduced and 75 are non-resident, 92 are sea or shore birds, and 114 are true land birds (of which 105 are passeresines). Of 104 native birds, 97 are endemic forms with 31 endemic species. The best represented and most widely distributed of the land birds are the following: the jungle fowl, introduced; pigeons and doves, five native genera; swiftlets, one genus; kingfishers, one genus; Old World warblers, two genera; Old World flycatchers, four resident genera; starlings, one resident genus; honey-eaters, two genera; white-eyes, two genera; and weaver finches, two genera. Rarer, or more restricted, resident land birds are the following: the osprey; megapodes; owls, two genera; goatsuckers, one genus; and cuckoo shrikes, one genus; and the Ponape lory; the Mariana crow; and the white-breasted wood swallow of Palau. Not mentioned by Baker are a large white introduced cockatoo and a fair-sized red and green parrot, both on Nguruk-dabel. Non-resident land birds include two genera of cuckoos, a roller, three thrushes, and a few additional species of the preceding families. The sea and shore birds include shearwaters, petrels, tropic birds, boobies, man-o'-war birds, herons, bitterns, ducks, rails, crakes, plovers, curlew, snipe, sandpipers, and terns.

The most important insectivorous land birds are swiftlets, flycatchers, warblers, white-eyes, and nightjars. Less important are kingfishers, owls,
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cuckoos, megapodes, drongo (introduced, Rota), swallows (non-resident), starlings, crows, and honey-eaters. Among the sea and shore birds the most important insectivores are probably the rails, crakes, bitterns, herons, plovers, curlews, and tattlers.

**Reptiles**

There are about 36 species of reptiles belonging to 18 genera. About eight species are endemic, and 10 are widespread or recently introduced. The monitor lizard *Varanus indicus* is found on most of the Marianas and Carolines, and has been introduced to a few atolls. *V. salvator*, as well as *V. indicus*, is found on Yap. Skinks are found on almost every island. Representatives of the genera *Emoia, Mabuia, Lygosoma*, and *Dasia* are widespread; *Ablepharus* occurs in the Carolines; and *Riopa* is found in the Carolines and Marshalls. Geckos are present on practically every island and are often represented by several species. The genera include *Gehyra, Lepidodactylus, Gymnodactylus, Perochinus, Hemidactylus*, and *Gecko*. All of these lizards are very important insect feeders. Snakes are few in Micronesia. Palau may be the only group with native species. Four species are found on Babelthuap: two species of *Typhlops* (one endemic); a subarboreal colubrine, *Dendroaphis lineolatus*; and a small boa, *Enygrus carinatus* (Brown, in press). Two species of snakes appear to have become established on Guam recently. *Typhlops braminus* has been there some 50 years. Sea snakes are common, but they probably never feed on insects. The estuarine crocodile, *Crocodilus porosus*, is found only in Palau. Another crocodile, introduced by the Japanese and kept in enclosed tidal ponds, is said to have escaped and established itself in Palau; but this may not be a different species.

**Amphibians**

There are only two amphibians in Micronesia. The only native one is the small endemic frog *Platymanitis pelewensis* found in Palau. The other is the introduced giant toad *Bufo marinus*, which thrives almost everywhere; for instance, on Ponape from the mangrove swamps to the highest summits. It was introduced to the southern Marianas (Guam in 1937; Saipan and Tinian, between 1939-1941; Rota in 1944); and to Palau, Yap (in 1939-1940), Truk, Ponape and Kusaie, and to Ngaiangl Atoll. On an atoll, it is a menace because it contaminates the limited sources of fresh water. Townes (1946), who examined stomachs of *B. marinus* on Tinian, found that it did not feed on many more harmful insects than on beneficial ones. In Palau I found termites, scavenging insects, earthworms, and a blind snake in stomachs. Rat-eating monitor lizards frequently die from feeding on the toads.
According to Schultz (1953), there are no true fresh-water fishes in Micronesia, except an introduced eel in the Marianas. Other fishes are present in streams on the principal high islands, but are not true fresh-water fishes. Since Trichoptera are present on these islands, the fishes presumably feed upon them. The mud-skippers, or mangrove puppies (Periophthalmus spp.), are abundant in the mangrove tidal areas and undoubtedly feed upon many insects, particularly small flies, some of which breed in mangrove mud.

**TERRESTRIAL INVERTEBRATE FAUNA**

The great majority of the Micronesian terrestrial invertebrates are insects. A second important group, the terrestrial arthropods other than insects—including the spiders, ticks, mites, centipedes, millipedes, scorpions, isopods, and amphipods—are also to be included in this series of publications. A few other arthropods, such as land crabs, hermit crabs, and some shrimps, are more or less terrestrial or live in fresh water; but they will not be covered in the series. The robber crab (Birgus latro) is found on some islands and is a coconut pest. A land crab (Cardisoma hirtipes) feeds on melons and pumpkins in Saipan. It is caught in a bamboo trap (Esaki, 1940).

The next important group is the Mollusca. Land snails of several types are found on the high islands, and a few are found on the atolls. The genus Partula is well-developed in the Marianas, and has been the subject of detailed study, including speciation, by Crampton (1925). A greater variety of mollusks is found in the Carolines, including some fresh-water snails. Slugs are present, and a conspicuous pest on many islands is the introduced giant African snail, Achatina fulica (Lange, 1950b). It is now found in the Marianas, the Bonins, Palau, Truk, and Ponape. Mosquitoes may breed in the accumulated empty shells in damp seasons, adding to the snail’s nuisance value. It is not as important in Micronesia as it might be because of the limited cultivation of vegetable crops. The only “native” crop it seriously affects is papaya. The predaceous snail, Gonaxis kibuesiensis, has been introduced to Agiguan for a control experiment.

Other terrestrial invertebrates include earthworms of a few species and a few of the lower groups of animals, most of which are widely distributed human or animal internal parasites, as well as a few fresh water forms. Small terrestrial leeches occur on Truk, Ponape, and Kusaie.

It hardly need be said that the marine animal life of Micronesia is extremely rich. Its distribution is not well enough known to draw conclusions as to what evidence may be correlated with the terrestrial zoogeography with a view to determining such questions as elevation and submergence of islands,
former possible connections between island groups, former stepping stones, and different ocean currents of the past.

ECOLOGY

The subject of insect ecology is immense, even on small islands, and I can do little more here than introduce the subject and point out that island ecology has received exceedingly little attention. The accumulation of ecological data has been limited, since most of the field workers in entomology in Micronesia have been primarily concerned with either elemental information concerning a few economic insects or the amassing of specimens to make possible a knowledge of the fauna. Even when host or habitat data have been recorded with specimens, it is difficult to correlate information or to make deductions and generalizations. Furthermore, many of the records have been dispersed to the collaborating specialists with the specimens for study. A fuller analysis and coordination of the information must await publication of the systematic reports and further field work with emphasis on ecology.

Among the studies already carried out in Micronesia, the most extensive and inclusive one for an entire geographical unit is that of Usinger and La Rivers (1953). Later studies were made by E. T. Moul (1954) on Onotoa Atoll in the southern Gilberts and by Marston Bates on Ifalik Atoll in the west-central Carolines. Ecological data on many species of Guam flies have been reported by G. E. Bohart and me (1951). Studies of individual insects include that of Lange on the Mariana coconut beetle *Brontispa mariana* (1950a), my own on the coconut rhinoceros beetle *Oryctes rhinoceros* (1953b), that of Doutt on the red coconut scale *Furcaspis oceanica* (1950b) and *Brontispa* (1950a), that of Dorsey on the Peleliu gnat (1947), and that of Reeves and Rudnick on Guam mosquitoes (1951). Numerous host records and other data have been reported by Esaki (1940, 1943, 1952), Townes (1946), Oakley (1946, 1953), and Alicata (1948). Much unpublished data were accumulated by some of the above workers, and also by the various participants in the Pacific Science Board entomological survey of Micronesia. (See field work.)

The following section on atoll ecology is taken almost entirely from Usinger and La Rivers' "The insect life of Arno" (1953), a report on field work done during the 1950 Coral Atoll Expedition of the Pacific Science Board, and used with the authors' permission. The data on high islands is based largely on my experience in Palau and other parts of the Carolines and in Guam, and part of it comes from some of the above-mentioned sources.
Gressitt—Introduction

ATOLL INSECT ECology

On atolls, as elsewhere, insects are the most numerous land animals. This well-known phenomenon is a function of their small size and high reproductive potential. The land arthropods of Arno Atoll (map, fig. 60) are estimated at 500 species, as compared with 96 species reported by Van Zwaluwenburg (1943) from Canton Island, a dry atoll. These species must be abundant to maintain themselves, as most of the higher terrestrial animals live on them. Thus insects are an early link in many of the food chains, many serving as primary converters of green plants into animal food.

Of equal importance to the grazers are the scavenging ants and cockroaches, and the wood-boring beetles and termites which, aided by bacteria and fungi, restore dead wood to humus. Other katabolic agents include flies and beetles which help in the decay of fallen fruit, dung, and carrion.

Another portion of the insect fauna, at least one-fourth, are predators and parasites, which eat other insects. And some—including mites, lice, and louse flies—are parasites on birds and rats.

A vital function of insects is pollination. On Arno probably three-fifths of the higher plants are insect pollinated. The single Arno bee, a leaf-cutting Megachile, collects pollen, nests in dead Scaevola twigs, and visits Triumfetta, Scaevola, Wedelia, and other flowers.

The above activities are basic to any community of plants and animals and are independent of man. Thus, with few exceptions, the insects are not much different on the uninhabited islets than in the villages. Many of the insects undoubtedly arrived before the first natives and had achieved a state of equilibrium which may have changed little with the advent of man. The housefly, house mosquito, domestic cockroaches, and lice are notable exceptions.

ANIMAL COMMUNITIES AND HABITATS

It might not be expected that 12 square kilometers of practically level land of similar origin and fairly uniform composition should present such a variety of distinct plant and animal associations. In spite of superficial similarity, there are at least four distinct terrestrial communities and several distinct but interrelated strata within each. In addition, there is the marine environment inhabited by water striders.

MARINE INSECTS

The fact that there are almost no marine insects is puzzling; but this lack must be related to the depth of the oceans and to the better adaptation of insects to terrestrial life, as well as to the better adaptation of crustaceans to marine life. However, one group, the marine water striders, has overcome these
difficulties by occupying the surface of the ocean. These striders have also permanently lost their wings. *Halobates micans* lives on the open ocean and on deep parts of the lagoon. Those blown onto the beach by strong winds are quite awkward on land, where they are probably eaten by golden plover by day and by ghost crabs by night. *H. mariannarum* occurs in large numbers in protected coves, as on the ocean side of Takleb and in the lagoon at the north horn of Arno. It differs slightly from its relatives in the Marianas and Carolines, suggesting that it has long been isolated from them. Presumably, this species feeds on plankters which rise to the surface at night. The fact that *Halobates* are not eaten by fishes suggests that the median metasternal scent gland repels the fishes. *Halovelia*, which is much smaller, is even more local, as it is found in small embayments. The male is minute and rides on the back of the female, preventing their separation.

**THE STRAND**

By day the beaches are clean, with few insects other than robber flies capturing small flies. At night the ghost crab (*Ocyzode ceratophthalma*) swarms over the beaches. Insects often seemed scarce to Usinger and La Rivers, but during some nights at low tides a small, white cricket was found in great numbers. These are weakly positively phototropic, gradually orienting themselves toward the lamp, and they leap at the slightest disturbance. They are apparently omnivorous and eat their injured fellows and flying ants, but presumably they feed principally on vegetation. This cricket and the ghost crab form two successive links in the chain of conversion of plant materials for animals of greater size. Ghost crabs were seen to catch about one cricket for each 10 attempts. Crab spiders were also numerous on the beaches at night, particularly on the rocks and vegetation bordering the sand. Geckos were also found in this environment, likewise searching for insects.

Insects are scarce in the intertidal zone, contrary to the situation in the *Halophila* tide pools of Samoa or the beaches of Hawaii. However, human feces are deposited in the intertidal zone and this attracts numerous flies that would otherwise be absent. Mangroves are a special association in a few places, such as the lagoon at Bikarej; but the only insects they seem to harbor are marine striders.

**INNER BEACH**

This community is occupied by such characteristic plants as *Scaveola*, *Messerschmidia*, *Guettarda*, *Pipturus*, and *Cordia*—each with a distinct fauna (figs. 65, 66)—and *Pemphig*, mostly on raised ledges, which appeared barren of insects. Also present are a leaf-mining agromyzid fly which makes con-
Figure 65.—Insect damage to strand or atoll plants: a, dark mottling caused by a sooty mold growing in honey dew deposited by plant lice on Scorcola frutescens; b, larva of Prosopis sita and its damage to foliage of Figna marina, Jaluit; c, caterpillar of Utetheisa pulchellaidea on its host, Messoremiidius argentus, Likiep (adult is a checkered white, black, and red day-flying moth); d, Caphyllium inophyllum damaged by two kinds of caterpillars, one feeding in terminal shoots, the other a leaf miner, Likiep. (Townes, 1946.)
spicuous serpentine burrows in the thick *Scaevola* leaves; a small endemic *Compydoloma* bug on *Scaevola*; caterpillars of the *Achaea* moth on *Cordia*; the day-flying moth *Utetheisa* (fig. 65, c), the adult with red and black spots on white background, on *Messerschmidia*; and the blue *Hypolimnas* butterfly on *Sida*.

A rich habitat in this zone is the *Scaevola* and *Messerschmidia* thickets which have been burned to provide space for coconuts. Usinger and La Rivers noted that two scolytid beetles, one cerambycid, and several small predaceous rove beetles were attracted to dead or dying limbs with browned leaves still attached. Other predators in the beetle galleries were two anthocorids and a *Ceratocombus* bug.

**OPEN WOODLAND**

Upon approaching an atoll, one first notes the tall palms on the horizon (fig. 53). Coconuts and *Pandanus* comprise most of the forest, and they alone rise above the strand scrub in the narrow parts of Arno. This forest, whether seeded naturally or planted, is an open type with spacing allowing sunlight to reach the ground.

Arno is singularly free of coconut pests. The red coconut scale is the most conspicuous pest on fronds and green husks. The boots, skirts, and trunks have more insects, some gathering for the protection afforded them. There are several cockroaches, small bark lice, earwigs, ants, and other small insects, most of which fall prey to the abundant skinks.

On Arno, *Pandanus* is less attractive to insects than coconut, perhaps because it provides less protection. Only at the bases of the fronds is a micro-habitat found, where rain water accumulates. Elsewhere in Micronesia this water sometimes sustains dragonfly naiads and mosquito larvae; but on Arno moisture was sufficient only for earwigs and small beetles during the period of the study. *Pandanus* fruits are large, and high in sugar content when ripe. When decaying on the ground they harbor an association of vinegar flies (*Drosophila*), fruit beetles (*Nitidulidae*), and numerous predators (*Staphylinidae*, *Anthocoridae*, *Cryptostemmatidae*, and an active white mite).

The ground cover in the open woodland consists of such low plants as *Vigna marina* (fig. 65, b), *Wedelia* (fig. 59, c), *Fleurya*, and in open areas, the sedge *Fimbristylis* and associated grasses such as *Lepturus*. Sometimes this growth is choked by the parasitic vine, *Cassytha*. Insects are abundant: a red spider mite (*Tetranychus*), on the undersides of *Vigna* leaves; the hopping plant bug (*Halticus*), spotting and withering *Vigna* and *Fleurya*; the cosmopolitan green plant bug (*Trigonotylus*), on grasses; some other true bugs, including the herbivorous sedge bugs (*Ninus* and *Orthotyloleus*) and *Nysius*
plies, Pachybrachius nigriceps and P. pacificus, and the predaceous Nabis capsiformis, on Fimbriostylis. That the lone predator is not sufficient to keep this association in check is attested by the enormous numbers present wherever the plants grow. The Nysius is of particular interest because it is found only on the islands remote from air bases in the Marshalls, whereas N. pulchellus, from Guam, is found exclusively on Majuro and Kwajalein. Presumably

![Image of insect damage to atoll plants]

Figure 66.—Insect damage to atoll plants: a, feeding holes made by adult weevils (Trigonops sp.) on Scaevola frutescens; b, caterpillar Bodamia exclamationis being attacked by several small gnats (Forcipomyia) on Terminalia, Likiep Atoll. (Townes, 1946.)
N. picipes is an old resident in the Marshalls, yet it is indistinguishable from typical Wake Island specimens.

**CANOPY WOODLAND**

The richest zone on Arno is in the wider parts of the islets where humus has accumulated and breadfruit grows. Here one finds a dense growth of trees 15 to 25 meters tall, with foliage so dense that much of the ground is shaded. Taro pits have long been dug in such places, augmenting the accumulation of humus and the maintenance of moist conditions. There are buttressed trunks of breadfruit with epiphytic bird's-nest ferns, a moss (Calypere tenerrum), a thick, low undergrowth of Polypodium fern, and decaying logs with Polyporus and Schizophyllum fungi.

Decaying logs contain elaterid larvae, lucanid larvae and adults, termites, ants, Machilis and a red collembolan, wood roaches, earwigs, predaceous rove beetles, scorpions, pseudoscorpions, centipedes, earthworms, isopods, millipedes, and several land snails. On the fungi growing on logs are fungus beetles (Ciiidae and Endomychidae), mycetophilid gnats, and various predators, including skinks and birds.

Tree holes are frequent, and the endemic mosquito (*Aedes marshallensis*) breeds in the contained waters. The eggs are laid at the water’s edge, and the pale larvae feed on the organic matter at the bottom of the holes. Mosquitoes are abundant in spite of their limited habitat. However, they are retiring in habit and seldom troublesome, though they were involved in outbreaks of dengue fever on neighboring atolls during World War II. This mosquito, being an efficient vector, required control, but only in limited areas because of its short flight range.

Taro pits provide an interesting problem. Surrounded by luxuriant tropical vegetation, these bodies of shallow water should, by mainland standards, be teeming with life. Yet they are almost devoid of insects. A fresh-water snail is common, and a few blood worms live in the mud; but few adult midges emerge, as most are eaten by the dragonfly naiads. On Arno these fierce predators appear to be over-adapted to their niche. The only other arthropod of any consequence in fresh water is a scarce reddish shrimp. Mayflies, caddisflies, water beetles, and bugs are all absent. The depauperate fresh-water fauna is not so surprising when one considers the nature of a coral atoll. Arno has fairly heavy and uniform rainfall and fares better than most atolls. Fresh water is scarce and seasonal on most atolls, and fresh-water life is thus hazardous. Even on Arno, the only endemic of aquatic habit is the tree-hole mosquito. The dragonflies are all strong-flying immigrants, and the others may be recent accidental immigrants. The adult dragonflies dart swiftly in the open forest, catching gnats and other small insects on the wing. The more delicate damsel-
flies were seen only in the vicinity of the taro pits on the widest part of Arno Island. Damselfly naiads were not seen; but dragonfly naiads were common in wells, cisterns, and taro pits, existing precariously in danger of hurricane or drought.

Herbivorous insects are not conspicuous in the canopy forests but are, nevertheless, abundant. A large red corizid bug is found on Allophyllus and the bird's-nest fern (Asplenium nidus); a small but sly spider mite, on breadfruit leaves; and a host of small saprophagous and parasitic insects in fallen rotting breadfruit, as in the rotting Pandanus fruit. The productivity of one rotten breadfruit in terms of individual Drosophila flies is enormous.

**INSECTS AND NATIVE CULTURE**

Lice and bed bugs accompanied the island peoples in their wanderings to these isles and probably also the housefly, its enemy Hermetia, the Australasian and Oriental cockroaches, ants, rotten-fruit insects, scale insects, mites and aphids attached to coconuts, breadfruit, Pandanus, banana, taro, arrowroot, papaya, and lime trees. The dengue-yellow fever mosquito, Aedes aegypti, came in drinking water, as it has throughout the tropics. It is so closely associated with man that it breeds only in cisterns and other drinking-water containers. Four species of termites, of as many genera, attack man-made structures or native woods. Each has in its gut distinctive Protozoa which convert cellulose to nutritive material. Most of the above pests, except for the housefly, are scarce and create few problems.

**AGRICULTURAL PESTS**

At the time of the Usinger-La Rivers study there were no agricultural pests of any significance on Arno. Among reasons for this unusual situation are the limited number of atoll crops, the lack of vegetable cultivation other than taro, the limited commerce, and the low populations of herbivorous insects. The latter is attributed to the particular ecological relationship existing on Arno between herbivores and predators. Normally, herbivores predominate, but protected habitats on Arno are few and predaceous insects and vertebrates (skinks and others) are very numerous. Thus the population equilibrium of crop-feeding insects is below the threshold of economic damage.

**ECTOPARASITES**

Both the house rat and the Polynesian rat were found to be infested with lice (Hoplopleura) and two species of parasitic mites (Laelaps). Herons were infested with parasitic flies (Ornthoica) and mites; noddies, with bird lice (Austromenopon), hippoboscid flies, and mites.
Scorpions and centipedes are much feared by the atoll peoples, but though they may be bitten frequently, their fears are probably exaggerated. The bite of the black widow spider is more serious. However, this spider is absent on Arno, though it has been introduced to some neighboring islands. Ticks, chiggers, and fleas were not found on Arno, and they are probably absent from most atolls.

An unusual pest is the so-called “bao in jekaro” (bird in the jekaro), an oedemerid beetle with strong emantharic poisoning properties. It is attracted to light and to the jekaro, the sap from the inflorescence of the coconut. If a bao falls into the sap and is swallowed, it produces kidney disturbances; if crushed on the skin, it produces a blister.

Ectoparasites of man include lice and, presumably, the tropical bed bug, although bed bugs were found only on Majuro. Lice are rather common, especially head lice, and the Marshallese engage in a louse-catching ceremony. Typhus is absent.

