THE COCONUT RHINOCEROS BEETLE

(*Oryctes rhinoceros*)

WITH PARTICULAR REFERENCE TO THE PALAU ISLANDS

BY

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BULLETIN 212

HONOLULU, HAWAII
PUBLISHED BY THE MUSEUM
1953

KRAUS REPRINT CO.
New York
1971

NOVEMBER 1, 1953

Reprinted with the permission of the original publisher
KRAUS REPRINT CO.
A U.S. Division of Kraus-Thomson Organization Limited

Printed in U.S.A.

This book was printed with the financial assistance of the Trust Territory of the Pacific Islands and the Pacific Science Board of the National Research Council.

FOREWORD

To one who is concerned with developing a mutually productive relationship between scientific research and the administration of an area such as the Trust Territory of the Pacific Islands, the publication of Dr. Gressitt's monograph on the coconut rhinoceros beetle is a significant event. Quite apart from its scientific merit, Dr. Gressitt's report is notable on a number of counts. Certain of these deserve mention.

The presence of the rhinoceros beetle in the Palau Islands is a serious threat to the copra economy of the entire Trust Territory. The sensible first step in meeting this threat is a program of field research designed to make available the essential information on the characteristics and habits of the beetle. Dr. Gressitt's monograph is a very important contribution to this research. It is a pleasure to point out that both the field research and the publication of the monograph were supported by private institutions and government agencies, and represent fruitful collaboration among the Pacific Science Board, the Office of Naval Research, the Bishop Museum, the New Zealand Administration of Western Samoa, the Administration of American Samoa, and the Trust Territory of the Pacific Islands, all of which assisted Dr. Gressitt.

The present monograph is not only an example of successful collaboration among a number of agencies and institutions. It also shows in a tangible way that the administration of the Trust Territory of the Pacific Islands is aware of the importance of scientific research in solving problems concerned with the economic welfare of the peoples of the Trust Territory. The publication of the monograph is, furthermore, concrete evidence of the recognition by the administration of the Trust Territory of American responsibilities under the Trusteeship Agreement with the Security Council of the United Nations. Finally, it should be pointed out that Dr. Gressitt's report on the rhinoceros beetle will be of value not only to the Trust Territory, but also to all areas in the western Pacific confronted by the depredations of this serious pest.

FRANK E. MIDKIFF
HIGH COMMISSIONER OF THE
TRUST TERRITORY OF THE
PACIFIC ISLANDS

ERRATA

Page 13, line 8: For *The coconuts* read *Many of the coconuts.*

Page 18, legend under figure 5: For *b* read *c,* for *c* read *b.*

Page 76, line 25: For *of* read *and.*

PREFACE

This study was made under the auspices of the Invertebrate Consultants Committee for the Pacific, of the Pacific Science Board (National Academy of Sciences-National Research Council), and was supported by a grant from the Office of Naval Research, United States Navy. My assignment was to make an ecological study of the coconut rhinoceros beetle in the Palau Islands of the western Caroline Islands and, briefly, in Samoa.

I am indebted to many people for assistance during the course of this study. Special appreciation is expressed to Mr. Harold J. Coolidge, Executive Director of the Pacific Science Board, and to Dr. C. E. Pemberton, Chairman of the Invertebrate Consultants Committee for the Pacific. I am also indebted to Miss Ernestine Akers and Mrs. Lenore Smith of the Pacific Science Board.

Facilities and assistance were provided by the Trust Territory of the Pacific Islands, particularly through Mr. Robert P. Owen; by Mr. H. W. Simmonds of Fiji who accompanied Mr. Owen and