Three mosquitoes are commonly encountered on atolls: the common house or night-biting mosquito of the tropics, *Culex quinquefasciatus*, and two day biters, *Aedes aegypti* and *A. marshallensis*. The first was not found on Arno, making bed nets unnecessary. The pantropic dengue-yellow fever mosquito, *A. aegypti*, originally a tree-hole breeder in Africa, is common, but only in the immediate vicinity of human habitations. Its eggs are laid at water’s edge in cisterns and other drinking-water receptacles, and the larvae feed on the bottom. Adults have silver-banded legs and lyre-shaped markings on the thorax, and they bite indoors in daytime. Dengue fever was temporarily introduced to some Marshall atolls during wartime, but yellow fever has never been known there. The native *A. marshallensis* is also a day biter and a close relative of *A. aegypti*. It breeds in tree holes and in half coconut shells in the forest, and it is abundant but not a vicious biter. This species belongs to the group characterized by *pseudoscutellaris* which carries non-periodic filariasis in Fiji and Samoa, but no evidence of the disease was seen on Arno.

Cockroaches and houseflies are of importance in general sanitation. The housefly is an important transmitter of disease organisms, and the only really unpleasant aspect of life on Arno. The combination of unscreened privies, defecation in exposed intertidal zone, unscreened houses, and unprotected food favor the fly and the high rate of amoebiosis. Skinks and *Hermetia* flies are not capable of keeping the housefly population sufficiently low.

**Interrelations of Insects with Plants and Animals**

The food cycle, or food web, becomes exceedingly complex, even for a small association. However, some of the Arno food chains are shown in the following tables (7-11). Quantitative data, and calculations of biomass, are
### Atoll Strand Community

<table>
<thead>
<tr>
<th>Herbivore</th>
<th>Sand cricket</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saprophages</td>
<td>Housefly (human feces; daylight)</td>
</tr>
<tr>
<td>Predators</td>
<td>Marine water strider (blown onto beach)</td>
</tr>
<tr>
<td></td>
<td>Herring</td>
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<td></td>
<td>Ghost crab</td>
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<td>Plover</td>
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<td>Tattler</td>
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</table>

### Marine Insect Community

<table>
<thead>
<tr>
<th>Herbivores</th>
<th>Pelagic plankters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predators</td>
<td>Marine water striders (three kinds: open ocean, tidepool, and cove)</td>
</tr>
</tbody>
</table>

| *Dotted lines between groups of predators indicate that those in lower groups prey upon members of groups above them.* |

### Table 8—Atoll inner beach community

<table>
<thead>
<tr>
<th><strong>A. Foliage stratum</strong></th>
<th><strong>Plant bugs</strong>: Scaevola aphids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbivores</td>
<td>Leaf-mining fly: Scaevola</td>
</tr>
<tr>
<td>Precaptors</td>
<td>Scavengers</td>
</tr>
<tr>
<td>Ants</td>
<td>Endermidia, Messerschmidia, Sida</td>
</tr>
<tr>
<td>Ladybird beetles</td>
<td>Syrphid fly</td>
</tr>
<tr>
<td>Syrphid fly</td>
<td>Geckos</td>
</tr>
<tr>
<td>Geckos</td>
<td>Green lacewing</td>
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<tr>
<td>Green lacewing</td>
<td>Spiders</td>
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<tr>
<td>Spiders</td>
<td>Skinks</td>
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<tr>
<td>Skinks</td>
<td>Cerambycid beetles</td>
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<tr>
<td>Cerambycid beetles</td>
<td>Predaceous bugs</td>
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<tr>
<td>Predaceous bugs</td>
<td>Skinks</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>B. Bark and dead-wood stratum</strong></th>
<th><strong>Predaceous bugs</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood borers</td>
<td>Bark beetles</td>
</tr>
<tr>
<td>Predators</td>
<td>Staphylinid beetles</td>
</tr>
<tr>
<td>Spiders</td>
<td>Predaceous bugs</td>
</tr>
<tr>
<td>Geckos</td>
<td>Skinks</td>
</tr>
<tr>
<td>Golden plover</td>
<td>Cerambycid beetles</td>
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</tbody>
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<table>
<thead>
<tr>
<th><strong>C. Ground stratum</strong></th>
<th><strong>Ghost crab</strong></th>
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<tbody>
<tr>
<td>Herbivore</td>
<td>Sand cricket</td>
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<tr>
<td>Predators</td>
<td>Crab spider</td>
</tr>
<tr>
<td>Rock gecko</td>
<td>Ghost crab</td>
</tr>
<tr>
<td>Golden plover</td>
<td>Heron</td>
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</tbody>
</table>
unavailable. However, herbivores of small size were most numerous. In general, species are listed in order, starting with herbivores, then scavengers, and then the successive groups of predators, members of each group preying on members of preceding groups. Most of the food chains end with lizards. The skinks, in particular, are the most numerous land vertebrates. They are also preyed upon occasionally by cuckoos, herons, chickens, and even a land crab; but none of these latter are generally distributed or depend primarily on

Table 9.—Atoll open woodland community

<table>
<thead>
<tr>
<th>A. Coconut-Pandanus stratum</th>
<th>Herbivores: coconut scale</th>
<th>Scavengers: bark lice, cockroaches</th>
<th>Predators: earwigs, spiders, skinks (night)</th>
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<table>
<thead>
<tr>
<th>C. Fallen green coconut stratum</th>
<th>Herbivores: rats</th>
<th>Scavenger: mosquito larvae: detritus</th>
<th>Predators: fruit beetles (nitidulids), spiders, predaceous mites, skinks</th>
</tr>
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<table>
<thead>
<tr>
<th>D. Rotten Pandanus fruit stratum</th>
<th>Saprophagous: vinegar flies</th>
<th>Predators: staphylid beetles, predaceous bugs, geckos</th>
<th>Predators: fruit beetles (nitidulids), spiders, predaceous mites, skinks</th>
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<td>gradient</td>
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<thead>
<tr>
<th>E. Soil stratum</th>
<th>Saprophagous: earthworms, sowbugs</th>
<th>Scavengers: Thysanuara, hermit crabs</th>
<th>Predators: geckos (night), hermit crabs, ground skink (day)</th>
</tr>
</thead>
</table>
lizards for food. The lizards do have endoparasites, including stomach nematodes and rectal flagellates.

The significance of these data from the viewpoint of atoll ecology is that the majority of the food chains are independent of man. Only in the immediate vicinity of villages is the picture significantly altered and in such places man

Table 10.—Atoll canopy woodland community

<table>
<thead>
<tr>
<th></th>
<th>Herbivores:</th>
<th>Scavengers:</th>
<th>Predators:</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Breadfruit stratum</td>
<td>corizid bug: bird's-nest fern</td>
<td>mosquito larvae: detritus, tree holes</td>
<td>gerocos (night)</td>
</tr>
<tr>
<td></td>
<td>spider: breadfruit leaves</td>
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<tr>
<td></td>
<td>Scavengers:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Underbrush stratum: Allophylus, Pipturus, Terminalia, Pisonia, Cordia</td>
<td>aphids</td>
<td>leafhoppers</td>
<td>ladybird beetles</td>
</tr>
<tr>
<td></td>
<td>Herbivores:</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Scavengers:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. Fallen log stratum</td>
<td>fungus flies</td>
<td>ants</td>
<td>spiders</td>
</tr>
<tr>
<td></td>
<td>Saprophagous:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. Rotten breadfruit stratum</td>
<td>vinegar flies</td>
<td>rove beetles</td>
<td>geckos</td>
</tr>
<tr>
<td></td>
<td>Saprophagous:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. Soil stratum</td>
<td>earthworms</td>
<td>Thysanura</td>
<td>millipedes</td>
</tr>
<tr>
<td></td>
<td>Sowbugs</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Collembola</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Scavengers:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. Taro pit-aquatic stratum</td>
<td>snail</td>
<td>midge larvae</td>
<td>dragonfly naiad</td>
</tr>
<tr>
<td></td>
<td>Herbivore:</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Scavenger:</td>
<td></td>
<td></td>
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<td></td>
<td>Predators:</td>
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</tbody>
</table>
enters the basic atoll food chains mainly via chickens and pigs. Aside from this, man has moved into the atoll biota and made his own niche.

Aicultural processes are proceeding at an accelerated rate on atolls, as elsewhere, and the biota is bound to change. The depauperate nature of the biota (few species of plants and animals as compared with a mainland area), and of even greater importance, its disharmonic nature (absence of certain types, with gaps or ecologic vacua), make atolls peculiarly susceptible to disruptive influences. The limited economy of the people, based on so few crops, could be ruined by failure of one of the staples. Thus the dispersal of dangerous pests must be prevented. Owing to wartime activity and air transport, Majuro, and to a greater extent Kwajalein and Enewetak, received pests such as the migratory locust, another grasshopper, the black widow spider, the night mosquito, an Odynerus wasp, and a tick. These, bed bugs, fleas, the coconut Brontispa beetle, and the copra beetle were not found on Arno by Usinger and La Rivers. Pests from farther parts of Micronesia, such as the coconut rhinoceros beetle, the giant African snail, and a malaria mosquito, should also be quarantined against.

<table>
<thead>
<tr>
<th>Table 11.—Atoll human community</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Man</strong>, an omnivore: eats fish, coconut, breadfruit, taro, pandanus, bananas, papaya, etc.</td>
</tr>
<tr>
<td>Ectoparasites: lice, bedbugs</td>
</tr>
<tr>
<td>Endoparasites: amoebae, hookworms, etc.</td>
</tr>
<tr>
<td><strong>Domestic animals</strong></td>
</tr>
<tr>
<td>Dog, a scavenger: copra, garbage</td>
</tr>
<tr>
<td>Pig, a scavenger: soil insects, roots</td>
</tr>
<tr>
<td>Chicken, an omnivore: copra, ground insects, skinks</td>
</tr>
<tr>
<td>Cat, an omnivore: rats, etc.</td>
</tr>
<tr>
<td><strong>Household vermin</strong></td>
</tr>
<tr>
<td>Rats: eaten by cat; ectoparasites: mites and lice</td>
</tr>
<tr>
<td>Cockroaches: Evania parasite</td>
</tr>
<tr>
<td>Termite: wood</td>
</tr>
<tr>
<td>Mosquito: cisterns; dragonfly naiaid predator</td>
</tr>
<tr>
<td>Housefly: privies; Hermetia predator</td>
</tr>
<tr>
<td>House gecko: predator on house insects</td>
</tr>
</tbody>
</table>

On Onotoa, a dry atoll in the southern Gilbert Islands, Moul (1954) found only about 80 species of land arthropods in his general study of terrestrial ecology in 1951. The number of plant species is very limited. Among the phytophagous groups were leafhoppers, an aphid, a few bugs, some Microlepidoptera, five noctuid moths, the Ultheisna moth, a sphinx moth, the butterflies Hypolinus and Precis, a skipper, a katydid (Phisidae), an oedemerid beetle, a weevil, and a few others. Scavengers included springtails, roaches, a cricket, a termite (possibly in a drift log), the copra beetle, dermestid and nitidulid beetles, craneflies, the housefly, the Chrysomyia fly, ants, and rats.
Predators included *Halobates*, a green lacewing, a damselfly, three dragonflies, ladybird beetles, staphylinid beetles, a syrphid fly, a few wasps, spiders, centipedes, geckos, skinks, terns, golden plover, and the coconut crab. Mosquitoes were found breeding in old coconut shells and taro pits.

On Ngaiangl, a wet atoll very close to Palau, I found evidence of a much larger fauna than that of Arno Atoll, including many of the common Palau insects (see insect fauna of Micronesia). This is correlated with the existence of a richer flora than is found on most atolls (Gressitt, 1952, 1953a), which is also directly related to the proximity of Babelthuap. This may represent close to the maximum biota for an atoll, except for those close to continental areas or possessing more introduced plants and having more extensive commerce.

In the accompanying food-chain tables, dotted lines between groups of predators indicate that members of each successive group may feed on those in groups above. Similar dotted lines in chains of saprophagous insects indicate ecologic succession.

**HIGH ISLAND INSECT ECOLOGY**

Compared with the ecology on atolls like Arno, which are distant from continents or high islands, insect ecology in groups like Palau and the southern Mariana Islands is very complicated. Though still much simpler than in most continental areas, it is not yet well enough understood to make a clear presentation of basic relationships. Since some aspects have received more attention than others, the picture presented here will be unbalanced. The following notes are based primarily on Palau. Some of the types of insects mentioned, even including some families, are not found in some (even in any) of the other high island groups. Information on flies primarily concerns Guam; and some of these species are introduced and do not occur in other island groups.

The Palau Islands display a great variety of ecological communities, as may be judged from the descriptions of geography and vegetation. Some situations—the high, narrow, uninhabited coral ridges; the almost “shoreless” undercut nature of the same islands (fig. 27); and the lowland jungle on volcanic Babelthuap, continuous with mangrove and nipa swamps (figs. 24, 25) on one hand and upland forest on the other—are more or less unique for Micronesia. Some are rare elsewhere. The phosphate environments of Angaur and Peleliu are also uncommon. The fact that the Palaus also include barrier reef islets, slightly raised reef islands, small volcanic islets, a very young atoll, and a submature atoll, makes them a very rich field for the study of island ecology. Some environments, like the low areas or sea-level “lakes” within some of the high coral islands, have hardly been investigated at all. However, the Palaus, lacking high altitudes, are almost without real cloud forest; and they com-
I nsects of M i cronesia—V o l. 1 , 1 9 5 4

Pletely lack the dwarf vegetation on open crests and other specialized high environments of P onape and K usaie. Perhaps the total land arthropod fauna of the Palaus is in the neighborhood of 5,000 species, or 10 times that of Arno.

Not only does Palau have a much richer fauna than does an atoll, but the biota is of a much more harmonic nature. That is, with more types of insects present, there are fewer ecologic vacua and the food chains have more steps and more complicated inter-relationships. From the economic standpoint, this may mean that the introduction of a new insect pest of a native crop is potentially more dangerous on an atoll, where its niche may not have been previously occupied, and where competitors and natural enemies may be few or lacking. Thus on a rich high island more enemies and competitors may be expected. Again, more pests become established on the high islands, not only because of more extensive commerce, but because hosts are present which may be lacking on atolls. The introduction of Micronesia’s most serious pest, the coconut rhinoceros beetle (Oryctes), though unprecedentedly serious in Palau, is an even greater threat to an atoll where the entire economy is dependent upon the coconut palm. In Palau the agriculture is potentially more diversified than on an atoll, though the present customs of the people do not make for such diversification.

Among groups of insects in Palau and not found on most of the atolls are the following: a preying mantid, a leaf insect, a horsefly, biting midges, jumping plant lice, cicadas, ant lions, brown lacewings, the caddisfly, predaceous elaterids, prionid beetles, rhinoceros beetles, June beetles, leaf beetles (except Brontispa), swallowtail butterflies, water bugs, water beetles, many parasitic insects, a velvet ant (mutillid), and many families of bugs, moths, beetles, flies, and wasps. Of these, the mantid, the leaf insect, the horsefly, rhinoceros beetles (two kinds), and the velvet ant are not found elsewhere in Micronesia, except that the mantid has been introduced to Guam, Saipan, and Truk, and two additional mantids have been introduced to Guam in recent years. A horsefly has also been found recently on Guam. Also lacking on most atolls are the giant African snail, the frog, the toad, the monitor lizard, snakes, several types of birds, the monkey, and the wild pig. Small terrestrial leeches are reported from Truk, Ponape, and Kusiaie; and they may also be in Palau.

The beach, strand, and coastal plain ecology of high islands is similar to the situation on atolls, but with the involvement of many added species of animals in the above groups, as well as of additional plants.

The mangrove association is well-developed in Palau (figs. 25, 29), but few insects have been noted in it. Besides the Peleliu gnat (Culicoides), which breeds in mangrove mud (Dorsey, 1947), a few herbivorous insects were noted on mangrove trees, including leaf beetles of the genus Rhyparida,
a small longicorn beetle (lamIID), and bag worms (in Truk), on Rhizophora; and scale insects on Bruguiera on Saipan. Little evidence of insect attack is seen on the trees. Marine water striders are often abundant on tidal portions of rivers in the mangrove zone; in sunken river mouths on Babelthuap, particularly in those opening into Ngaremedu Bay; in mangrove passages such as that between Sokehs and Ponape; and in other mangrove areas and river mouths on Ponape, Kusaie, and other islands.

Fresh-water environments are much better developed on the older volcanic islands than on atolls and raised coral islands. Thus on Babelthuap, Ponape, and Kusaie, and in southern Guam and parts of Saipan, there are permanent rivers, numerous streams, and even some ponds or small lakes (at least on Babelthuap and Saipan). All of these islands possess caddisflies (except perhaps Saipan) and other water insects. Streams are short and, in part, temporary in Yap and Truk; and Yap has some very small ponds, most of them formed by bomb craters. In spite of these limited niches, Yap has the widest variety of aquatic insects in Micronesia, with a mayfly, three caddisflies, and numerous bugs and beetles. There may be no fishes in fresh water on Yap. Taro pits are present on all the inhabited volcanic islands, as well as on low coral islands. Perhaps the largest continuous taro area in Micronesia is found on the west-central portion of Peleliu. On northeast Peleliu is one of the largest mangrove bays (fig. 29), though parts of it were burned or destroyed by oil during the war.

Around small rapid streams and waterfalls, particularly on Ponape, numerous tetrigid grasshoppers and interesting large and small crickets are found. Their roles are not completely understood, but some of them must be omnivorous and some must feed on flies or caddisflies near the water, or even on aquatic larvae.

The water in pitcher plants (fig. 41, d) breeds an endemic Aedes mosquito, at least on Babelthuap and Koror, and its larvae have a few small predators. Likewise tree holes are breeders of Aedes mosquitoes on various islands, as they are on Arno. Aedes mosquitoes breed also in shells of dead giant African snails, in opened coconuts, in war wreckage, in steps cut on coconut palm trunks, and so forth.

The accumulated water in the axils of Pandanus and Freycinetia leaves is an interesting environment (fig. 24), rich in the very damp areas. In lowland jungle on Ponape it was particularly noted to include various small fly larvae and damselfly naiads. In the axils containing more debris than water were found mites, isopods, millipedes, centipedes, and other forms. Aedes pandani, which breeds in this environment on Guam, is a pestiferous day biter in the Guam forests.
Table 12.—Lowland rainforest community

<table>
<thead>
<tr>
<th>A. Palm stratum</th>
<th>Nectar, pollen:</th>
<th>Lepidoptera (adults)</th>
<th>flies (adults)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>bees</td>
<td>oedemerid beetles</td>
<td>thrips</td>
</tr>
<tr>
<td>Herbivores:</td>
<td>Brontispa beetle</td>
<td>Furcaspis oceanica (and parasites)</td>
<td>Oryctes rhinoceros (Palau)</td>
</tr>
<tr>
<td></td>
<td>Segestes (katydid)</td>
<td>weevils</td>
<td>small moth larvae</td>
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<tr>
<td>Scavengers:</td>
<td>ants</td>
<td></td>
<td>Acanthograeffia (phasmid)</td>
</tr>
<tr>
<td>Predators:</td>
<td>Chelisoches (earwig)</td>
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<table>
<thead>
<tr>
<th>B. Pandanus–Freycinetia stratum</th>
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<tr>
<td>Herbivores:</td>
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<td>Scavengers:</td>
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<td>Predators:</td>
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<table>
<thead>
<tr>
<th>C. Forest tree, shrub, and vine stratum</th>
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<td>Herbivores:</td>
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<td>Scavengers:</td>
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<td>Parasites:</td>
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<td>Predators:</td>
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* Dotted lines between groups of predators indicate that those in lower groups prey upon members of groups above them.
The lowland rainforest environment is exceedingly rich in variety of inhabitants, and the ecological relations are poorly understood. In a dark damp forest one may gain the impression that insects are extremely scarce, with almost none to be seen on the wing and very few to be obtained by sweeping vegetation with a net. However, one may come across a tall flowering *Heterospathe* palm and, in the stillness, hear the buzzing of wild bees and other insects. In lengthy searching of logs and decaying vegetation, a great variety of small scavenging and predaceous insects and other arthropods may be found. In the crowns of *Pandanus, Freycinetia*, various palms, *Thoracostachyum* (fig. 5, b), and other plants with large petioles, other interesting environments occur, with herbivores including hispid beetles, weevils, long-horned grasshoppers, and others, and with predators including earwigs, centipedes, geckos, skinks, and birds. This environment, in relation to the introduced coconut rhinoceros beetle (*Oryctes*), was recently treated by me (1953b), including the beetle’s larval environments. These latter involve various sorts of decaying vegetation, from wood to garbage and manure,
which harbor large varieties of scavenging beetle larvae, fly maggots, mites, millipedes, isopods, amphipods, and others, as well as predaceous centipedes, scorpions, carabid and elaterid beetles, geckos, skinks, monitor lizards, and others.

In forest clearings and village areas, the lowland rain forest environment merges with the coastal strand and open woodland environments. Transition also takes place between the rain forest and mangrove on one hand and the upland forest on the other. Some of the insects, like some of the plants, may be found in several of the environments. The palms and pandanus, for instance, may be found on beaches, open hillsides, jungle, and swamps merging with mangrove (fig. 24, 25). The *Pseudopinanga* palm, however, is hardly seen out of wet jungle, though it is found from well-elevated hillsides to the edge of mangrove. More insects, particularly of the leaf-eating herbivores, are found in the partly cleared or picked-over forests, the open woodlands, the clearings, and the cultivated areas with bits of native vegetation remaining. Naturally, the various predators are found in greater abundance in these environments also.

The various forms of decaying vegetation, carrion, and excrement are great breeders of flies and their predators. These were more thoroughly studied on Guam (Bohart and Gressitt, 1951), where there occur many introduced species. With the presence of cattle, buffalo, horses, and other domesticated animals not found on atolls, more environments exist for the breeding of these insects. An important source of fly-breeding on the high islands, particularly where there are roads and vehicles, is the carcasses of crushed giant toads and giant African snails. The toads then come to feed on the flies attracted to the dead toads and snails, and live snails come to feed on their dead relatives, and thus more of them are crushed by vehicles, providing continued added fly-breeding situations. Seasonally, fallen breadfruit rotting on the ground provides a great source of breeding for flies of many species, including many of those closely related to man and to disease transmission. Rotting coconuts are a similar source (fig. 70). The introduction of dung beetles may prove helpful in reducing the amount of scattered animal excrement available for fly-breeding, but this does not influence the breeding of flies in rotting breadfruit. The introduction of carrion beetles might help to reduce fly-breeding in the limited carrion environment.

On some islands—and this was particularly noted in Truk, where much breadfruit is preserved in the ground for later eating—the places where the breadfruit is prepared and pounded provide a rich environment for a variety of arthropods in the decaying refuse. These include mites, springtails, various other primitive insects, millipedes, isopods, amphipods, beetle larvae, and such predators as anthocorid bugs, pseudoscorpions, centipedes, geckos, and
### Table 13.—Aquatic communities

<table>
<thead>
<tr>
<th>Classification</th>
<th>Habitat</th>
<th>Herbivores</th>
<th>Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Marine</td>
<td>surface stratum</td>
<td>plancters</td>
<td>Halobates (marine strider)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Halovelia (small marine strider)</td>
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<tr>
<td>B. Brackish</td>
<td>mangrove water stratum</td>
<td>Culicoides pelioliensis (gnat)</td>
<td>small crustaceans</td>
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<tr>
<td></td>
<td></td>
<td>Periophthalmus fish</td>
<td>Bufo marinus (toad)</td>
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<td></td>
<td></td>
<td>mangrove crab</td>
<td>snakes</td>
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<td></td>
<td></td>
<td></td>
<td>crocodile</td>
</tr>
<tr>
<td>C. Brackish:</td>
<td>mangrove mud stratum</td>
<td>notonectid bugs</td>
<td>Ochthera canescens (ephydrid)</td>
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<tr>
<td></td>
<td></td>
<td>Paraclius germanus (dolichopodid)</td>
<td>damselsfly naiads</td>
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<tr>
<td></td>
<td></td>
<td>dytiscid beetles</td>
<td>dragonfly naiads</td>
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<td></td>
<td>water striders</td>
<td>shrimps</td>
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<td></td>
<td></td>
<td>crabs</td>
<td>large shrimps</td>
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<td>snakes</td>
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<tr>
<td>D. Stagnant:</td>
<td>pond and taro pit stratum</td>
<td>mosquito larvae</td>
<td>corixid bugs</td>
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<td>syrphid fly larvae</td>
<td>midge larvae (tendipedids)</td>
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<td>small crustaceans, etc.</td>
<td>hydrophilid beetles</td>
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<td>notonectid bugs</td>
<td>Ochthera canescens (ephydrid)</td>
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<td>Paraclius germanus (dolichopodid)</td>
<td>damselsfly naiads</td>
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<td>dytiscid beetles</td>
<td>dragonfly naiads</td>
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<td>water striders</td>
<td>shrimps</td>
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<td>crabs</td>
<td>large shrimps</td>
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<td></td>
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<td>snakes</td>
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</tr>
<tr>
<td>E. Stream, waterfall, and pond (non-stagnant) community</td>
<td>mayfly (Yap)</td>
<td>snails</td>
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<tr>
<td></td>
<td></td>
<td>tetrigid grasshoppers</td>
<td>crickets</td>
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<td></td>
<td></td>
<td>mosquito larvae</td>
<td>tendiped larvac</td>
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<td>other fly larvae</td>
<td>hydrophilid beetles</td>
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<td></td>
<td></td>
<td>caddisfly larvae</td>
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<td></td>
<td></td>
<td>water striders</td>
<td>water bugs</td>
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<td>dytiscid beetles</td>
<td>dragonfly naiads</td>
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<td>shrimps</td>
<td>crabs</td>
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<td>fishes</td>
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<td></td>
<td></td>
<td>bittern</td>
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<tr>
<td>F. Pitcher plant (Nepenthes) stratum</td>
<td>Aedes mosquito larvae</td>
<td>moth larvae</td>
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<td></td>
<td></td>
<td>fly larvae</td>
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<td></td>
<td></td>
<td>spiders</td>
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<tr>
<td>G. Tree hole stratum</td>
<td>Aedes mosquito larvae</td>
<td>Ochthera canescens (ephydrid)</td>
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<td></td>
<td></td>
<td>spiders</td>
<td>Paraclius germanus</td>
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<tr>
<td>H. Pandanus and Freycinetia axil stratum</td>
<td>mites</td>
<td>mosquito larvae</td>
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<td></td>
<td></td>
<td>midge larvae</td>
<td>isopods, millipedes</td>
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<td>damselfly naiads</td>
<td>centipedes</td>
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<td></td>
<td></td>
<td>geckos</td>
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</table>
Table 14.—Open woodland, clearings, cultivated and village areas community

<table>
<thead>
<tr>
<th>A. Coconut stratum (see lowland rainforest: palm stratum)</th>
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<tbody>
<tr>
<td><strong>Herbivores:</strong></td>
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<td><strong>Scavengers:</strong></td>
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<td><strong>Predators:</strong></td>
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<table>
<thead>
<tr>
<th>B. Pandanus stratum (see lowland rainforest: Pandanus-Freycinetia stratum)</th>
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<tbody>
<tr>
<td><strong>Scavengers:</strong></td>
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<td><strong>Predators:</strong></td>
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<table>
<thead>
<tr>
<th>C. Fruit and ornamental tree stratum (breadfruit, mango, papaya, citrus, etc.)*</th>
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<tbody>
<tr>
<td><strong>Herbivores:</strong></td>
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<td><strong>Scavengers:</strong></td>
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<td><strong>Predators:</strong></td>
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<table>
<thead>
<tr>
<th>D. Cultivated crops: sugar cane, maize, cassava, taro, melons, sweet potato, etc.*</th>
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<tbody>
<tr>
<td><strong>Herbivores:</strong></td>
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<td><strong>Scavengers:</strong></td>
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<td><strong>Predators:</strong></td>
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<table>
<thead>
<tr>
<th>E. Rotting wood stratum (see lowland rainforest: D. dead stumps, logs, and other decaying vegetation stratum)</th>
</tr>
</thead>
</table>

* See section on economic entomology for specific records.
Table 14.—Open woodland, clearings, cultivated and village areas community—Continued

<table>
<thead>
<tr>
<th>F. Rotting coconut stratum (fallen green, ripe, or opened only for drinking)</th>
<th>Saprophages:</th>
<th>flies (larvae and adults):</th>
<th>Atherigona orientalis</th>
<th>Cadrema bilineata</th>
<th>Chrysmyia megacephala</th>
<th>Sarcophaga &quot;peregrina&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scavengers:</td>
<td>hermit crabs (also predators)</td>
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<tr>
<td>Predators:</td>
<td>rats (also scavengers)</td>
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<tr>
<td>G. Rotting breadfruit and Pandanus fruit stratum</td>
<td>Saprophages:</td>
<td>flies (larvae and adults):</td>
<td>Cecidomyids</td>
<td>Chaetodrosophilella quadrilineata</td>
<td>Drosophila melanogaster, etc.</td>
<td>Notogramma stigma</td>
</tr>
<tr>
<td></td>
<td>Scavengers:</td>
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</tr>
<tr>
<td></td>
<td>Predators:</td>
<td>predaceous mites</td>
<td>anthocorid, ceratocombid bugs</td>
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<tr>
<td>H. Garbage and compost stratum</td>
<td>Saprophages:</td>
<td>flies (larvae and adults):</td>
<td>Milichiella lacteipennis</td>
<td>Physiphora aenea</td>
<td>Tubifera arvora (rare)</td>
<td>Ophyra chalcogaster</td>
</tr>
<tr>
<td></td>
<td>Parasites:</td>
<td>Spalangia, etc. (in fly puparia)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predators:</td>
<td>Hermetia illucens (also saprophagous)</td>
<td></td>
<td>Microchrysa flaviventris (also saprophagous)</td>
<td>earwigs</td>
<td>Pseudozaena (carabid beetle)</td>
</tr>
</tbody>
</table>

† Dotted lines under saprophagous insects indicate groups representing ecological succession.
Table 14.—Open woodland, clearings, cultivated and village areas community—Continued

<table>
<thead>
<tr>
<th>I. Carrion stratum</th>
<th>Saprophagous:</th>
<th>Predators:</th>
</tr>
</thead>
<tbody>
<tr>
<td>flies (larvae and adults):</td>
<td>Lucilia cuprina</td>
<td>Hermetia illucens (also saprophagous)</td>
</tr>
<tr>
<td>Chrysomyia megacephala</td>
<td>Sarcophaga dux, S. “peregrina”</td>
<td>robber flies (on adults)</td>
</tr>
<tr>
<td>Sarcophaga ruficornis</td>
<td>Chrysomyia rufifacies (also predaceous)</td>
<td>rats</td>
</tr>
<tr>
<td>Sarcophaga gressitti, S. kmabi</td>
<td>Megaselia scalaris, M. stuntzi</td>
<td>histerids</td>
</tr>
<tr>
<td>Puliciphora wymani, P. nigrosterna</td>
<td>Diploneura cornuta</td>
<td></td>
</tr>
<tr>
<td>Physiphora aenea</td>
<td>Chrysomyia “nigripes”</td>
<td></td>
</tr>
<tr>
<td>Rhinia testacea</td>
<td>Parafannia molluscovora</td>
<td></td>
</tr>
<tr>
<td>Atherigona orientalis</td>
<td>Discomyzma maculipennis</td>
<td></td>
</tr>
<tr>
<td>Pseudexesta prima</td>
<td>Pannia pusio</td>
<td></td>
</tr>
<tr>
<td>Ophyra chalcogaster</td>
<td>Hecamede persimilis</td>
<td></td>
</tr>
<tr>
<td>beettles:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermestes sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Necrobia rufipes (copra beetle)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>J. Excrement stratum</td>
<td>Saprophagous:</td>
<td>Parasites:</td>
</tr>
<tr>
<td>flies (larvae and adults):</td>
<td>Sarcophaga ruficornis (human, horse)</td>
<td>Spalangia, etc. (in fly puparia)</td>
</tr>
<tr>
<td>Chrysomyia kmabi (pig, human)</td>
<td>Sarcophaga gressitti, S. dux (human)</td>
<td></td>
</tr>
<tr>
<td>Chrysomyia megacephala (human)</td>
<td>Lucilia cuprina (human)</td>
<td></td>
</tr>
<tr>
<td>Musca sorbens (pig, cow, etc.)</td>
<td>Musca vicina (horse)</td>
<td></td>
</tr>
<tr>
<td>Ophyra chalcogaster (pig, etc.)</td>
<td>Atherigona orientalis (human)</td>
<td></td>
</tr>
<tr>
<td>Stomoxys calcitrans (cow, pig, heaps)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megaselia scalaris (human)</td>
<td>Megaselia suis (pig)</td>
<td></td>
</tr>
<tr>
<td>Leptocera femorina (pig)</td>
<td>Paralimnina aequalis (pig)</td>
<td></td>
</tr>
<tr>
<td>Allotrichoma spp. (pig)</td>
<td>Milichiella lacteipennis (cow, horse)</td>
<td></td>
</tr>
<tr>
<td>Desmometopa sp. (cow, horse)</td>
<td>Lonchaea filifera (pig)</td>
<td></td>
</tr>
<tr>
<td>Drosophila spp. (human)</td>
<td>Tubifera arvora (heaps, liquid)</td>
<td></td>
</tr>
<tr>
<td>Psychoda sp. (pig)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lyctoria sp. (human)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>introduced coprid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>J. Excrement stratum</td>
<td>Predators:</td>
<td></td>
</tr>
<tr>
<td>beettles:</td>
<td>Microchrysa flaviventris</td>
<td></td>
</tr>
<tr>
<td>Atherigona orientalis</td>
<td>(heaps)</td>
<td></td>
</tr>
<tr>
<td>histerid beetles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>skinks</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
skinks. In Truk and Babelthuap a similar environment, that of rotting banana stalks, contained numerous chiggers. These commenced to bite the hands immediately during the search for specimens or the gathering of material for Berlese funneling.

The high coral island environment in southern Palau has not been adequately investigated. It obviously includes many endemic forms of insects, just as it does plants. The *Gulubios* palms on the high ridges undoubtedly embrace an interesting stratum. *Pandanus* and various of the scrubby trees harbor otiörhynchine weevils. Fresh-water environments are extremely limited; but in old cisterns at a former Japanese station near the destroyed lighthouse at Ngaremediu, high on northeastern Ngurukdabel, dragonflies, water striders, and other aquatic insects were observed.

On the summit of Mount Unibot on Ton Island, the highest peak of Truk, I found an interesting relationship between an ant (*Odontomachus haematoda*) and a peculiar plant, *Baloniella pedicellaris*. The ant, which is perhaps the largest in Micronesia, is black with very long mandibles, and has both a bite and a painful sting. The plant belongs to the Balanophoraceae and is parasitic on the roots of trees. There were several large nests of the ant surrounding and almost covering clumps of the plant growing close to the trunks of some trees of moderate size. The nests consisted largely of accumulated debris of volcanic dirt and vegetable fragments, with many openings, particularly near the top of the yellow, fleshy plants, which were 8 to 12 cm. high. The nests were 35 cm. or more broad and contained moderate numbers

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### Table 14.—Open woodland, clearings, cultivated and village areas community—Continued

<table>
<thead>
<tr>
<th>Herbivores:</th>
<th>Saprophages:</th>
<th>Scavengers:</th>
<th>Predators:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gryllotalpa (mole cricket)</td>
<td>oribatoid mites</td>
<td>ants (also predaceous)</td>
<td>mites (including chiggers)</td>
</tr>
<tr>
<td>Thysanura</td>
<td>millipedes</td>
<td>hermit crabs (also predaceous)</td>
<td>blind snake (Typhlops)</td>
</tr>
<tr>
<td>millipedes</td>
<td>earthworms</td>
<td></td>
<td>scorpions</td>
</tr>
<tr>
<td>earthworms</td>
<td></td>
<td></td>
<td>geckos</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>rails</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>toad</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>monitor lizard</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
of the ants. When undisturbed, the ants walked slowly over the crowns of the plants or stood still on them, apparently imbibing some fluid or sticky secretion on the surface. When indirectly disturbed, the ants ran around with jaws outspread, occasionally snapping them audibly, and, more rarely and when excited, attempting to bite the crowns of the plants. That a symbiotic relationship of some extent existed seemed quite evident. How important a part of the ant's food the plant secretion is, or what its nature was, was not determined. Nor was it determined whether the ant offers more than general protection to the plant, or whether it has anything to do with its fertilization or dispersal. Herbarium specimens of the same plant from the same locality bear no notes regarding ant nests. This ant is well known, and elsewhere it often makes small nests under the skirts of coconut palms, and under the bark of dead trunks.

Table 15.—High cloud forest association (Ponape and Kusaie)

<table>
<thead>
<tr>
<th>Association</th>
<th>Herbivores</th>
<th>Scavengers</th>
<th>Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Cyathea tree fern stratum</td>
<td>cossonine weevils in petioles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Pandanus, Freycinetia, and Thoracostachyum stratum</td>
<td>Trigonops weevils, tetrigoniid grasshoppers, elaterid, etc., beetles</td>
<td>rynchophorine weevils, large crickets</td>
<td>ants, wood borers, earwigs, carabid beetles, geckos, flycatchers (Rhipidura, etc.), white-eyes (Zosterops, Rukia), kingfisher (Halcyon; eats geckos)</td>
</tr>
<tr>
<td>C. Shrub and dwarfed tree stratum</td>
<td>otiorynchine weevils, cerambycid beetles</td>
<td>roaches, Apterygota</td>
<td>earwigs, spiders</td>
</tr>
</tbody>
</table>

Among some of the characteristics of the biota on high islands are the scarcity of leaf beetles (chrysomelids), June beetles, and large caterpillars. Among the dominant herbivores are leaf-eating weevils (mostly otiorynychids), other types of weevils in more protected environments, and moth larvae (Microlepidoptera), also often found in protected situations. Among predators, spiders, geckos and skinks are abundant and, in damp and covered environments, centipedes and others. In general, there are more types of herbivores and scavengers than are found on atolls, and also more parasitic insects and small predators; but geckos and skinks are likewise of the greatest
importance as insect predators, and are extremely abundant, as there are not many large predators. Monitor lizards are important, but they have been much reduced in numbers on most islands, as a result of eating the introduced toad and of being hunted because they feed on chickens.

Table 16.—Human community

<table>
<thead>
<tr>
<th>Man: omnivorous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ectoparasites: lice, bedbugs, fleas, ticks, mites, chiggers</td>
</tr>
<tr>
<td>Endoparasites: amoebae, hookworms, Ascaris, Trichuris, etc.</td>
</tr>
</tbody>
</table>

**Domestic animals**

| Dog: scavenger (copra, garbage) |
| Pig: scavenger (copra, soil insects, roots) |
| Chicken: omnivore (copra, soil insects, skinks) |
| Cat: omnivore (rats, etc.) |
| Cattle, water buffalo: herbivores |
| Horse: herbivore |

**Household vermin and biters**

| Rats: eaten by cat; ectoparasites: mites, lice, fleas |
| Cockroaches: Evania parasite |
| Termites: wood |
| Ants: scavengers and predators |
| Biting midges (Culicoides): mangrove mud, streams |
| Mosquitoes: cisterns, half coconut shells, etc.; dragonfly naiaad predators |
| Housefly: privies, Hermetia predator |
| Horsefly: larvae prey on worms and grubs in mud |
| Stable fly: cattle manure |
| Centipedes: also useful predators |
| Scorpions: predators |
| Oedemerid (toddy) beetles: larvae in rotting wood |
| Geckos: feed on many of above |

The preceding tables (12-16) of high island food chains are not complete, and some include only a small part of the stratum or community. Many environments are completely omitted. Much of the data refers to Palau, but most of the fly records apply to Guam (Bohart and Gressitt, 1951).

For high island beach and strand communities, see atoll food chains, tables 7 and 8. To these lists should be added various introduced species, or native insect groups lacking on atolls, particularly on plants not found on atolls, and added parasites and predators, including ant lions, carabids, the frog (Palau only), the toad, the monitor lizard, additional birds, and others.
ECONOMIC ENTOMOLOGY

Because of the limited insect fauna of Micronesia, and because of the relatively small number of plants cultivated there to date, the number of known insect pests in the islands has not been very great. However, with increased commerce, particularly aviation, the number of pests is rapidly increasing and the danger to local agriculture and to neighboring areas is mounting. In 1936 Swezey (1940) found 50 species of insect pests on Guam which did not then occur in Hawaii, and more have since reached Guam from the Philippines. Biological control, as in Hawaii, Fiji, and other isolated island groups, is of the greatest potential importance in Micronesia. (See Pemberton, 1953, and in press; Maehler, 1949.)

Most of the recorded economic insects are listed here under their hosts. Some of the pests mentioned may be wrongly identified, and this will be rectified in forthcoming papers in the series; but since information on economic insects is scarce, some even inaccessible, space is devoted to them here. Distribution mentioned refers only to records as pests.

INSECTS WHICH ATTACK CROPS

The principal insects recorded from the various crops in Micronesia are listed below, with brief notes, under the crops, which are arranged alphabetically. Many of the records are from Fullaway (1912), Vandenberg (1926-1933), Esaki (1940, 1943, 1952), Swezey (1940), Swezey et al., (1942, 1946), Oakley (1946, 1953), Townes (1946), Bryan (1949), and Gressitt (1953b). Some are unpublished records of K. L. Maehler, M. M. Ross, R. P. Owen, J. W. Beardsley, G. D. Peterson, and O. N. Liming.

HOST PLANTS

AGAVE

The scale insect Aonidiella orientalis (Newstead) was found by Oakley to be abundant on Agave sisalana on Rota.

AVOCADO (PERSEA)

The Oriental fruit fly, Dacus (Strumeta) dorsalis Hendel, is a serious pest of avocado in the Mariana Islands. This fly was introduced to Saipan after 1928 and a few years earlier than 1935, by which time it was abundant and was attacking mango in particular. It was probably introduced from Okinawa, according to Esaki (1952). It was found on Guam December 19, 1947 by Maehler, having reached Tinian and Rota earlier.

Aspidiotus destructor Signoret has been noted recently on avocado on Guam by Peterson.
BAMBOO (BAMUSA AND OTHERS)

The scale *Asterolecanium bambusae* (Boisduval) has been noted on bamboo on Guam, by Fullaway, and Beardsley has found *Asterolecanium* on Koror and Ponape.

BANANA (MUSA)

The banana weevil, or banana root borer, *Cosmopolites sordidus* (Germar) was abundant in Guam by 1936 according to Swezey. By 1939 it had reached Saipan where it was common by 1940. It was recorded from the Bonin Islands in 1914. In 1947 the histerid *Plaesius javanus* Erichson was introduced from Fiji to Guam for the control of the weevil; establishment of the histerid was confirmed by Ross in February 1949. In 1948 T. R. Gardner introduced the hydrophilid *Dactylotermum hydrophiloides* MacLeay to Palau from Malaya for control of the weevil, but establishment has not been determined. In 1946 Oakley found a hydrophilid presumably feeding on the weevil larvae in Yap. In early 1954 the histerid *Leionota* sp. was shipped to Guam and Palau by Krauss from Trinidad, via Honolulu. Another banana weevil, *Polythus mellerborgi* (Boheman) was also common on Guam by 1936, and was found on Saipan in 1946; but it is not an important pest.

Other banana pests include the scales, *Aspidiotus destructor* Signoret and *Coccus viridis* (Green), which attack occasionally; the banana aphid, *Pentalonia nigronervosa* Coquillet, which occurs in Guam, Palau, and Ponape, but is not serious; and the derbid *Proutista moesta* (Westwood).

The locust *Valanga excavata* (Stål) was presumed to have fed on banana leaves on Tinian (Oakley).

A pyraustid moth *Nacoleia* sp., is a banana scab moth in the Carolines, its serpentine galleries disfiguring the fruit. *Prodenia litura* (Fabr.) was found as a pest by Swezey, who introduced *Telenomus nawai* Ashmead for control. (See figure 65, b.)

The June beetle *Holotrichia mindanaoana* (Brenske) feeds on banana leaves on Guam and Saipan, and another species is present in Palau. The Chinese rose beetle, *Adoreus sinicus* Burmeister, was found on Guam in February 1949 by Maehler and has since spread to Saipan, Tinian, and Rota. The Oriental fruit fly (see avocado) attacks ripe fruit.

BEANS (PHASEOLUS)

*Aphis laburni* Kalt is widespread and attacks various beans, according to Esaki; and *A. medicaginis* Koch was found sparsely on beans in the Marianas by Oakley. The leafhopper *Empoasca pitiiensis* Metcalf attacks beans also.

The heteropterans *Riptortus* sp., *Leptoglossus membranaceus* [australis (Fabr.)], *Nezara viridula* Linn. and *Halticus tibialis* Reuter are recorded by
Esaki, and the membracid *Leptocentrus taurus* (Fabr.) is recorded for the Marianas by Oakley.

The gracilariid moth *Acrocercops* sp. is a leafminer on many islands; and the olothreutid moth *Cryptophlebia carpophaga* [ombrodelta (Lower)] was found in pods on Guam in 1936 by Swezey. The phycitid moth *Etiella zinckenella* (Treitschke), was also found in pods on Guam by Swezey. The pyraustid *Nacoleia diemanalis* (Guenée), a leafroller, was found on Guam in 1936 by Swezey, and probably the same species was found in *Vigna* on Tinian by Oakley. The pyraustid moth *Maruca testulalis* (Geyer) is a pod borer in Guam and Saipan. Esaki also mentions some noctuid caterpillars. One of them is *Prodenia litura* (Fabr.); another, *Chrysodeixis* (“Plusia”) *chalcites* (Esper), was noted on Guam by Swezey. *Argyroloce carpophaga* (Walsingham) is said to occur on Guam. The butterfly *Lampides boeticus* (Linn.) is a widely distributed pest.

The chrysomelid *Pagria* sp. was noted on Guam in 1951 by Peterson; and the Chinese rose beetle, *Adoretus sinicus* Burmeister, is a serious defoliator. The scoliid *Campomeris marginella modesta* Smith was introduced for *Adoretus* control in 1951.

The mining fly *Melanagromyza phaseoli* (Coquillet) was found on Guam in 1950 by Owen, and in 1952 on Truk.

**BEETS (BETA)**

The Hawaiian beet webworm *Hymenia recurvalis* (Fabr.), was found on Guam by Fullaway in 1911, and he also mentioned an *Apanteles* parasite and a carabid predator, *Chlaenius biguttatus* [flavoguttatus MacLeay]. He also noted an aphid.

**BERMUDA GRASS (CYNODON)**

*Antonina* sp. was found by Fullaway on the roots of Bermuda grass on Guam in 1911, and it was found recently in Palau and Truk by Beardsley. The pyraustids *Marasmia venilialis* (Walker) and *Psara licarsisalis* (Walker), as well as army worms, grasshoppers, and leafhoppers were cited as grass pests in general by Swezey.

**BREADFRUIT (ARTOCARPUS)**

The scale *Icerya aegyptiaca* (Douglas) is, at times, a damaging pest on breadfruit, at least in some of the central and western Carolines and the Marshalls. It is checked by *Rodolia pumila* Weise, *R. cardinalis* (Mulsant), and *Rodolia* sp. in Palau. Beardsley has recently introduced *Rodolia* sp. to Nomwin. *R. pumila* was introduced from Rota to Truk in 1947. from Saipan
to Ulithi in 1948, and to Kwajalein and Nama in 1949, by Langford; and these introductions were reported as successful. In 1948 an Indian *Rodolia* was introduced to Guam and Majuro, and establishment was confirmed initially at one release point above Agana, Guam on mealybug on croton (Maehler). An apparent lepidopteran larval predator of *Icerya* was noted by Oakley. The scale *Vinsonia stellifera* Westwood is common, according to Esaki. *Aspidiotus destructor* Signoret occasionally affects breadfruit (see coconut). Mealybugs are also sometimes common, as is the fulgoroid *Phacicephalus* sp. An aphid was noted by Fullaway. *Xenaleurodes artocarpi* Takahashi, endemic to Palau, is often quite prevalent on the under sides of leaves.

The Oriental fruitfly, *Dacus dorsalis* Hendel, rarely infects breadfruit (see avocado); but other fruit flies, including *Dacus frauenfeldi* Schiner, commonly attack breadfruit in the Carolines and Marshalls.

The weevil *Aclees porosus* Pascoe attacks the terminal shoots of breadfruit in the western Carolines, causing considerable pruning and die-back on Yap. Euglenid beetles were noted on the leaves by Oakley.

An unidentified moth borer of the terminal shoots also occurs in Palau and Truk. Its work may be secondary to that of *Aclees*.

**Cabbage (Brassica)**

The moths *Hellula undalis* (Fabr.), *Prodenia litura* (Fabr.), and *Crocodolomia binotalis* Zeller were reported from Guam by Swezey; *Adoxophyes angustilineata*” by Oakley. Beardsley found *Prodenia* and *Crocodolomia* attacking Chinese cabbage in Palau.

The aleyroid *Bemisia tabaci* Gennadius was observed on cabbage on Saipan by Esaki. An agromyzid fly, probably recently introduced, was found in Chinese cabbage on Guam by Owen; and Peterson notes *Hallicus insularis* Usinger, *Aphis gossypii* Glover, and *Adoretus sinicus* Burmeister.

**Cacao (Theobroma)**

A mealybug, *Pseudococcus* sp., was observed on Rota by Oakley.

The longicorn *Nanyohammus luteosparsus* Matsushita is said by Esaki to be destructive in Palau. He also reports a scolytid beetle under bark and a weevil (?Trigonops) in young shoots.

Fullaway was informed of a large lepidopterous borer on Guam in 1911. Beardsley found a red-banded thrips on young trees on Ponape in 1953.

**Cassava (Manihot)**

Army worms are reported as occasionally damaging cassava by Esaki, who also reported the black scale *Saissetia nigra* (Nietner) as common but not
serious. The scale *Pseudaulacaspis pentagona* (Targioni) was reported on Saipan by Oakley, and it was found in 1954 in Palau, Yap, and Truk by Beardsley. Cassava is relatively free from insect attack.

**CHILI PEPPER (CAPSICUM)**

*Epilachna philippinensis* Dieke (fig. 69) may be the most important pest in the Marianas.

The scale *Pseudaulacaspis pentagona* (Targioni) was noted on Saipan, *Aphis gossypii* Glover in Truk, and a grasshopper and some lygaeid bugs on Tinian, all by Oakley.

**CITRUS**

The scale insects *Icerya aegyptiaca* (Douglas), *Coccus viridis* (Green), *Lepidosaphes groveri* (Packard), *Parlatoria proteus* (Curtis), and *Aoniella aurantii* (Maskell) are considered important by Esaki. He considers *Pseudococcus citri* (Risso), *Ferrisia virgata* (Cockerell), *Ceroplastes floridensis* Comstock, and *Parlatoria pergandii* Comstock (on Ponape) less important. *Icerya aegyptiaca* is controlled by *Rodolia*, and the mealybugs are controlled by *Cryptolaemus montrouzieri* Mulsant, which was introduced to Guam by Fullaway, and which was later established in Saipan and Palau. *Aoniella aurantii* and *Pseudococcus citri* were found on Guam in 1911 by Fullaway. *Lepidosaphes beckii* (Newman) has also been recorded from citrus. *Aspidiotus destructor* Signoret was noted on Guam by Peterson. *Aoniella inornata* McKenzie was reported from Yap and Truk by Oakley, and *Aspidiotus lataniae* Signoret, from Truk. *Icerya purchasi* Maskell is found on Guam; but it is controlled by *Rodolia cardinalis* (Mulsant) introduced in 1926. *Pseudococcus adonidum* (L.) is reported from Truk by Oakley. *Coccus hesperidum* (L.) has been recorded from Guam.

*Aphis medicaginis* Koch was found on new leaves of orange on Saipan by Oakley. The aleyrodid *Auleurocanthus spiniferus* (Quaintance) was found on Guam in 1951 by Peterson, who introduced *Prospaltella smithi* Silvestri, *Amitus hesperidum* Silvestri and *Eretnocerus serius* Silvestri for its control. The first is established and effective, according to Peterson.

The swallowtail *Papilio xuthus* L., which feeds on citrus and *Triphasia* in the larval stage, was introduced into the Marianas from Japan. The citrus leafminer, *Phyllocnistis citrella* Stainton, a gracilariid moth, is found in the southern Marianas (Guam since 1927) and Palau. It is perhaps the worst pest of citrus on Guam. *Prays endocarpa* Meyrick has been recorded from citrus fruits on Guam and *P. citri* Miller, from Palau and Yap. *Othreis fullonia* (Clerck), a noctuid, attacks citrus in the Marianas and Palau.
The Oriental fruit fly is a pest of citrus in the Marianas (see also avocado), and other species occur in the Carolines.

The weevil Dacalus sp. was reported from lemons on Yap by Oakley. A buprestid beetle, recorded as Agrilus auriventris Saunders by Esaki and as A. occipitalis (Eschscholtz) by Sweeney and Oakley, damages twigs and leaves. This buprestid, the above citrus leafminer, and a disease called gummosis have rendered most citrus on Guam unproductive.

Coconut (Cocos)

Coconut is the most important crop of Micronesia. The currently most serious pest, though only in the Palau, is Oryctes rhinoceros (L.), the coconut rhinoceros beetle. This species was not present before World War II, and was probably introduced from southern Asia in 1942. The adult bores in the crown of palms (fig. 67, b), pandanus, pineapple, sugar cane, and other plants; and the grubs feed on dead vegetable material of many sorts. The beetle has caused the destruction of over one-half the coconut palms of the Palau. Its population was enabled to build up to a very high level because of lack of natural enemies and control and as a result of conditions of war, including the killing of palms, which provided ample larval food. The damage by the beetle is now lessening, primarily as a result of gradual elimination of excess larval food in the form of logs and stumps of palms killed by the beetles. This has been accomplished largely by the control crew, who drag the logs to the rivers or sea with the aid of water buffaloes. The earlier, very large populations of the beetles are greatly diminished.

Other control methods include the introduction of natural enemies. The parasite Scolia ruficornis Fabr. from Zanzibar was proved to have been established in late 1953, after several attempts were made to introduce it during 1947 to 1949 by Compere, Williams, and Abbott; and in 1951 by Krauss. Krauss also sent the histerid Placodes ebeninus Lewis from East Africa. Gardner introduced Scolia patricia/is plebeja (Gribodo) in 1948, but there is no evidence of establishment. In 1952, the histerid Pachylist er chinensis Quesnel was introduced from Samoa to Palau, as Simmonds, Owen, and I found it fed on young grubs in Samoa. In early 1954, the histerid Leonota sp. was sent from Trinidad by Krauss. In 1951 Steinhaus went to Palau to introduce the milky disease, Bacillus popilliae, but results were inconclusive. I studied the ecology of the beetle in 1951. Centipedes, monitor lizards, certain carabid and elaterid beetles, and some birds are among other natural enemies.

Three coconut beetles of the genus Bronisla are endemic to Micronesia. B. mariana Spaeth (Planispa castaneipennis Chujo) caused very serious damage to palms on Saipan after the war; on Tinian, where there were fewer palms; and on Rota. It was probably introduced to Saipan from Yap or Truk.
after 1931. Esaki also records it from Ulithi, Fais, Sorol, Woleai, Ifalik, Faraulep, Elato, Lamotrek, and Satawal. Oakley noted it on Nomwin in 1946, and in 1952 Beardsley found it on Losap and East Fayu. It was serious on East Fayu. This beetle may be native to Yap, and may have spread eastward, then northward. It has not yet reached Guam. Lange introduced *Haackeliana*

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*Figure 67.—Insect damage to coconut palms in Palau, 1951: a, fronds skeletonized by long-horned grasshopper, *Segestes unicolor*, Melekeok, Babelthuap; b, palm killed by *Oryctes rhinoceros* and *Brentispa paluensis* (former has amputated several fronds in earlier feeding inside of growing portion, latter has fed between new leaflets, causing them to shrivel when frond opened), Ngiwal, Babelthuap.*
Brontispa Ferrière and Tetrastichus brontispa (Ferrière) to Saipan and Rota in 1948 (1950a). The latter has become established and effects fair control. Of less importance than Brontispa mariana is B. chalybeipennis (Zacher), found on Ponape, Kusaie, and most of the Marshalls. Esaki lists it from Arno, Majuro, Aur, Maloelap, Wotje, Ailuk, Mejit, Utirik, Ebon, Jaluit, Ailinglapalap, Namu, and Kwajalein. Maulik renamed it, from Namorik, B. namorikia. Recently it has been noted on Mili and Kili. Esaki suggests that these species may not be native to Micronesia, as he found them only on coconut palms, and as he found them without parasites. However, they have not been found elsewhere. They are normally not serious pests, except when they spread to new areas. On Ponape I found a dead B. chalybeipennis in a Pandanus axil under Esorrhiza and Ponapea palms, with no coconut palms within a considerable distance. In the shaded forest areas the hispids have low populations. The third species, B. palauensis (Esaki and Chujo) = B. yoshinoi Barber, is found only in Palau (fig. 67, b), and does little damage, except that it sometimes helps Oryctes rhinoceros to kill palms.

All three Brontispa are extremely narrow and flattened and about 7 to 9 mm. long. The first, B. mariana, is brown; B. chalybeipennis is steel blue to bluish green, and B. palauensis is blue. Both larvae and adults feed between the still-folded upper surfaces of the leaflets of the new fronds. The adults leave when the fronds open out. The earwig Cheilocheles morio (Fabr.) is a predator of members of this genus.

The coconut scale Aspidiotus destructor Signoret has, from time to time, done serious damage to coconut palms in Micronesia. Esaki states that the scale was introduced to Yap from the Philippines in 1892 and that the most serious damage in Yap was done during 1905 to 1906. About 1899 it was introduced from Yap to Palau, where it caused serious losses in 1908. In 1911 it was carried from Yap to Saipan, where the worst damage was done in 1915 to 1916. Much damage was done on Rota in 1920. It was introduced to Guam from Saipan at about the same time, or possibly as early as 1911; and severe damage occurred in 1924 to 1925. A minute coccinellid beetle, Telsimia nitida Chapin, native in the Marianas, proved a useful predator on this scale, and Vandenberg mentions the parasites Aphelinus and Aspidiotiphagus on Guam in 1925. Ponape received this coconut scale during German times, and serious damage occurred in 1938 to 1939. In 1939, Esaki introduced Telsimia nitida from Saipan to Ponape. Maehler found a Cybocephalus predator in Palau in 1948, and Beardsley found it in Ponape in 1954, as well as an Aphytis parasite in Palau, Truk, and Ponape.

Furcaspis oceanica Lindinger, the red coconut scale, is endemic to Micronesia, being widely distributed in the Marshalls and Carolines. In its native areas it is normally not a serious pest, occuring primarily on the bases of the petioles, and rarely on the leaflets. The scale was first found in Saipan in
1943, by Fujishima, and it later became very serious. In 1948 it completely covered the fronds of many trees on Saipan. Doult (1950b) discovered the parasite Anabrolepis oceanica in Ulithi in 1948 and introduced it to Saipan. The scale also occurs on Exorrhiza ponapensis and Ponapea ledemanni in Ponape, Exorrhiza carolinensis in Truk, and on Nypa fruticans and Pandanus spp. *E. ponapensis* is said by Esaki to be the original host plant.

Other scale insects reported from coconut include *Lepidosaphes duponti* Green on Saipan and Guam; *L. meegregori* Banks on Guam and Tinian; *Lepidosaphes* sp. in Palau, and *Icerya aegyptiaca* (Douglas) in Ulithi (all Oakley); *Lepidosaphes* sp. on Guam in 1911 (Fullaway); *Aonidiella inornata* McKenzie in Palau [and Truk], *Pseudococcus saipanensis* Shiraiwa in the Marianas, Carolines, and Marshalls; and *P. oceanicus* Takahashi in Truk (Esaki); *P. cocosis* on Guam (Fullaway); and *Chrysomphalus* sp.

The aleyrodid *Aleurocanthus palaenensis* Kuwana is found on coconut in Palau. Other coconut pests include the long-horned grasshopper *Segestes unicolor* Redtenbacher which feeds on the leaflets of coconut palm fronds, sometimes leaving only the midribs (fig. 67, a). It may cause great damage locally. It occurs in Palau and is also a pest in New Britain. Another long-horned grasshopper, *Phisis pectinata* (Guerin) is a widely distributed feeder on coconut-frond leaflets. Esaki records it from Saipan, Palau, Yap, Truk, Ponape, Kusaie, Jaluit, and Wotje. Locusts which feed on coconut leaflets in addition to other plants include several species of the genus *Valanga* in the Marianas and the western and central Carolines.

Of several species of stick insects which feed on coconut or other plants, the most important are members of the genus *Acanthagraefferia*. Esaki records *A. denticulata* (Redtenbacher) from Pagan, Saipan, Rota, and Guam, stating that it probably occurs on the islands between Pagan and Saipan. He also records *A. modesta* Günther from Truk, and possibly the same species or *Graeffia coccophaga* Newport, from Ponape.

The coconut moths *Agonoxena pyrogramma* Meyrick and *A. argaula* Meyrick have been recorded from Guam or the Carolines, but they may be misidentifications. Swezey reared *Macrocentrus pallidus* Fullaway from *Agonoxena "pyrogramma,"* which may be the most serious coconut pest currently on Guam.

The coconut weevil, *Diocalandra frumenti* (Fabr.) was common on Guam by 1936, and it was found in Ulithi, Palau, and Truk in 1946 by Oakley. The sugar-cane weevil, *Rhabdoscelus obscurus* (Boisduval), which bores in damaged coconut palms, is widespread. It was found on Guam in 1911 by Fullaway.

A pentatomid bug was found in abundance on coconut flowers on Saipan by Oakley. Some Fulgoroidea (Cixiidae and Derbidae) feed on coconut in the Carolines and Marshalls but are not important, according to Esaki.
The June beetle *Holotrichia mindanaoana* (Brenske) feeds on coconut fronds on Guam, according to Oakley. Oedemerid beetles, *Sessinia* and *Eobia*, known as toddy beetles, feed on the male flowers of the coconut palms and are abundant and widespread. *Caroliniella*, and perhaps another genus of cerambycids, feeds in the petiole bases in the Carolines. The copra beetle *Necrobia rufipes* (DeGeer) is a widespread pest.

The termite *Nasutitermes brevirostris* (Oshima) frequently builds its nest on the side of a living palm and makes a covered passage to the crown (fig. 24, a).

**COFFEE (COFFEA)**

The scales *Ferrisia virgata* (Cockerell), *Ischnaspis longirostris* (Signoret), and *Pulvinaria psidii* Maskell were reported on Saipan and Ponape; *Pseudococcus brevipes* (Cockerell) and *Pseudococcus* sp. were recorded from Guam; *P. citri* (Risso) and *Coccus viridis* (Green), from Saipan (Oakley); and *Saissetia hemisphaerica* (Targioni), *Pulvinaria psidii*, and *Pseudococcus* sp. were found by Fullaway on Guam in 1911.

A gracillariid moth was recorded from the base of clusters of young berries by Esaki.

A scolytid, *Stephanoderes hampei* (Ferrière), was found by Oakley to be seriously damaging coffee berries on Saipan in 1946; but it was not found on Rota or Guam, and was less abundant on Ponape.

**COTTON (GOSSYPiUM)**

It is possible that cotton is no longer planted in Micronesia, though the Japanese did plant it on Saipan, Palau, Yap, and Ponape; and some has been grown on Guam. The pink bollworm *Pectinophora gossypiella* (Saunders) was reported as common on Saipan by Esaki. *P. scutigera* (Holdaway) was reported by Oakley from cotton and *Thespesia*. *Earias fabia* (Stoll) was said to be important in Saipan and Palau (Esaki) and Guam (Fullaway), and *E. cupreociridis* (Walker) and *Cosmophila eosa* Hbn. *Anomis* sp.] were reported from Palau. The pyralid *Diaphania indica* (Saunders) was reported by Esaki. *Prodenia litura* (Fabr.) is also present.

The pyrrhocorid *Dysdercus megalopygus* Breddin was reported from Palau and Yap; the pentatomid *Nezara viridula* Linn., from Palau; the coreid *Leptoglossus membranaceus* [australis (Fabr.)] and the lygaeid *Oxyacarus bicolor* (Stål), from Saipan and Palau, by Esaki; and *O. bicolor* (as *O. lugubris*), from Guam by Oakley.

*Aphis gossypii* Glover, *Ferrisia virgata* (Cockerell), and *Saissetia nigra* (Nieter) were recorded by Fullaway and Esaki. Species of *Pseudococcus*, including *P. citri* (Risso), and *Asterolecanium* sp., have also been recorded. *Coccus elongatus* (Signoret) was observed on Timian by Oakley.
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The anthribid Aracercus fasciculatus (DeGeer) and a nitidulid were reported by Esaki as attacking bolls.

cowpeas (Vigna)

The moth Acrocercops sp. is a leaf miner found on Saipan and Guam by Oakley. The phalaenid defoliator Anticarsia irrorata (Fabr.) was also found on Guam by Oakley, and by Swezey.

Aphis medicaginis Koch was found on Saipan by Oakley, as well as elsewhere on other hosts. Pseudaulacaspis pentagona (Targioni) was found on Saipan by Oakley.

Prodenia litura (Fabr.) was noted on Vigna marina in the Marshalls by Townes (fig. 65, b).

Cucurbit (Cucurbitaceae)

Aphis gossypii Glover, injurious to cucurbits and widely distributed in Micronesia, was found on Guam in 1911. Coccinellid predators of the genera Coelophora and Coccinella are present. The leaf-footed plant bug, Leptoglossus membranaceus [australis (Fabr.)] was reported by Esaki from western Micronesia and Ponape, and by Usinger and Oakley from Guam. Megymenura affine Boisduval was noted in Truk in February 1948 by Maehler. A small lygaeid was reported from Tinian by Oakley, as well as Ferrisia virgata (Cockerell), Nezara viridula (L.) and Pseudococcus citri (Risso) were reported from Truk, and Icerya aegyptiaca (Douglas), from the Marshalls by Oakley. The mirid Halticus tibialis Reuter is destructive in eastern Micronesia and the Marianas. Both H. tibialis and H. insularis Usinger occur on Guam. Empoasca pityiensis Metcalfe was noted on Guam by Peterson.

Several cucumber beetles are harmful in western Micronesia. Aulacophora quadriraculata (Fabr.) is in the Marianas, and Esaki suspects that it was introduced to Saipan from Samoa during the German regime. A. similis (Olivier), A. marginalis Chapuis, and A. flavomarginata Duivier are recorded from Palau; and A. similis entered Guam in 1951. One species occurs on Yap, but none is found on Truk or eastward.

The melon fly Dacus (Strumeta) cucurbitae Coquillet was introduced to Guam in 1936 or slightly earlier. It did not occur on other islands of Micronesia until at least 1942. The Japanese, on taking Guam in December 1941, imposed a quarantine; but the fly was found on Saipan in July 1943, on Tinian a few days later, and on Rota the following month, when it was also intercepted at Yokohama as maggots in melons. Dacus dorsalis attacks melons rarely.
The pyralid *Diaphania indica* (Saunders) was reported by Esaki as widespread and by Swezey for Guam. The army worm *Prodenia litura* (Fabr.) and a geometrid were recorded as occasional pests by Esaki.

**Eggplant** (Solanum)

The phytophagous lady beetle *Epilachna philippinensis* Dieke, which attacks solanaceous plants (fig. 69) is destructive on Guam, Saipan, Tinian, and Rota. It was first found in November 1948, by Maehler, on *Cestrum diurnum* growing along the Agana air strip. *Adorectus* also causes damage to the foliage of eggplant.

A number of minor pests are recorded from the Marianas by Esaki and Oakley: *Myaeus persicarum* (Sulzer), *Ferrisia virgata* (Cockerell) *Saissetia nigra* (Nietner), and *S. hemisphaerica* (Targioni), *Leptocentrus taurus* (Fabr.), *Nezara viridula* (L.), *Conocephalus* sp. and a thrips. The cutworm *Chrysodeixis chalcites* (Esper) was found in abundance on Guam by Oakley, but it was parasitized by the ichneumonid *Echthromorpha conopleura* Krieger. Esaki recorded *Pinnaspis strachani* (Cooley) from Ponape. *Aphis gossypii* Glover, and *Leptoglossus australis* (Fabr.) were noted on Guam by Swezey and Usinger, and *Empeasca pitiensis* Metcalf was noted by Peterson.

**Fig** (Ficus carica)

The pyraustid moth *Sylepta derogata* (Fabr.) was reported by Oakley to defoliate fig seedlings on Guam. It is parasitized by *Echthromorpha conopleura* Krieger, an ichneumonid. The leafhopper *Tartessus swezeyi* Metcalf feeds on *Ficus*.

**Guava** (Psidium)

The olethreutid *Spilonota holotephrus* Meyrick was noted on Guam by Swezey in 1936. *Dacus dorsalis* is also a pest of guava in the Marianas.

**Kapok** (Ceiba)

The black scale *Saissetia nigra* (Nietner) has been recorded; and Fullaway noted it from Guam in 1911, with the parasite *Tomocera* sp.

**Maize** (Zea)

The migratory locust *Locusta migratoria danica* L. is a serious pest on Saipan (fig. 68). It also occurs on other Mariana Islands and on Truk, Kwajalein, and Majuro. *Valanga excavata* (Stål) occurs in the southern Marianas, and *Aioloopus tamulus* (Fabr.) is another locust on maize in the Marianas.
The "European corn borer" *Pyrausta nubilalis* (Hübner), common in the Marianas (fig. 68), was recorded from Guam in 1911. The ichneumonid parasite *Zaleptopygus flavo-orbitalis* (Cameron) ("Cromastus") and the tachinid *Lydella stabulans grisescens* Rob.-Desv. ("Ceromasia lepida," "Masicera senilis") were introduced to Guam from Japan by Vandenberg in 1931. The former also attacks other leaf-rolling moths on Guam, according to Swezey, but the latter is said by Peterson to have died out on Guam, Saipan, and Tinian.

![Figure 68](image_url)

The ichneumonid parasite *Exeristes roborator* (Fabr.) has been introduced to Guam several times but apparently has not become established. Other parasites have recently been sent to Guam from the Moorestown, New Jersey, laboratories. The "corn earworm" *Heliothis armigera* (Hübner) is widely distributed and harmful (fig. 68). The pyraustid moth *Marasmia trapezalis* (Guenée) is a maize leafroller, found on Guam in 1911 by Fullaway and on Saipan, Tinian, and Rota by Oakley. Swezey reared *Apanteles guamensis* (Holmgren) from it on Guam. The cotton moth *Prodenia litura* (Fabr.) is also recorded (fig. 65, b). The butterfly *Melanitis leda* (L.) was reared on Guam in 1911 by Fullaway.

The "corn leafhopper" *Peregrinus maidis* (Ashmead) is common in Saipan and Palau but not very serious, according to Esaki. Fullaway recorded it from Guam in 1911, and Oakley has found it in Yap. It is controlled by the bug *Cyrthorhinus lividipennis* Reuter and also, on Guam, by the mymarid egg...
parasite *Anagrus flavescens* Waterhouse. *Cicadulina bipunctella* (Matsumura) occurs on Guam.

*Aphis maidis* Fitch is widespread. Predators are coccinellids *Coccinella arcurata* (Fabr.) and *Coeolophora inaequalis* (Fabr.), the larvae of *Syrphus pusillus* Macquart, and a hemerobid.

The pentatomid *Nesara viridula* (L.) was noticed on Truk, and the mirid *Creontiades pallidifer* (Walker) was found on Guam by Oakley.

The June beetle *Holotrichia mindanaoana* (Brenske) attacks the roots of maize in the larval stage and feeds on the plant as an adult (Guam and Saipan) and a related species occurs in Palau. *Anomala sulcatula* Burmeister attacks maize in the Marianas. The Chinese rose beetle *Adoretus*, both larva and adult, is a serious pest on Guam, Saipan, Tinian, and Rota. The anthribid *Araecerus fasciculatus* (DeGeer) and the rice weevil *Calandra oryzae* (L.) were noted by Fullaway in dry maize on Guam in 1911.

The agromyzid fly *Pseudonapomyza spicata* (Malloch) is a maize leaf-miner on Guam and Saipan. It is parasitized by *Hemiptarsenus semialbicollis* (Girault).

**Mango (Mangifera)**

The scale insects *Vinsonia stellifera* Westwood, *Coccus mangiferae* Green, *C. acuminatus* Green, *Ceroplastes floridensis* Comstock, *Phenacaspis indicans* Banks, *Ishnaspis longirostris* (Signoret), *Chrysomphalus aonidium* (L.), and *Aspidiotus destructor* Signoret were reported by Esaki. *Lepidosaphes mcgregori* Banks was noted on Guam by Swezey. Oakley reported *Asterolecanium pustulans* (Cockerell) for Guam; *Ceroplastes rubens* Maskell, for Guam and Saipan. *Ferrisia* is known from mango; Fullaway noted *Pseudococcus* sp. on the roots; and tropiduchid and derbid hoppers were mentioned by Esaki.

*Heliothrips haemorrhoidalis* Bouček was reported on young foliage by Esaki.

The Oriental fruit fly *Dacus (Strumeta) dorsalis* Hendel is an important pest in the Marianas (see avocado). Oakley found 50 percent infestation on Rota and 25 percent on Saipan and Tinian. *Dacus (Strumeta) frauenfeldi* Schiner was reported in Yap and Truk by Oakley; and a species noted from Ponape by Esaki may attack mango.

Leaf beetles of the genera *Rhypana* or *Phytorus* are frequently abundant on mango on most of the high island groups, though they also feed on other trees. Damage is sometimes very severe. The longicorn beetle *Niphohannus korolensis* Matsushita is said by Esaki to bore in mango stems in Palau.

The noctuid moth *Othisis fullonia* (Clerck) is recorded by Esaki, and *Bombotelus jocosatrix* (Guénée) is reported for Guam by Swezey.
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OKRA (HIBISCUS)

*Aphis gossypii* was reported for Saipan and Tinian, together with a coccinellid predator and a predaceous syrphid larva, possibly *Syrphus pusillus* Macquart, by Oakley. *Baris fabia* (Stoll), an agrotid, was observed on Tinian and Guam by Oakley. *Empoasca pilensis* Metcalf and *Adoretus sinicus* Burmeister were noted on Guam by Peterson. Beardsley notes *Anomis* and *Baris* in Palau.

ONION (ALLIUM)

*Thrips tabaci* Lindeman, the onion thrips, is a pest in Saipan and Palau, according to Esaki.

The cotton moth *Prodenia litura* (Fabr.) also attacks onions.

ORNAMENTAL PLANTS

The Chinese rose beetle, *Adoretus sinicus* Burmeister, is a serious pest of many ornamentals on Guam, and *Adoretus* was found in Palau in 1947. *A. sinicus* had reached Saipan, Tinian, and Rota by 1953. It has a wide range of host plants and is particularly harmful to rose and *Acalypha*. The scoliid *Camposomeris marginella modesta* (Smith) was introduced to Guam from Hawaii for control of the beetle in 1950, and it is established. An *Adoretus* from Japan was intercepted in quarantine in Guam in 1911 by Fullaway. *Protactia fusca* (Herbst), a cetonid, was found established on Guam in January 1954 by Peterson and Liming. The cetonid is a flower feeder and very rarely eats foliage.

The aleurocid *Aleurocanthus spiniferus* (Quaintance) was found on rose (*Rosa*) on Guam in 1951 by Peterson (see citrus).

*Croton* (*Codiaeum*) is attacked by the scales *Icerya aegyptiaca* (Douglas), *Pseudococcus citri* (Risso), and *Lepidosaphes tokionia* (Kuwana); and cycads (*Cycas*) are attacked by *Cerothrips rubens* Maskell, *Lepidosaphes euryae* Kuwana, *L. cocculi* Green, and *Parlatoria proteus* Curtis, according to Esaki. *Icerya purchasi* Maskell is present on Guam, but is controlled by *Rodolia*.

*Morinda* is attacked by *Saissetia* sp.; *Erythrina*, by *Saissetia oleae* (Bernard).

PANDANUS

*Oryctes rhinoceros* (L.) bores in the crown of *Pandanus* in Palau, killing the plants.

A small moth larva cuts oval holes in the leaves of *Pandanus*. Mealybugs are common and several gryllacridid grasshoppers, particularly *Salomona carolina* Willense, feed on the leaves. Large stick insects were found doing extensive feeding in Kusaie by Gates Clarke and on Ebon in the Marshalls by Beardsley. The one found in the Marshalls is *Megacrania batesi* Kirby.
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PAPAYA (CARICA)

*Aspidiotus destructor* Signoret was reported by Esaki and *Aonidiella comperei* McKenzie by Oakley. Both have coccinellid predators. The Oriental fruit fly was reported on Tinian by Oakley.

PEANUT (ARACHIS)

The mealybug *Ferrisia* sp. and the scale *Saissetia* sp. were noted on Guam in 1911 by Fullaway. *Aphis laburni* Kalt was reported by Esaki.

PIGEON PEA (CAJANUS)

The butterfly *Lampides boeticus* (L.) and the moth *Maruca testulalis* (Geyer) were reported on Guam by Oakley, who also noted an unknown leaf tier, a coreid bug, and a moth larva in the Marianas. The scale *Saissetia* sp. is also recorded.

PINEAPPLE (ANANAS)

*Pseudococcus brevipes* (Cockerell), the pineapple mealybug, is recorded from the southern Marianas by Esaki and Oakley, from Palau by Takahashi, and from Truk by Oakley. It is said to be controlled on Guam by the coccinellid *Cryptolaemus montrouzieri* Mulsant, introduced in 1911, and by *Nephus* sp. The scale *Chrysomphalus bromiliae* Leonardi (*anassarum*) was recorded by Esaki.

RADISH (RAPANUS)

The cabbage webworm *Hellula undalis* (Fabr.), a pyralid, was noted on Guam in 1911 by Fullaway, and on Tinian in 1946 by Hadden (Oakley). *Prodenia litura* (Fabr.) was incriminated by Esaki. The aphid *Rhopalosiphum pseudobrassicae* (Davis) was reported for Guam by Oakley.

RICE (ORYZA)

Rice cultivation has been attempted sparingly in Rota, Guam (fig. 17, a), Palau, and Ponape and has almost been abandoned. It failed in Palau because of the rice bug *Leptocorisa acuta* (Thunberg), which is widely distributed (Esaki). This bug was first noted on Guam in 1918. The pentatomid *Nezara viridula* (L.) was reported by Esaki and Oakley. *Creontiades* sp. was noted for Guam by Swezey.

Swezey found the leafhoppers *Nephotettix bipunctatus* (Fabr.) and *Nilaparvata lugens* (Stål) in abundance on Guam rice in 1936. The predaceous bug *Cyrtorhinus lividipennis* Reuter probably attacks both of these leafhoppers.
The sugar-cane mealybug *Trionymus sacchari* (Cockerell) was noticed on Rota and Ponape (Oakley). *Pseudococcus* sp. was noted on Guam in 1911 by Fullaway. The fulgoroid *Sogata furcifera* Horvath was reported on Ponape by Esaki, as well as some delphacids. The grasshoppers *Aiolopus tamulus* (Fabr.) and *Euconocephalus* sp. were observed on Rota and Guam by Swezey and Oakley; and *Euconocephalus* sp. and *Oxya* sp. were noted on Ponape by Oakley.

The pyralid *Cnaphalocrocis medinalis* (Guenée) was reported as common by Esaki. Gelechiid moth larvae and the leafroller *Susumia exigua* (Butler) were observed on Guam, and *S. exigua* was found on Rota. Of parasites of *S. exigua*, *Apanteles guamensis* (Holmgren) was noted by Swezey on Guam and *Brachymera* sp. was associated on Guam and seen on Rota, by Oakley. *Spodoptera maurita* (Boisduval) has also been recorded, as well as *Nymphula fluctuosalis* Zeller and *Tatobatus biannulalis* (Walker). The butterfly *Melanitis leda* (L.), found on Guam, attacks rice in India.

The rice weevil *Calandra oryzae* (L.), which attacks stored rice on Guam, was present in 1911.

**Sorghum**

*Aphis maidis* Fitch was found on Tinian and Guam, accompanied by coccinellid predators *Coelophora* and *Coccinella*, and also on Truk, by Oakley. The corn leafhopper, *Peregrinus maidis* (Ashmead) was reported for Guam in 1911 by Fullaway. *Pseudococcus boninensis* (Kuwana) and *Neomaskellia bergii* (Signoret) were noted in Truk by Oakley.

The European corn borer and another moth were noticed on Tinian by Oakley.

**Soursop and Sweet Sor (Annona)**

The coccids *Saissetia nigra* (Nietner), *S. olearia* (Bernard), *S. hemisphaerica* (Targioni), *Pulvinaria psidii* Maskell, *Coccus elongatus* (Signoret) and some mealybugs were reported by Esaki. *Pseudococcus* sp. was reported from Palau by Oakley. *Ferrisia* also feeds on soursop.

A fruit fly, perhaps *Dacus dorsalis* Hendel, was found by Oakley in ripe soursop fruits on Saipan.

**Sugar Cane (Saccharum)**

The sugar-cane borer *Rhabdoscelus obscurus* (Boisduval), a widespread and serious pest, was found on Guam in 1911 by Fullaway. The tachinid parasite *Microcromasia sphenophori* (Villeneuve) was introduced to Guam from Hawaii in 1926 and 1927 by Vandenheuvel, and from Guam to Saipan.
in 1928; but it died out in Guam in 1929 and was never established in Saipan, according to Esaki.

The migratory locust *Locusta migratoria danica* L. was reported by Oakley for Saipan, Tinian, Rota, and Guam. *Oxya intricata* (Stål) was noted from Truk and *Oxya* sp. from Ponape, by Oakley.

A sugar-cane leafhopper, *Perkinsiella thompsoni* Muir, is only moderately abundant. The myrnarid *Paranagrus optabilis* Perkins and an *Ootetarstichus* are established in Guam as its parasites, according to Swezey.

The sugar-cane mealybug *Trionyxus sacchari* (Cockerell) was noted from Guam in 1911 by Fullaway, Esaki also reported the pineapple mealybug *Pseudococcus brevipes* (Cockerell), the sugar-cane white fly *Neomaskeilia borgi* (Signoret) from western Micronesia, and the derbid *Proutista maesta* (Westwood). Oakley reported the *Trionyxus* from Truk, and Swezey noted all four from Guam, as well as *Pseudococcus boninis* (Kuwana) and its parasite *Aphycus terryi* Fullaway.

The borer *Grapholitha schistaceana* (Snell, v. Voll.) and other pyralids were recorded by Esaki. The former may have been introduced from Formosa. The Philippine parasite *Trichogramma chilonis* Ishii, introduced from Japan by Konishi in 1935, proved effective in control. According to Esaki it had been introduced earlier from the Philippines to Japan as a possible natural enemy of the rice-stem borer (*Chilo simplex* Butler).

The June beetle *Anomalia sulcata* Burmeister was found by Swezey on Guam in 1936. Esaki failed to find it in Saipan and Tinian in 1936, but it was introduced to Saipan about that time, as one was taken in 1935 and another in 1936, both by other Japanese. The beetle, which bred extensively in farm-yard manure applied in the cane fields, had become a serious pest on Rota by 1937; and by 1939 it had become equally serious on Saipan. The grubs damaged the newly planted cane shoots. Konishi introduced *Campsoneris annulata* (Fabr.) to Saipan from Manila in 1940 for control, and it had become abundant by the following year.

The dynastid *Anarmonotum rufum* Arrow bores in cane, but it is known only from Palau and it is rare. A false wire worm of the tenebrionid genus *Gonocephalum* was reported from the Mariannas by Esaki.

**SWEET POTATO (IPOMOEA)**

The common sweet potato weevil *Cylas formicarins* Fabr. is widespread in Micronesia, but it is absent on many atolls. The weevil *Euscepes postfasciatus* (Fairmaire) was not mentioned by Esaki, but it was recorded from Guam by Fullaway in 1911, and from Rota, Guam, Palau, and the central Carolines and Ponape by Oakley in 1946. It was also found on Saipan by Maceiler in 1949. A weevil, *Dacalus* sp., was found abundant and injurious to vines on Rota, Yap, Palau, and Woleai by Oakley, who also reported the
weevil *Trigonops* sp. on leaves on Rota. A weevil of the genus *Sphaeropterus* was reported by Maehler as causing damage in the Palau.

The scale *Pulvinaria* sp. was found on sweet potato. The pentatomid *Brachypalpus* sp. was noticed on leaves on Rota by Oakley, and the mirid bug *Hallicus tibialis* Reuter was reported as widespread by Esaki. The mirid bug *Creontiades straminus* (Walker) was found in small numbers on leaves on Rota and in the central Carolines by Oakley.

The gracilariid moth *Acrocercops* sp. was noted in the Carolines by Oakley, with a parasite, *Apanteles* sp. in Palau. Beardsley noted *Pachyserca nipponalis* (Walker) in Palau. The sphyngid *Herse convolutus* (L.) and the nymphalid butterfly *Precis villova* (Fabr.) were reported by Esaki. Swezey noted *Trichogramma* sp. parasitizing *H. convolutus*. *Prodenia litura* (Fabr.) was noted in Truk by Townes, and in Ponape and Jaluit by Oakley. The nymphalid *Hypolimnas bolina* (L.) was reported in the Carolines by Oakley.

The tortoise beetle *Cassida circumdata* Fabr. was noted on Guam in 1947 by Maehler and in 1953 in Truk and Palau by Beardsley. A gallerucid, *Aulacophora* sp., was noticed in Yap by Oakley.

**TARO (COLOCASIA AND OTHER GENERA)**

The taro leafhopper *Tarnophagus prosferina* (Kirkaldy) was recorded by Esaki from Palau, Truk, Ponape, and Kusaie, and by Oakley from Rota, Guam, Kapingamarangi, and Majuro. Vandenberg noted it on Guam in 1927. Its eggs are fed upon by the mirid *Cyriochinus fulvus* Knight, which was introduced successfully in 1947 to Guam and the Carolines. On Guam, *Tarnophagus* has a dryinid parasite, *Haplogonatopus vitiensis* Perkins, with the encyrtid hyperparasite *Echthroragonatopus exuioxus* Perkins. *Aphis gossypii* Glover, the cotton aphid, is known from Guam. Probably the same species was noted on Saipan, Rota, the Carolines, and Ailinglapalap by Oakley, who reported coccinellid and syrphid predators. Swezey noted an *Aphelinus* parasite. The fulgoroid *Phaecephalus* sp. was noted in the Hall Islands by Oakley. *Lamaena caliginea* (Stål), *Empoasca pitiiensis* Metcalf, and *Aphis gossypii* Glover were noted on Guam by Peterson. *Pseudococcus* sp., from the Carolines and Likiep, and *Iscaea aegyptica* (Douglas) from the Carolines, were noted by Oakley.

The cotton moth *Prodenia litura* (Fabr.) was noted on Guam in 1927 by Vandenberg, and in the eastern Carolines by Townes and Oakley. The sphingids *Hippotion* sp. and *Theretra* spp. were recorded from Palau by Esaki.

**TERMINALIA**

*Phytotus* sp., *Trigonops* spp., *Adoretus sinicus* Burmeister, *Selenothrips rubricinctus* (Giard), a skipper, and some undetermined moths have been
noted on Guam by Peterson. The fruit of *T. catappa* is one of the favorite hosts of *Dacus dorsalis* Hendel. Townes noted *Bodanaia* larvae on Likiep (fig. 66, b).

**Tobacco (Nicotiana)**

The mirid bug *Cyrtopeltis tennis* Reuter was noted on tobacco on Guam in 1911 by Fullaway, and in the Marianas and Carolines in 1946 by Oakley. *C. nicotianae* (Koningsberger) was found on Guam by Usinger. Grasshoppers were reported by Swezey.

The noctuid moths *Heliothis assulta* Guenée and *Prodenia litura* (Fabr.) were reported as destructive by Esaki and Swezey. *Heliothis armigera* (Hübner) was noted from Guam by Fullaway in 1911 and from Rota in 1946 by Oakley.

**Tomato (Lycopersicon)**

The girdling bug *Cyrtopeltis tennis* Reuter was reported from Saipan, Rota, and Guam by Oakley. *Aphis gossypii* Glover and *Empoasca pilicinis* Metcalf have been noted on Guam by Peterson.

The cotton moth *Prodenia litura* (Fabr.) was reported from Saipan and Tinian by Oakley, and the corn earworm *Heliothis armigera* (Hübner) was reported from Guam by Peterson. Beardsley found *Prodenia* and *Chrysoilex chalcites* (Esper) in Palau.

The lady beetle *Epilachna philippinensis* Dieke (fig. 69) is one of the worst pests on Guam, and also occurs on Saipan, Tinian, and Rota. The parasitic fly *Paradexoides epilachnæ* Aldrich was introduced in 1950 and 1952, but has not been recovered. The melon fly, *Dacus cucurbitae* Coquillett does damage on Guam. *D. dorsalis* rarely attacks tomato.

**Yams (Dioscorea)**

The scale *Aspidiotus destructor* Signoret was reported by Oakley.

The tortricid *Adoxophyes angustilineata,* and the moths *Chrysoideis chalcites* (Esper) and *Diaphania indica* (Saunders) are mentioned by Oakley.

**Beneficial Insects**

Of general predators, mantids were lacking in Micronesia, except for one species found in Palau; but recently at least three kinds have been introduced to Guam and one to Saipan and Truk. Asilid flies are moderately represented in the Marianas and Palau Islands, but elsewhere are largely restricted to beach-inhabiting species. Dragonflies and damselflies are moderately represented on all islands. Syrphid flies play an active role in Guam, Palau and elsewhere, as do green and brown lacewings.
Parasites, and some coccinellid or other beetle predators, when known or established, have been mentioned above with their pest hosts.

Several insects which feed on the weed Lantana camara were sent to Ponape from Hawaii in 1948 and 1949. Of these, the tingid Teleonemia scrupulosa Stål and the olothetaeid moth Epinotia lantana (Busck) became established and are doing well in controlling lantana.

Figure 69.—Epilachna philippinensis and damage to tomato, Guam. (U. S. Navy.)
INSECTS OF MEDICAL AND VETERINARY IMPORTANCE

As to insects of medical importance, the vectors of many serious insect-borne diseases are fortunately lacking; and the importance of quarantines in keeping them excluded cannot be overestimated. At the present time, malaria, yellow fever, the various sleeping sicknesses, bubonic plague, typhus, and other such diseases are probably absent, though Philippine laborers undoubtedly have latent malaria. Vectors of malaria and yellow fever are present. One species of *Anopheles* (*A. subpictus* Grassi) was found on Guam in the village of Inarajan, southern Guam in March 1948 by an Army Survey Team. Among other mosquitoes, there are several native species of *Aedes*, in addition to the introduced *A. aegypti* (L.) which could carry yellow fever. Dengue fever is present, and occasionally is rather common. It is carried by *A. aegypti* and *A. albopictus* (Skuse). Type B encephalitis has occurred on Guam in recent years, and it may be transmitted by *Culex quinquefasciatus* Say and *Aedes albopictus*. *A. pandani* Stone, on Guam, is a particularly annoying day biter. Reeves and Maehler report collecting several thousand off a man’s back in less than an hour. *A. albopictus* is said to breed in empty giant African snail shells on Guam. *Culex quinquefasciatus* is widely distributed, and is the vector for filariasis, which is present but which rarely develops into conspicuous elephantiasis in Micronesia. Introduction of the cannibal mosquitoes *Toxorhynchites brevipalpus* and *T. splendens* from Honolulu to Guam for mosquito control was made in early 1954 by Peterson. Mosquito breeding situations are discussed above under ecology.

The Oriental bedbug, *Cimex hemipterus* (Fabr.) is present, but it is apparently not very abundant. Fleas are present, but rarely become numerous. The common sandy and damp environment of villages appears to be unfavorable for the breeding of fleas, though it favors flies. Dog and cat fleas are present, but the human flea appears to be rare. The human louse and pubic louse are present.

The small biting gnat *Culicoides pellionensis* Tokunaga, at times abundant on Peleliu, breeds in mangrove mud (Dorsey, 1947). It is said to have been introduced to Truk during or just after the war. The bites are painful and annoying, but no disease is known to be transmitted by this fly. Another species, *C. esakii* Tokunaga, present on Ponape in the damp forests, breeds in mountain streams. A large horsefly (*Tabanus*) is present in Palau, and one has been found recently on Guam. The stable fly *Stomoxys calcitrans* (L.,inn.) is present on Guam.

Various filth flies are of significance to public health and become abundant where breeding media are not destroyed. Those considered most important on Guam in 1945 to 1946 (Bohart and Gressitt, 1951) were *Chrysomyia megacephala* (Fabr.) *Musca sorbens* Wiedemann (fig. 70), *M. vicina* Macquart,
Atherigona orientalis (Schiner), Sarcophaga ruficornis Fabr., Lucilia cuprina Wiedemann, Ophyra chalcogaster Wiedemann, Sarcophaga dux Thompson, S. knabi Parker, S. grossiti Hall and Bohart, and Physiphora aenea (Fabr.). Chrysomyia megacephala and Sarcophaga grossiti were observed on human sores or cuts. Additional species are listed in the section on ecology.

Figure 70.—Houseflies (Musca sorbens) on opened green coconuts; these flies breed in coconuts much less commonly than do Atherigona and Scholastica. (Townes, 1946.)

The copra itch mite Pyremotes ventricosus (Newman) is widespread and common and causes irritation to tender skin. Other itch mites and chiggers are present, some of them being limited to sandy or coral-rock areas. One is common on the high coral islands of Palau, another, in compost and debris in coral sand village areas on Babelthuap and in Truk. Some of these are harvest mites (Trombicula spp.), of which one is also recorded from Yap.

The most prevalent and annoying stinging insects in Micronesia are the wasps—Kopalidia marginata zundaica v. d. Veicht in the Mariana and Palau Islands, and Polistes spp.—and the ants Solenopsis geminata rufa Jerdon (fire ant), Odontomachus haematoda (L.), and Camponotus spp.

A black widow spider, Latrodectus geometricus Koch, has been introduced to Guam and several other parts of Micronesia. Large centipedes, Scolopendra subspinipes Leach and S. morsitans L., are common and widespread. A very large millipede, Polyconoceras callosus Karsch, is common in damp places in parts of Palau and a similar kind is common in Truk (fig. 38). They have a brown acid secretion which is squirited from glands and is painful to tender skin and dangerous to eyes. The scorpions Isometrus maculatus (DeGeer) and Hormurus australasiae (Fabr.) are widely distributed, but they rarely bother people.
Gressitt—Introduction

Oedemerid beetles of the genera Eobia and Sessinia, called toddy beetles, are widespread and commonly attracted to lights. Many people suffer severe skin irritation on contact with the bodies of these beetles, which contain a substance in the nature of cantharidin. When ingested with toddy in which a beetle has drowned, severe irritation of the kidney and hemorrhage of the urinary tract may occur.

Insects of veterinary importance include a number of the flies, fleas, ticks, and others which also attack man and which are mentioned above. The warble fly of cattle, Hypoderma lineatum (De Villiers), has been introduced to Guam. Various mites and lice of fowls and other domestic animals are present. The cattle tick Boophilus annulatus australis (Fuller) is found on Guam, Palau, and Ponape, and on the latter island is known to carry bovine piroplasmosis (Texas cattle fever). Another cattle tick, Amblyomma cyprium Neumann, is known from Guam. The chicken lice Lipoptena caponi (L.) Menopon gallinae (L.), and Oxyuris angularis Peters were found on Ponape by Alicata (1948). He also found the mites Pterolichus obiusus Robin and Megninia cubitalis (Megnin) on chickens on Ponape, and the mite Laelaps echidinus Berlese on rats on Ponape.

FIELD WORK

In conjunction with the systematic reports to follow this introduction, it may prove helpful in assessing the actual total terrestrial arthropod fauna of Micronesia to evaluate the field work of the various collectors. Though this cannot be done precisely, the following information may serve to further an understanding of the relative equivalence of the collections, to better estimate the fauna, and to suggest future work to fill the probable gaps.

Since the principal components of the combined collections were made primarily by different individuals on different islands, the results from the different islands are not equivalent. Not only has more time been spent on some islands, but the collectors have used different methods and have concentrated on different habitats and on different groups according to their interests, experience, or circumstances. Nevertheless, those sent on general assignments did make special efforts to produce balanced collections.

It should be pointed out that collecting in Micronesia is far from simple, for the type of collecting to which one may be accustomed in temperate continental areas may produce little results. The meager results in comparison to those of collecting in continental tropics is striking. The conspicuous fact is the scarcity and insignificance of the insects, and the difficulty with which they are obtained. Most are small and live in unexposed situations. Large day-flying insects are particularly scarce, and large insects in general are rare. Collectors who specialized in collecting in the hidden and protected niches, ob-
tained more of the typical minute native fauna and endemics. Special mention in this connection must be made of H. S. Dybas, who obtained two most remarkable collections for the Chicago Natural History Museum and for the Pacific Science Board.

To provide relevant information, data on the various collectors are presented (table 17), followed by a list of the collectors with notes and brief biographic data. A third section presents notes on collecting localities and methods of a few of the field workers.

Table 17.—Geographical summary of important Micronesian collections

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Table continued...
Among the high islands, the collecting coverage has been fairly extensive on Saipan and Guam, but insufficient in the Carolines, northern Marianas, Volcano Islands, and the Bonins. Among the atolls, the collecting has been extremely uneven. Arno in the Marshalls has had good coverage, and Ifalik in the Carolines and Onotoa in the Gilberts have had moderate coverage. Other atolls have been visited briefly or not at all. The visits to many atolls were of only a few hours’ duration. Townes, Fosberg, Beardsley, and others spent periods of a few days each on several atolls.

For future field workers in the area, Fosberg and Sachet (1953) have compiled a handbook for work on atolls which is also helpful on other islands. The entomology section was prepared by Usinger.

DATA ON COLLECTORS

ADAMS, PHILLIP A.: Graduate student, University of California, later Harvard University; made principal Ponape entomological survey for Pacific Science Board, in 1950. Collected in mountainous area, and lowlands. Specialist in Neuroptera.

ASAHIYA, EIZO: Physiologist, Hokkaido University (brother of Syoziro Asahina); collected in Bonin Islands in 1932. Most of specimens in Kyushu University and S. Asahina collection.

BAILEY, STANLEY F.: Entomologist at University of California, Davis. As Navy entomologist on Guam, collected Thysanoptera in 1945.

BAKER, R. H.: Ornithologist, University of Kansas, then with U. S. Naval Medical Research Unit No. 2; collected bird and mammal parasites and some miscellaneous insects on Guam, Palau, and a few of the Carolines in 1945 (1951).

BATES, MARSTON: Entomologist-Zoologist at University of Michigan; participated in 1953 coral atoll program of Pacific Science Board, on Ifalik Atoll in the west-central Caroline Islands.

BEARDSLEY, J. W.: Assistant entomologist of the Trust Territory of the Pacific Islands (now with Hawaiian Sugar Planters’ Association Experiment Station), stationed in Koror, 1952-1954, worked on various pests and made general collections in Carolines and Marshalls, particularly in Palau and Truk.

BERTRAM, ROBERT E.: Member of United States Army; made a small collection on Iwo Jima and the Bonin Islands in late 1945 and 1946. Collection in Bishop Museum.

BOHART, RICHARD M.: Collected insects on Guam and Rota in 1945, while a member of U. S. Naval Medical Research Unit No. 2. Made the Pacific Science Board entomological survey for northern Mariana Islands and Bonin Islands in 1951. Specialist in mosquitoes, higher wasps, and Strepsiptera, University of California, Davis.

BROOKS, D. J.: Entomologist, Ohio State University; collected, with Holder, on Agrihan in 1945; specimens in U. S. National Museum.


BRYAN, EDWIN H., JR.: Curator of collections at Bishop Museum; made a trip to Guam in 1936 and several visits to atolls of the Marshalls with U. S. Army Intelligence during latter part of World War II.
CATALA, RENÉ: Zoologist from Institut Scientifique d'Océanie, Noumea, New Caledonia; made a collection at Tarawa, Gilbert Islands, in 1950, and presented much of the material to Bishop Museum.

CHAFFEE, R.: United States serviceman; collected on Guam at end of World War II.

CLAGG, C. F.: Navy entomologist, Pearl Harbor; collected briefly on Kwajalein, 1953.


DADO (DATO), KANE MATSU: Japanese administrator in Bonin Islands, 1929-1935; made a collection, now in the National Institute of Agricultural Sciences, Tokyo, in 1930.

DAVIS, C. J.: Entomologist, Board of Agriculture and Forestry, Hawaii; collected on Agiguan in 1954; specimens in Bishop Museum.

DAVISON, C. O.: Member of U. S. Naval Medical Research Unit No. 2; collected some parasites of vertebrates and other insects with R. H. Baker in 1945.


DOUSSON, C. 0.: Member of U. S. Naval Medical Research Unit; collected some parasites of vertebrates and other insects with R. H. Baker in 1945.

ECKE, J. W.: United States serviceman; collected mosquitoes and other insects in the northern Gilbert Islands in 1944 and presented them to Bishop Museum.

ESAKI, TATE: Entomologist of Kyushu University, Fukuoka, Japan; in charge of entomological investigations for the Japanese administration of Micronesia before World War II, making several trips to the high island groups and some atolls, 1936-1940. His extensive collections are from Pagan, Tinian, Saipan, Rota, Palau, Yap, Woleai, Truk, Ponape, Kusaie, Jaluit, and Wotje. Emphasis was placed on economic insects and less time was spent in the higher areas of Truk, Ponape, or Kusaie. Has written much on economic, as well as systematic, entomology of Micronesia (1940, 1943, 1952). Specialist in Hemiptera and Lepidoptera; series of reports published on his collections from Micronesia.

FORD, E. J., JR.: Plant Quarantine inspector, Honolulu, who collected on Angaur in 1944; specimens in Bishop Museum.


FREY, DAVID: Specialist in fresh-water Crustacea, University of Indiana; collected fresh-water insects in Guam, Yap, and Palau in 1946, while a member of U. S. Naval Medical Research Unit No. 2. The only person to collect a representative of Ephemeroptera in Micronesia (Yap).

FULLAWAY, D. T.: Entomologist from Board of Agriculture and Forestry, Honolulu; did entomological work on Guam in 1911. Collections in U. S. National Museum and Bishop Museum.

FURUKAWA, HARUO: Professor in Tokyo who published on Bonin Island Orthoptera and butterflies; visited Chichi Jima, Bonins, in March 1927. Material in his own collection.


GOSS, RICHARD J.: Entomologist at Brown University; made the Pacific Science Board entomological survey of Yap while a graduate student at Harvard University, 1950.

GRESSITT, J. L.: Collected on Guam as member of Naval Medical Research Unit No. 2 from May to August 1945, mostly with G. E. Bohart, working on flies and doing light-trapping and incidental collecting; also from November 1945 to January 1946, after Bohart's departure (Bohart and Gressitt, 1951). Made ecological study of *Oryctes rhinoceros* (1953b) in Palau for Pacific Science Board in 1951. In winter of 1952-1953 partially resurveyed principal islands of the Carolines, attempting to fill apparent gaps in the collections. Collected for a few days with J. F. G. Clarke on Ponape and Kusie.

HADDEN, Fred C.: Entomologist, then with U. S. Commercial Company, collected pests on Saipan in 1946. Collection at Hawaiian Sugar Planters' Association Experiment Station, Honolulu.


HARDCASTLE, A. B.: Member of U. S. Naval Medical Research Unit No. 2 on Guam; collected parasites of vertebrates, particularly Acarina, during 1945.

HIRAYAMA, S.: Professional collector; Bonin specimens in Hokkaido University.

HORNOSTEO, H. G.: Former staff member of Bishop Museum; collected some insects on Guam between 1922 and 1927.

HOSAKA, E. Y.: Botanist of Hawaii Agriculture Experiment Station; collected some insects on U. S. Commercial Co. expedition in Trust Territory in 1946. Specimens in Bishop Museum.

IKEDA, HAYATO: Marine zoologist, Kyushu University; collected insects in Bonin Islands (Chichi Jima and Haha Jima) on several visits between 1935 and 1940. Specimens at Kyushu University, Fukuoka.

ISSIKI, S.: Collected in Marianas, 1939; specimens in Taiwan Agric. Research Inst.


KONDO, YOSHIO: Malacologist, Bishop Museum; collected on Bishop Museum Caroline Islands Expedition in 1936, and for Pacific Science Board in Bonins and Marianas in 1949 and on Agiguan in 1952.

KONDO, I.: Collected in Truk, 1944, 1945; specimens in Saikyo University, Kyoto.

KRAUSS, NOEL L. H.: Entomologist of the Board of Agriculture and Forestry, Hawaii; collected pests on Guam in 1946 and on Saipan in 1947; made entomological survey of western Caroline atolls, Palau, Yap, and Guam for Pacific Science Board in 1952.

KUWANA, INOKICHI (S. I.): Late coccidologist; collected in Bonins in 1905 and 1912; collection at National Institute of Agricultural Sciences, Tokyo.

LANGE, W. HARRY: Economic entomologist at University of California, Davis; made survey of *Brontispa mariana* on Saipan and collected its natural enemies in Malaya and Indonesia for the Pacific Science Board.

LANGFORD, D. B.: Biological control specialist for Trust Territory of the Pacific Islands, 1947-1948; introduced beneficial insects, and did some collecting on various islands, including some of the Caroline atolls.
LA RIVERS, IRA: Entomologist from University of Nevada; studied ecology of insects of Arno Atoll with R. L. Usinger in 1950 for Pacific Science Board.


MATSUMURA, SHOGEN: Entomologist at Hokkaido University, now retired; made a collecting trip to the Bonin Islands in 1905. Collection, named by Matsumura and others, in Hokkaido University.

MATSUMITA [MATSUSHITA], DENGU: Japanese entomologist, now apiary dealer; collected insects in Japanese Mandated Islands in 1940 and 1942, particularly on Saipan, Tinian, and Rota, and also on Palau. Most of collection presented to Bishop Museum by Nodoka Hayashi of Tokyo.

MEAD, ALBERT R.: Zoologist from University of Arizona; worked on giant African snail for Pacific Science Board; collected in Bonin Islands, northern Marianas, Saipan, and Truk in 1949.

MILLER, R. E.: Public health doctor from Hanover, New Hampshire; studied insects on Kapingamarangi Atoll in 1950, collecting a few mosquitoes and flies. Specimens in Bishop Museum.

MOTOSE AND ISE: Collectors of Bonin specimens, 1931, in National Institute of Agricultural Sciences, Tokyo.

MOU, EDWARD T.: Botanist from Rutgers University; studied terrestrial ecology and collected insects on Onotoa Atoll, Gilbert Islands, for 1951 Pacific Science Board atoll survey (1954).

MUROKAMI, SHISO: Marine zoologist, now at Nagasaki; collected on Tobi (Tokobei) Island in 1938. Specimens at Kyushu University, Fukuoka.


OKO, ZENYEMON: Japanese entomologist who, with Y. Kondo, participated in Bishop Museum Caroline Islands Expedition in 1936. Most of the insects taken were Lepidoptera, Cicadidae, and larger species in other groups.

OSHiro, YOSHIo: Amateur entomologist from Honolulu; collected for Bishop Museum while a defense worker at Eniwetok in 1951.


POHLHEIMUS, T. W.: Collected Lepidoptera at Kwajalein in the Marshalls, 1945; presented specimens to Bishop Museum.


REEVES, WILLIAM C.: Medical entomologist, Hooper Foundation, University of California; collected several times on Guam (1951).


RUDNICK, A.: Medical entomologist, School of Public Health, University of California; studied mosquitoes on Guam with Reeves, 1949.

SAKAGAMI, SOCHI (F. S.): Animal ecologist of Hokkaido University; collected on Marcus in 1952.

SAKIMURA, K.: Entomologist, Pineapple Research Institute, Honolulu; collected pineapple pests and natural enemies in Bonins, Yap, and Palau in 1934.

STUNTZ, JOHN R.: Member of U. S. Naval Medical Research Unit No. 2 on Guam; worked with George Bohart and me on flies, and collected miscellaneous insects. Most specimens given to California Academy of Sciences.

SWEZEY, OTTO H.: Entomologist, Hawaiian Sugar Planters' Association; conducted entomological survey of Guam in 1936, assisted by R. L. Usinger. Did much rearing and collecting of host data, particularly for Lepidoptera. The Swezey-Usinger collection of about 1,000 species, together with material taken by Fullaway, Oakley, and Bryan, was the basis of Bishop Museum's "Insects of Guam, I and II" (1942, 1946).

TOSAWA, N.: Collected on Chichi Jima; material in various Japanese collections.


UCHIYAMA, SHIGETARO: Economic entomologist in Palau, 1922-1927; in Ponape, 1927-1933; and in Saipan, 1933-1936. Later retired on Ponape to cultivate Derris. Specimens in Kyushu University, Japan, and Bishop Museum.

USINGER, ROBERT L.: Collected with O. H. Swezey on Guam, 1936, while on staff of Bishop Museum. All groups of insects taken, with much valuable data. In 1950 went from University of California to participate in Pacific Science Board Arno Atoll study, where detailed data were accumulated on ecology of atoll insects; assisted by Ira La Rivers (1953). Wrote on Heteroptera of Guam and Marshall Islands.


WARTON, GEORGE W.: Acarologist, now at University of Maryland; as member of U. S. Naval Medical Research Unit No. 2, collected mites and other parasites of vertebrates on Guam in 1945.

YASUMATSU, KIEZO: Entomologist with Kyushu University, Fukuoka, Japan; participated with Esaki in surveys of Japanese Mandated Islands, particularly Pagan, Saipan, and Truk (1940). Reported on field work (1940, 1941) and also on various groups of Hymenoptera.

YOSHIMURA, SEICHIRO: Student who collected with Yasumatsu on Pagan, Saipan, and Truk in 1940. Collection at Kyushu University.

YOSHINO, TSUYOSHI (Go): Economic entomologist for Japanese administration of Mandated Islands; worked particularly in Palau, but also on Saipan; stationed in Palau 1930-1936, 1937-1940 or later; and Saipan, 1936-1937. Collections scattered, but some in Kyushu University. Many specimens labeled as taken by him in Palau may actually be from Ponape, the Marshalls, or even Celebes.
COLLECTING LOCALITIES AND METHODS

The following notes are presented with the hope of serving future field workers as well as aiding in evaluation of the collections forming the basis of this series. The information is incomplete and is by no means balanced. Some of it has been kindly supplied by certain of the field workers, and the rest has been gathered from available reports and my own experience.

**BONIN AND NORTHERN MARIANA ISLANDS**

These groups were surveyed in 1951 by R. M. Bohart (1951). His time was very limited on some islands and not sufficient on any, though interesting collections were obtained. He visited Chichi Jima, Muko Jima, Haha Jima, Agrihan, Pagan, and Alamagan, in addition to Saipan and Rota. He used a Berlese funnel on Saipan and Chichi Jima, and used sweeping methods, primarily, on all islands. On Haha Jima and Muko Jima he found the faunas poorer than on Chichi Jima.

**SAIPAN**

H. S. Dybas did extensive collecting in all environments in late 1944 and in 1945. His large series of all types of insects suggests that he must have obtained quite a large proportion of the insect fauna. Since there had been extensive damage to the vegetation at that time, he was able to exploit the existence of great amounts of decaying plants of all sorts and make a particularly good sampling of the native fauna. Dybas also worked on Tinian, Rota, and Guam in 1945.

Townes, Oakley, Maehler, Owen, Langford, R. M. Bohart, and many others also collected on Saipan.

**GUAM**

The work of Swezey and Usinger laid emphasis on careful host and habitat data, and much information has been published (1940, 1942, 1946). At the time of their work, in 1936, many of the present roads were non-existent, or were paths or wagon trails, and the northern half of the island was largely untouched forest. In the meantime, extensive clearings have been made for airstrips, military bases, or farms. Some of these are now covered with secondary growth. During 1945, when George Bohart and I, as well as Richard Bohart and others, were based at Naval Medical Research Unit No. 2 (NaMRU-2), many of these roads and clearings were being developed, and excellent opportunities for some kinds of collecting existed. The NaMRU-2, was located at Point Oca at the north end of Agana Bay (figs. 15; 16, a), on
a relatively low portion of the limestone plateau, sloping to the beach. This was covered with tall forest which was almost completely eliminated. We carried on extensive light-trapping here, and also at the top of the plateau above Point Ritidian at the north end of the island. Most of the trapping was done with a powerful electric light. At Point Oca and at many places in the central portion of Guam extensive bait trapping for flies was carried on, as well as other methods of sampling of adult and larval flies (Bohart and Gressitt, 1951). In addition, a moderate amount of general sweeping and beating was done in various parts of the island, particularly around farms and villages, and in secondary growth near Mount Santa Rosa or along the south coast. Many others have worked on Guam since 1945, particularly Maehler, Peterson, and Krauss.

**Palau**

The principal Palau survey was made by H. S. Dybas, in 1945 and 1947-1948. The war-time period was spent entirely in the southern islands, particularly Peleliu, whereas the later work was principally on or near Koror and in northern Babelthuap (1948). Dybas concentrated on the beating of woody or other native vegetation and on close and careful searching for minute forms in dead and decaying vegetation of all sorts, as well as in flowers, fruits, axils, fungi, soil, water, and other environments. On Koror, Dybas worked particularly along the tops of the elevated limestone ridges forming the eastern part of the island. Many species not found elsewhere were taken there. On Babelthuap, he worked principally at Ulimang on the northeast coast, and also at Ngerechelong on the northern peninsula. Ulimang is on a low coastal strip covered with coconut, strand, and swamp associations. Behind the village rises a ridge of hills in grass and sparse Pandanus, long cleared and partly terraced, as found in various parts of Babelthuap. Dense vegetation of trees and shrubs is restricted to valleys, ravines, and a partly wooded hilltop southwest of Ulimang.

Townes (1946) and Maehler (1949) did some effective field work, particularly on the volcanic portion of Koror and in southern Babelthuap (fig. 23, a). Their collections were made particularly by sweeping and searching on plants and are rich in Hymenoptera, Lepidoptera, and some other groups. Krauss (1953) worked especially on Koror and Ngarmalk (northwest Ulesehel), a limestone island near Koror. His collection is rich in small Hymenoptera and Diptera.

In 1951 I studied the ecology of the coconut rhinoceros beetle in Palau, working particularly at Ngiwal near the middle of the east coast of Babelthuap. This is a coconut-strand environment backed by swamps, hillside, and native jungle; and it has already been described in detail (1953b). Specimens were
taken incidental to the assigned work, mostly in decaying materials. My visit in December 1952 was partly to resurvey the above problem, and the remaining time was spent in jungle or clearings on the east side (Ngatpang) and north side (Ngaremese; fig. 23, b) of Ngaremedu Bay in west-central Babelthuap. Short visits were made to other islands. Each night two or three light traps were operated, as well as several Berlese funnels. The light traps were converted to Berlese funnels during the daytime (fig. 42, a), and various jungle debris processed in them. The funnels were simple cones with alcohol vials attached by tape to a short section of metal tubing at the apex of each cone. The debris was placed above two removable screens of different mesh near the top. Naphthalene was sprinkled over the debris and the top covered with paper and then a rag to keep out light and hold in the fumes, in order to repel the fauna down through the screens. This method was suggested to me by Dybas in 1952. Krauss used one of my funnels just before this trip, and several were left with Clarke on Kusaie some weeks later. One light trap consisted of a larger (50 cm.) funnel with apex fitted with a screw-top jar cover for receiving the cyanide jar. Jars of the same size, with alcohol, were used in converting to a Berlese funnel. One of the Berlese funnels, with screens removed, was used for another light trap, though it excluded large moths, cicadas, and dragonflies. Broad sheet-iron umbrellas were suspended immediately above the gasoline lanterns to keep rain out of the funnels. At Koror, a manufactured electric light trap was used in addition. Besides using the above methods, I did much sweeping, beating, and searching in logs, Pandanus, and so forth. J. W. Beardsley has recently collected much material at Koror and elsewhere.

Yap

The principal survey of Yap was made by Goss (1950). He collected in all the districts of Yap, using various collecting methods. He was one of the few to use a Berlese funnel extensively; he had an electric light trap, which he could use only at Kolonia; and he also used an aspirator and swept grass with a fine nylon net, besides using other methods. He worked particularly on economic plants and in grassland.

Townes, Oakley, Maehler, Owen, Beardsley, and I made shorts stops in Yap. Krauss spent more than two weeks there in 1952 and took many small flying insects, particularly Diptera and Hymenoptera. In 1952 I concentrated on light-trapping, Berlese funneling, and beating in native forest and on water insects, particularly on Mount Madaade (Matade). My other mountain locality, "Mount Gillifitz," is actually Mount Tabiwal, Gillifiz being a village to its north.
TRUK

The principal Truk survey was made by R. W. L. Potts (1949), who worked particularly on Wena (Moen), and visited Tonoas (Dublon), Nama, Fefan, Parem, Romanum, Fanapenges, Ton (Tol), Fano (Falo), and Pis. He noted that most of the islands provided similar environments, with only Wena, Tonoas, Ton, and to a lesser extent, Fefan, having a greater variety of native plants; and he noted that the most natural forest was on the steep southeast slope of Mount Unibot on Ton.

Potts worked extensively on the lower north slope of Mount Chukumong on Wena, and on the saddle between Chukumong and Mount Tonaachau to its north (fig. 39, a). This area is called Nantaku, the Japanese name, and was a farming area in Japanese times. It became the American administration and residence area, first called Civil Administration and then District Administration area. Potts' labels bear “Civ. Ad. Area.” Tonaachau is largely grassy, with Hibiscus; but Chukumong has mixed native and secondary growth, with the breadfruit-coconut zone (fig. 39, b) going quite high and merging with weed-invaded native growth, ivory nut palms, and the very tall Exorrhiza carolinensis palms.

Tonoas (Dublon) resembles Wena (Moen) in many of its environments, having much grass and many weeds invading the forests. Fefan is even more disturbed, with grassland extending high on the slopes, and with almost no natural forest. Pis is a low reef islet on the north side of the reef. Potts stressed the collection of flying insects and light-collecting. His collection is rich in Lepidoptera, ants, and some other groups.

In view of the scarcity of natural forest in Truk, I concentrated on the areas where it persists, particularly on the upper portion of Mount Unibot on Ton. I also worked some on Wena, Fefan, and just a bit on Tonoas.

At Mount Unibot on Ton, I ran one light trap in native forest on the steep ridge at 450 meters for several nights both before and after going to Ponape. Far fewer insects were taken than in a light trap at the foot of the mountain, but the fauna was quite different. Even with the beating during daytime, weevils and many other groups were unexpectedly scarce. I also gathered material from the ground or rotten wood for running in the Berlese funnels at this point, as well as at the extreme summit and at the foot of the mountain, in the area of the lower light trap, which was in a coconut-breadfruit area.

PONAPE

The principal Ponape survey was made by P. A. Adams in 1950. Adams worked in many environments in coastal areas on various sides of the island, as well as at some of the high mountains. He spent quite a bit of his time at the Agriculture Experiment Station, just south of Colonia, where there are
various environments, including a stream with a small dam, as well as many introduced plants. He also worked in the coconut groves and other farms at Madolenihm (Matalanim), in coconut-breadfruit areas elsewhere, and in native lowland forest at Nanipil.

H. S. Dybas worked for over a month on Ponape in 1948 and spent over half of his time in native forest, including the summits of some of the high mountains. He worked particularly with decaying vegetation and with the beating of native plants, thus collecting many of the small insects which dominate the endemic fauna. Since Dybas and Adams did not have Berlese funnels or effective light traps, I concentrated on these two methods of collecting, as well as on sweeping and beating in native forest at different altitudes, during my three weeks stay in 1953. Most of the time I ran one light trap at the Agriculture Experiment Station and the other in forests to the south, at Nanpohnmal and on the slopes (fig. 42, a) of Mount Temwetemwensekir (Tamatamansakir). Material for the Berlese funneling was obtained in these areas, and higher on Temwetemwensekir. The forest at Nanpohnmal was native jungle with clearings along the road to Nanipil. The road along the side of Temwetemwensekir went through some partly overgrown clearings and a few cultivated clearings, in otherwise natural forest.

KUSAIE ISLAND

J. F. Gates Clarke made the only extensive survey on Kusaie (1953). The work of Esaki, Ono, Townes, Oakley, and me was brief, but Clarke was on Kusaie from January 23 to May 3, 1953 and supplied most of the following information. His headquarters was Mutunlik, on a low hill (22 meters) on the south side of Lele Harbor and near the ocean (fig. 50, b, right background). He did extensive light-trapping there, and worked in the strand vegetation and coconut-breadfruit forest. “Hill 541” (altitude in feet) is close by, inland from Mutunlik. There are ferns, Derris and Freycinetia, as well as the aforementioned vegetation. Sensrik is near Mutunlik, on the south shore of Lele Harbor. Tafeayat and the river of the same name are behind mangrove at the inner end of the harbor, with Mount Tafeayat (fig. 51, a) to the south.

Lele (Lelu) Island, in the northeast, forms the north side of Lele Harbor (fig. 50, b). It is partly reef growth just above sea level, but it has a hill rising to just over 100 meters. The vegetation is strand, with coconut and Pandanus and large banyans, ferns, and shrubs among the ancient ruins behind the village.

Pukusrik (Pukesrik) is on the east coast near the north end—in mangrove swamp, including nipa palm—on the channel leading to Funaunpes. Funaunpes is a strand environment, with coconut and Pandanus and sand beach. Tafunsak is also strand, with secondary growth behind it, to the foot of Mount Matante.
Weye Cave, near Tafunsak, has a large opening in the face of a high cliff, is 30 meters deep, and has a high ceiling with many swiftlet nests. Water covers the floor, with droppings and debris. It harbors a crustacean, a mosquito larva, and a small strider.

Mount Matante, the high mountain in the north, is less steep than the rest. Clarke worked at various altitudes and to the summit (593 meters). The best collecting was in an environment dominated by *Cyathea* (300 meters) where light-trapping was done (fig. 49, b).

Fuinwukat (Mertens), to the southwest, and 465 meters high, is steep, with narrow ridges covered with ferns and *Freycinetia*. Yela Cave is near the middle of the northwest coast and near the mouth of the Yela River. The cave floor is dry, with several deep mounds of pure insect remains. In these, Clarke found some Coleoptera and a tineid moth not found elsewhere. Swiftlet nests were obtained from the low ceiling, and scavengers and parasites were taken. A light trap placed in front of the cave drew nothing from inside. Yela River runs through a long, flat valley. Mesophytic jungle dominates, with secondary growth toward the base of Fuinwukat and mangrove near the mouth.

Mwot is on raised land behind the beach toward the west end of Kusaie. The area is mostly in cultivation or secondary growth and the ridges terminating nearby are covered with a dense growth of *Hibiscus*. *Melochia* was seen only here and on Lele Island. Inmen, west of Mwot, is a seaward beach locality with strand vegetation and poor collecting. Sawokusa, at the extreme western tip, is also poor.

Mount Wakapp (490 m.) is in the center of the west part of Kusaie. It was named by the Kusaians for Margaret Walkup, a missionary who died in 1865. The ridge to it is quite rough. The *Ponapea* palm, which appears above 200 meters, is a natural host of the red palm scale, *Tutucapis*, which was sometimes very abundant. Higher up is the damp cloud forest, with ferns, tree ferns, epiphytes, and stunted trees.

Mount Fuinkol (Crozer), the highest peak on Kusaie, is in the center of the island. Clarke and I climbed it together, walking up the Fuinkol River. The upper portion is a typical narrow ridge with cloud forest. Some small weevils, an elaterid, and a few other insects, were taken on the summit.

Clarke estimated that he took over 700 species on Kusaie. He used the same modified Berlese funnels which I used, and a copy of my better light trap. The light trap was run 51 nights at 13 different stations, and it took long series of many species not otherwise collected. Clarke also did considerable beating, sweeping, and some rearing.

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Krauss, N. L. H.

Kubary, J.

Kubota, Nagahisa

Ladd, Harry S.

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This list is by no means complete, but it is intended to include principal islands, as well as villages, mountains, and islets at which insects have been collected. Other geographical features, such as reefs, banks, rocks, islets, capes, bays, and rivers, are omitted unless known to apply to specimen localities. Synonyms are only partially listed, and in most cases very similar spellings are omitted. Islets with the same name as the atoll or island group are usually not mentioned separately. A more complete listing of the islet names is made under the separate atolls in the geographical section.

The romanization of Micronesian place names is in a state of flux and until official action has stabilized the spellings, selection of the proper romanization is somewhat arbitrary. For most names, the best and latest maps have been followed, but in many cases widely used spellings differ greatly from the local pronunciations of the place name. For the most part, the previously used romanization thought to be closest to the local pronunciation of the name has been used; but it is quite possible that some wrong choices have been made.

It is unfortunate that erroneous spellings of many place names have been perpetuated on maps and used on even recent specimen labels, including my own. However, it is probable that the spelling of Micronesian place names will become stabilized during the next several years. Since these spellings are being carefully revised preparatory to the issuance of new maps, some of the proposed changes are being adopted in this work so that the data in this series will be more intelligible to the users of the future maps. Both the spellings on the labels and the presumed correct spellings will be used in text references to specimens in the forthcoming articles.

In the following list, the abbreviation \( A. \) is used for atoll, and \( \text{gr.} \) refers to group.

\[
\begin{align*}
\text{Abaian A.}, & \quad \text{Gilberts} \quad \text{lat.} \quad 1^\circ 49' \quad \text{N.} - \quad \text{long.} \quad 172^\circ 57' \quad \text{E.} \\
\text{Abanekeneke (Abenekeke) I.,} & \quad \text{Onotoa A., Gilberts} \quad \text{lat.} \quad 1^\circ 48' \quad \text{S.} - \quad \text{long.} \quad 175^\circ 32' \quad \text{E.} \\
\text{Abapao A.}, & \quad \text{Palau} \quad \text{lat.} \quad 7^\circ 08' \quad \text{N.} - \quad \text{long.} \quad 134^\circ 19' \quad \text{E.} \\
\text{Abemama A.}, & \quad \text{Gilberts} \quad \text{lat.} \quad 0^\circ 22' \quad \text{N.} - \quad \text{long.} \quad 173^\circ 53' \quad \text{E.} \\
\text{Abenekeneke (see Abanekeneke)} & \\
\text{Abo, Guam} & \quad \text{lat.} \quad 13^\circ 25' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 40' \quad \text{E.} \\
\text{Achugao, Guam} & \quad \text{lat.} \quad 13^\circ 16' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 39' \quad \text{E.} \\
\text{Achuguan, Saipan} & \quad \text{lat.} \quad 15^\circ 14' \quad \text{N.} - \quad \text{long.} \quad 145^\circ 45' \quad \text{E.} \\
\text{Addi (Addide) R.}, & \quad \text{Babelthuap} \quad \text{lat.} \quad 7^\circ 36' \quad \text{N.} - \quad \text{long.} \quad 134^\circ 35' \quad \text{E.} \\
\text{Aerik (Airikku, Aidik) I.,} & \quad \text{Rongelap A., Marshalls} \quad \text{lat.} \quad 11^\circ 27' \quad \text{N.} - \quad \text{long.} \quad 166^\circ 48' \quad \text{E.} \\
\text{Afenia (Affenia, Afeina),} & \quad \text{Saipan} \quad \text{lat.} \quad 15^\circ 07' \quad \text{N.} - \quad \text{long.} \quad 145^\circ 42' \quad \text{E.} \\
\text{Agana, Guam} & \quad \text{lat.} \quad 13^\circ 28' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 45' \quad \text{E.} \\
\text{Agana Spring, Guam} & \quad \text{lat.} \quad 13^\circ 28' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 46' \quad \text{E.} \\
\text{Agat, Guam} & \quad \text{lat.} \quad 13^\circ 24' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 39' \quad \text{E.} \\
\text{Aglayan, Guam} & \quad \text{lat.} \quad 13^\circ 16' \quad \text{N.} - \quad \text{long.} \quad 144^\circ 44' \quad \text{E.} \\
\text{Aguguan (Aguingan) I.,} & \quad \text{S. Mariana} \quad \text{lat.} \quad 14^\circ 51' \quad \text{N.} - \quad \text{long.} \quad 145^\circ 34' \quad \text{E.} \\
\text{Agol (see AoI)} & \\
\text{Agriculture Experiment Station,} & \quad \text{Ponape} \quad \text{lat.} \quad 6^\circ 58' \quad \text{N.} - \quad \text{long.} \quad 158^\circ 13' \quad \text{E.}
\end{align*}
\]
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Agrihan (Gregua) I., N. Marianas ........................................... lat. 18°46' N.—long. 145°40' E.
Aguijan (see Agigan)
Agulue (Akurue, Akulue) I., Ailuk, Marshalls ................................ long. 11°17' N.—long. 17°52' E.
Aiaki, Otoai-Aiaki I., Onotoa, Gilberts ................................ lat. 1°53' S.—long. 175°33' E.
Aidik (Airikku, Aeric) I., Rongelap A., Marshalls ................................ lat. 11°27' N.—long. 166°48' E.
Ailinginane A., Marshalls .................................................. lat. 11°08' N.—long. 166°29' E.
Ailinglapalap A., Marshalls .................................................. lat. 7°25' N.—long. 168°45' E.
Ailuk A., Marshalls ......................................................... lat. 10°20' N.—long. 169°56' E.
Aimelik (see Imelik)
Aimeong (Aimion), Babelthuap ........................................... lat. 7°32' N.—long. 134°32' E.
Aimion (see Aimeong)
Airai colony, Babelthuap .................................................... lat. 7°23' N.—long. 134°32' E.
Airai village, Babelthuap .................................................... lat. 7°21' N.—long. 134°34' E.
Airik (see Airok)
Airfield, Yap I., Yap ......................................................... lat. 9°28' N.—long. 138°03' E.
Airfields I and II, Ponape ................................................... lat. 6°56' N.—long. 158°11' E.
Airik (see Airok)
Airikku (see Aidik)
Airok (Airek) I., Ailinglapalap, Marshalls ................................... lat. 7°17' N.—long. 168°50' E.
Airok (Airk) I., Maloelap, Marshalls .................................... lat. 8°30' N.—long. 171°12' E.
Aiung (Aiyon), Babelthuap .................................................. lat. 7°43' N.—long. 134°37' E.
Ajayan, Guam ................................................................. lat. 13°15' N.—long. 144°43' E.
Alamagan (Concepcion) I., N. Marianas ................................ lat. 17°30' N.—long. 145°50' E.
Alatgue, Guam ................................................................. lat. 13°18' N.—long. 144°40' E.
Alcolon (see Ngerelong)
Alifan, Mt., Guam .............................................................. lat. 13°23' N.—long. 144°40' E.
Alilling, Guam ................................................................. lat. 13°16' N.—long. 144°40' E.
Alle (Erile) I., Ujae A., Marshalls ........................................ lat. 9°09' N.—long. 165°34' E.
Almagosa, Mt., Guam .......................................................... lat. 13°21' N.—long. 144°41' E.
Almeni (Arumeni) I., Bikar A., Marshalls ................................ lat. 12°15' N.—long. 170°08' E.
Almiokan (see Ngaremeskang)
Almongui (see Ngaremengui)
Alu (see Fallo)
Alutom, Mt., Guam .............................................................. lat. 13°26' N.—long. 144°43' E.
Amanites Pt., Guam ............................................................. lat. 13°52' N.—long. 144°48' E.
Amiagat, Mt., Peleliu, Palau ................................................. lat. 7°03' N.—long. 134°17' E.
Anatahan, N. Marianas ....................................................... lat. 16°21' N.—long. 145°40' E.
Anderson Field, Guam ........................................................... lat. 13°34' N.—long. 144°55' E.
Ane Jima (Perry I.), Haha Jima gr., Bonins ............................. lat. 26°03' N.—long. 142°08' E.
Angaur (Ngaur, Angauru) I., Palau ........................................ lat. 6°53' N.—long. 134°08' E.
Ani Jima (Buckland I.), Chichi Jima gr., Bonins ...................... lat. 27°07' N.—long. 142°10' E.
Anigu, Guam ................................................................. lat. 13°29' N.—long. 144°46' E.
Ant A., E. Carolines .......................................................... lat. 6°47' N.—long. 157°58' E.
Aol (Agol, Gol, Arugoru), Babelthuap ................................ lat. 7°40' N.—long. 134°39' E.
Aonon (see Aumon)
Aonteuma (Temuah) I., Onotoa A., Gilberts ................................ lat. 1°47' S.—long. 175°29' E.
Apemama (see Ahemama)
Apra, Guam ................................................................. lat. 13°29' N.—long. 144°40' E.
Arabaketsu (see Ngargarage) .................................................
Aragamaye (Aragame), Koror I., Palau ........................................ lat. 7°21' N.—long. 134°30' E.
Arakabesan (see Ngarkabesang)
Arakasao (see Ngarekesauaol)
Aramagan (see Alamagan)
Aramonogui (see Ngaremlengi)
Arunuka A. (Henderville), Gilberts.lat. 0°11' N.—long. 173°39' E.
Arekalong (see Ngerehelong)
Arekasoru (see Ngarekeseaul)
Aringel, Yap.lat. 9°30' N.—long. 138°05' E.
Armaten (see Ngeremetengel)
Arno A., Marshalls.lat. 7°05' N.—long. 171°42' E.
Arorae I., Gilberts.lat. 2°38' S.—long. 176°49' E.
Arubaketsu (see Ngarbaged)
Aruh (Aru), Ponape.lat. 6°56' N.—long. 158°29' E.
Arukoron (see Ngerehelong)
Arumaten (see Ngeremetengel)
Arumiongan (see Ngaremlekgang)
Arumizu (see Ngarmid)
Arunogui (see Ngaremlengi)
As Akin, Saipan.lat. 15°14' N.—long. 145°45' E.
As Gonno (Asukonno), Saipan.lat. 15°10' N.—long. 145°45' E.
As Lito (Asilito), Saipan.lat. 15°07' N.—long. 145°42' E.
As Teo, Saipan.lat. 15°11' N.—long. 145°46' E.
Asan, Guam.lat. 13°28' N.—long. 144°45' E.
Asias (see Ngasias)
Asiga Pt., Guam.lat. 13°19' N.—long. 144°46' E.
Asor 1., Ulithi A., Caroline.lat. 10°02' N.—long. 138°47' E.
Asukonno (see As Gonno)
Asuncion I., N. Marianas.lat. 19°40' N.—long. 145°24' E.
Auak (see Awakpah)
Aulong (Orooolong) I., Palau.lat. 7°16' N.—long. 134°17' E.
Aulptagel (see Ulebsehel)
Aulptagel, NW (see Ngarmac)
Aumon (Aomon) I., Eniwetok A., Marshalls.lat. 11°32' N.—long. 162°19' E.
Aur A., Marshalls.lat. 8°16' N.—long. 171°06' E.
Auru (see Ulebsehel)
Awakpah (Auak), Ul Distr., Ponape.lat. 6°57' N.—long. 158°16' E.
Babelthuap (Babeldaob) I., Palau.lat. 7°30' N.—long. 134°33' E.
Baleig gr. (Haha Jima, Coffin), Boninslat. 26°35' N.—long. 142°10' E.
Balabat (Barabat), Yap.lat. 9°30' N.—long. 138°08' E.
Banaderu, Saipan.lat. 15°17' N.—long. 145°49' E.
Baqjen (Banejin) I., Allak A., Marshalls.lat. 10°18' N.—long. 169°38' E.
Baqjen, Islet N. of (see Enejomaren)
Barabat (see Balabat)
Barriagada, Guam.lat. 13°29' N.—long. 144°50' E.
Beech Cove, Tinian.lat. 14°59' N.—long. 145°36' E.
Beechey gr. (Chichi Jima), Boninslat. 27°06' N.—long. 142°12' E.
Beirut, Mt. (see Piarrot)
Bekrak (Pigowak, Belrak) I., Utirik A., Marshalls.lat. 11°15' N.—long. 169°50' E.
Benig (Benik), Yap I., Yap.lat. 9°30' N.—long. 138°07' E.
Beru A., Gilberts.lat. 1°19' S.—long. 176°00' E.
Bigej I., Kwajalein A., Marshalls.lat. 8°53' N.—long. 167°46' E.
Bikakela (Bigatye1an g) I., Ailinglapalap, Marshalls.lat. 7°17' N.—long. 168°43' E.
Bikar A., Marshalls.lat. 12°15' N.—long. 169°56' E.
Bikarej (Bikareij) I., Arno A., Marshalls.lat. 7°15' N.—long. 171°38' E.
Bikatz (Bikat) I., Butaritari (Makin), Gilberts.lat. 3°10' N.—long. 172°42' E.
Bikom (Pykon) I., Uje1ang A., Marshalls.lat. 9°52' N.—long. 160°50' E.
<table>
<thead>
<tr>
<th>Location</th>
<th>Lat/Long</th>
<th>Notes</th>
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<tbody>
<tr>
<td>Bok (Bock) I., Ujae A., Marshalls</td>
<td>lat. 9°02' N.—long. 165°35' E.</td>
<td></td>
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<tr>
<td>Bolonaetok 1. (Sandspit on E. reef), Wotho, Marshalls</td>
<td>lat. 10°07' N.—long. 165°59' E.</td>
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<tr>
<td>Bolonaos, Mt., Guam</td>
<td>lat. 13°18' N.—long. 144°42' E.</td>
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<tr>
<td>Bonin (Ogasawara) Is., N. of Volcano Is.</td>
<td>lat. 27°00' N.—long. 142°10' E.</td>
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<tr>
<td>Borodino (see Daito Jima)</td>
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<tr>
<td>Breje I., Pokak A., Marshalls</td>
<td>lat. 14°37' N.—long. 169°00' E.</td>
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<tr>
<td>Busche (Matante), Mt., Kusaie</td>
<td>lat. 5°21' N.—long. 162°59' E.</td>
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<td>Buckland I. (see Ani Jima)</td>
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<td>Buiartun (see Tanyah)</td>
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<tr>
<td>Butaritari (&quot;Makin&quot;) A., Gilberts</td>
<td>lat. 3°02' N.—long. 172°48' E.</td>
<td></td>
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<tr>
<td>Caroline Is.</td>
<td>lat. 1°10° N.—long. 131°163° E.</td>
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<tr>
<td>Chalan Kanoa (Charan Canoa, Charanka), Saipan</td>
<td>lat. 15°09' N.—long. 145°43' E.</td>
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<tr>
<td>Chalan Laulau, Saipan</td>
<td>lat. 15°10' N.—long. 145°43' E.</td>
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<tr>
<td>Chalankeja (Charankeja), Lake Susupe, Saipan</td>
<td>lat. 15°09' N.—long. 145°43' E.</td>
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<tr>
<td>Chichi Jima (Beachey or Peel gr.), Bonins</td>
<td>lat. 15°09' N.—long. 145°43' E.</td>
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<tr>
<td>Chukumong (Teroken ), Mt., Wena I., Truk</td>
<td>lat. 15°09' N.—long. 145°43' E.</td>
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<td>Coffin gr. (see Haha Jima)</td>
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<tr>
<td>Colony (Kolonia, Yap)</td>
<td>lat. 9°30' N.—long. 138°08' E.</td>
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<tr>
<td>Colony (see Kolonia)</td>
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<tr>
<td>Cotal, Guam</td>
<td>lat. 13°24' N.—long. 144°43' E.</td>
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<td>Crozer, Mt. (see Fuinkol)</td>
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<tr>
<td>Daito Jima (Oagari, Borodino), W. Pacific</td>
<td>lat. 25°35' N.—long. 131°15' E.</td>
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<td>Dalap I. (see Telap)</td>
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<td>Darit I. (see Jaroj)</td>
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<tr>
<td>Dededo, Guam</td>
<td>lat. 13°30' N.—long. 144°49' E.</td>
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<tr>
<td>Dogol (see Dugor)</td>
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<tr>
<td>Donnay (Donni, Denni), Saipan</td>
<td>lat. 15°12' N.—long. 145°47' E.</td>
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<td>Dublon (see Tonoas)</td>
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<tr>
<td>Eil Malk (Mecherchar) I., Palau</td>
<td>lat. 7°29' N.—long. 146°10' E.</td>
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<tr>
<td>Elizabeth (see Majurirok)</td>
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<tr>
<td>Elluk (Eerukku) I., Utirik A., Marshalls</td>
<td>lat. 11°15' N.—long. 169°49' E.</td>
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Emertao, Babelthuap .............................................. lat. 7°30' N.—long. 134°33' E.
Emidji (see Imedj)
Enderby (see Puluvat)
Enebuoj (see Enibuoj)
Eneje Ito (Encherudo) I., Wotho A., Marshallss............ lat. 10°01' N.—long. 166°01' E.
Enelamoe (Islet N. of Baojen), Ailuk, Marshallss............ lat. 10°18' N.—long. 169°58' E.
Enelamaj (Eniyamieg) I., Ujuae A., Marshallss.............. lat. 9°12' N.—long. 165°31' E.
Enelap (Enyelabegan) I., Kwajalein, Marshallss............. lat. 8°47' N.—long. 167°37' E.
Enelap (Enimlap) I., Ujelan, Marshallss....................... lat. 9°49' N.—long. 160°52' E.
Enemonmon (Gibuiurii) I., Lae A., Marshallss.............. lat. 10°01' N.—long. 166°16' E.
Enebuoj (Enichero), Wotho A., Marshallss.................... lat. 10°10' N.—long. 165°58' E.
Enejomaren (Islet N. of Baojen), Ailuk, Marshallss........ lat. 10°44' N.—long. 167°41' E.
Enemalago (Enylamie), Ujae A, Marshallss.................... lat. 9°12' N.—long. 165°31' E.
Enikapkan (Ennylabegan) I., Kwajalein, Marshallss........ lat. 8°47' N.—long. 167°37' E.
Enellap (Enimlap) I., Ujelan, Marshallss....................... lat. 9°49' N.—long. 160°52' E.
Enelamoj (Enylamie) I., Ujae A, Marshallss.................... lat. 9°12' N.—long. 165°31' E.
Fukurozawa (near Fukuro, Mt.), Chichi Jima, Bonins...lat. 27°03' N.—long. 142°11' E.
Funaumes, Kusaie ...........................................lat. 5°22' N.—long. 163°01' E.
Fuyo Jima, Fuyo To (see Totiu)
Fuyu Shima (see Urnan)
Fwinkol (see Fuinkol)
Gabayanga, NC. Angaur, Palau ................................lat. 6°55' N.—long. 134°08' E.
Gachapar (Gatchapar, Gatapar), Gagil, Yap........lat. 9°14' N.—long. 145°23' E.
Gafuet I, C. Carolines ........................................lat. 9°14' N.—long. 145°23' E.
Gagil Distr., Yap..............................................lat. 9°33' N.—long. 138°11' E.
Gagil-Tomil “I.” (Gagil and Tomil Districts), Yap....lat. 9°32' N.—long. 138°10' E.
Gaingas (see Ngaiangas)
Gaisharu (see Ngchesar)
Gakipp (see Ngatelp)
Galdock (see Ngurdok)
Galmiskan (see Ngaremeskang)
Garakayo (see Ngergoi)
Garameo (see Ngermediu)
Garapan, Saipan ..............................................lat. 15°12' N.—long. 145°43' E.
Garard (see Ngarard)
Garasunao (see Ngardman)
Garudoroko (see Ngardololok)
Garukyoku (see Ngarekeu)
Garumisukan (see Ngaremeskang)
Garyo I. (see Heleu)
Gasupan (see Ngatpang)
Gatchapar (see Gachapar)
Gatschapar (see Gatchapar)
Gillifitz (Gillifitz, Girifitsu) village, Yap............lat. 9°33' N.—long. 138°08' E.
Gillifitz, Mt. (see Tabiwal, Mt.)
Gorak I., Palau..................................................lat. 8°02' N.—long. 134°41' E.
Goreor (see Koror)
Gorror (see Guror)
Greenwich (see Kapingamarangi)
Guadobuso-to (see Ngesebus)
Guam I., S. Marianas ..............................................lat. 13°25' N.—long. 144°45' E.
Gugewe I. (including Bweje), Kwajalein, Marshalls...lat. 8°50' N.—long. 167°44' E.
Guguan I., N. Marianas ...........................................lat. 17°19' N.—long. 145°51' E.
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Guror (Gorror), Yap I., Yap ....................................lat. 9°27' N.—long. 138°04' E.
Hagman (Kagman) Mt., Saipan ...............................lat. 15°09' N.—long. 145°47' E.
Hagman (Inai Hagman, Kagman) Pt., Saipan ..........lat. 15°09' N.—long. 145°47' E.
Hagoy (Hagoya), Lake, Tinian ..............................lat. 15°03' N.—long. 145°37' E.
Haha Jima (Coffin or Hillsborough I.), Bonins........lat. 26°40' N.—long. 142°09' E.
Haha Jima Retto (Bailey or Coffin gr.), Bonins .......lat. 26°35' N.—long. 142°10' E.
Halaihai, Saipan .............................................lat. 15°12' N.—long. 145°46' E.
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Haputo, Guam ....................................................lat. 13°35' N.—long. 144°50' E.
Hare (Hale) I., Kapingamarangi A., E. Carolines.....lat. 1°02' N.—long. 154°48' E.
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Heleu (Garyo) I., Ngemelis Is., Palau.................lat. 7°06' N.—long. 134°14' E.
Higashimuura (E. Village), Angaur, Palau ...............lat. 6°54' N.—long. 134°09' E.
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Hoga (Hokkaido) Mountain, Japan ........................lat. 40°50' N.—long. 141°45' E.
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I Naotan Pt., Saipan....................................lat. 15°05' N.—long. 145°45' E.
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Igudon (Igurin), Eniweto A., Marshalls....................lat. 11°21' N.—long. 162°14' E.
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Ineem, Kusai.............................................lat. 5°55' N.—long. 169°39' E.
Imelik (Imlidj) I., Jaluit A., Marshalls....................lat. 5°19' N.—long. 162°55' E.
Ina Hugman (See Hagman Pt.)..............................lat. 13°16' N.—long. 144°45' E.
Inarajan, Guam...........................................lat. 6°59' N.—long. 171°42' E.
Inen, Amoa..............................................lat. 6°59' N.—long. 171°42' E.
Inshappu (see Mwot)....................................lat. 7°22' N.—long. 151°50' E.
Ino Jima (see Iwo Jima)................................lat. 7°20' N.—long. 134°35' E.
Iwo (Iwo) Jima (Sulphur I.), Volcano Is....................lat. 11°29' N.—long. 141°19' E.
Jabwot I., Marshalls.....................................lat. 10°08' N.—long. 169°31' E.
Japitan I. (see Jobitan)................................lat. 7°01' N.—long. 158°13' E.
Japteen (Japutik) I., Ponape................................lat. 7°07' N.—long. 171°21' E.
Jeh (Jeh) I., Ailinglapalap A., Marshalls....................lat. 7°35' N.—long. 168°58' E.
Jenno I., Marshalls......................................lat. 10°08' N.—long. 169°31' E.
Jembe Bay, Palau ........................................lat. 7°22' N.—long. 151°50' E.
Inow (Iwo Jima).........................................lat. 7°20' N.—long. 134°35' E.
Iwayama Bay, Palau ......................................lat. 7°23' N.—long. 134°35' E.
Iwayama Bay, Palau ......................................lat. 7°23' N.—long. 134°35' E.
Iron, Mt., Fefan I., Truk..................................lat. 7°22' N.—long. 151°50' E.
Iwo (Iwo) Jima (Sulphur I.), Volcano Is....................lat. 24°47' N.—long. 141°19' E.
Jabwot I., Marshalls.....................................lat. 10°08' N.—long. 169°31' E.
Jabwot I., Marshalls.....................................lat. 10°08' N.—long. 169°31' E.
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Jabwot I., Marshalls.....................................lat. 10°05' N.—long. 168°59' E.
Jabwot I., Marshalls.....................................lat. 10°05' N.—long. 168°59' E.
Japtan I. (see Jobatan)................................lat. 7°01' N.—long. 158°13' E.
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Kabem (Kaben) I., Wotho A., Marshalls....................lat. 10°01' N.—long. 166°00' E.
Karaberu (see Ngeremmed)................................ lat. 7°01' N.—long. 158°13' E.
Kapir, Yap.................................................lat. 9°31' N.—long. 138°06' E.
Kapir, Yap.................................................lat. 9°31' N.—long. 138°06' E.
Kapir, Yap.................................................lat. 9°31' N.—long. 138°06' E.
Kapir, Yap.................................................lat. 9°31' N.—long. 138°06' E.
Karap (see Nikap Aru)....................................lat. 7°44' N.—long. 161°38' E.
Kayang (see Ngiangl A.)................................lat. 6°52' N.—long. 138°18' E.
Kayo To (see Fanapenges)................................lat. 6°52' N.—long. 138°18' E.
Kazan Retto (see Volcano Is.)..............................lat. 6°52' N.—long. 138°18' E.
Kemah Bay, Saipan .......................................lat. 15°14' N.—long. 145°48' E.
Kemah Bay, Saipan .......................................lat. 15°14' N.—long. 145°48' E.
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Keng, Yap I., Yap ........................................................................ lat. 9°31' N.—long. 138°08' E.
Kilange (Kirage) I., Arno A., Marshalls ................................................................ lat. 7°05' N.—long. 171°53' E.
Kili I., Marshalls ........................................................................ lat. 5°38' N.—long. 169°07' E.
Kiloken (Kilagen) I., Ujelang A., Marshalls ............................................................... lat. 9°49' N.—long. 160°56' E.
Kingsmill Is. (see Gilbert Is.)
Kinyo To (see Pole)
Kirage I. (see Kiliange)
Kirenen (Kiriniyan) I., Ujelang A., Marshalls ............................................................... lat. 9°50' N.—long. 160°50' E.
Kiriwitu, Rota ........................................................................ lat. 14°07' N.—long. 155°10' E.
Kita Iwo (Io) Jima (N. Iwo, San Alessandro), Volcano Is. ........................................ lat. 25°26' N.—long. 141°17' E.
Kita Mura (N. village), Saipan ........................................................................ lat. 15°15' N.—long. 145°48' E.
Kita Mura (Hokusang), Angaur, Palau ........................................................................ lat. 6°54' N.—long. 134°08' E.
Kiti Dist., Ponape ........................................................................ lat. 6°49' N.—long. 158°11' E.
Kiyose, Chichi Jima, Bonins ........................................................................ lat. 27°05' N.—long. 142°12' E.
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Knox Is. (see Narik A.)
Koiguru (see Goikul)
Kolonia (Ponape, Colonia), Ponape ........................................................................ lat. 6°59' N.—long. 158°13' E.
Kolonia (Yaptown, Colonla), Yap ........................................................................ lat. 9°30' N.—long. 138°08' E.
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Koror (Oreor, Goror, Kororu, Korol, Kareor) I., Palau ................................................ lat. 7°20' N.—long. 134°30' E.
Kubersoh, Mt. (see Kupwuriso)
Kuchma, Tonoas (Dublon) I., Truk ........................................................................ lat. 7°23' N.—long. 151°54' E.
Knop A., near Truk ........................................................................ lat. 7°04' N.—long. 151°55' E.
Kupwuriso (Kubersoh), Mt. (529 m.), Ponape ................................................................ lat. 6°56' N.—long. 158°15' E.
Kuria Is., Gilberts ........................................................................ lat. 0°14' N.—long. 173°23' E.
Kusai Is. (Ualan, Kuschai), E. Carolines ........................................................................ lat. 5°20' N.—long. 162°58' E.
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Kwajalein Atoll (Kwajlen), Marshalls ........................................................................ lat. 9°10' N.—long. 167°25' E.
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Kwateb (Kwadak) I., Kwajalein A., Marshalls ............................................................... lat. 9°01' N.—long. 167°43' E.
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Lae A., Marshalls ........................................................................ lat. 8°56' N.—long. 166°14' E.
Laguna, Pagan, N. Marianas ........................................................................ lat. 18°08' N.—long. 145°46' E.
Lamer, Yap I., Yap ........................................................................ lat. 9°28' N.—long. 138°05' E.
Lamolam, Mt. (406 m.), Guam ........................................................................ lat. 13°20' N.—long. 144°40' E.
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Langer (see Lenger)
Lasso, Mt. (172 m.), Tinian ........................................................................ lat. 15°02' N.—long. 145°37' E.
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Lele (Lele, Lelo) I., Kusaie ........................................................................ lat. 5°20' N.—long. 163°01' E.
Lenger (Langer) I., Ponape ........................................................................ lat. 6°59' N.—long. 158°14' E.
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Likiep A., Marshalls ........................................................................ lat. 9°54' N.—long. 169°08' E.
Likop (Likok), Ponape ........................................................................ lat. 6°54' N.—long. 158°19' E.
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Lojirun (Raajerun) I., Taka A., Marshalls ........................................................................ lat. 11°08' N.—long. 169°40' E.
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<td>Machar (Machar) I., Arno A., Marshall's</td>
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<td>Manto (see Mahnd)</td>
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<td>Map I., Yap</td>
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<td>Map I., Yap</td>
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<td>Marcus (Minami Tori Shima) I., E. of Volcano Is.</td>
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Olei Village, Saipan. lat. 15°10' N.—long. 145°43' E.
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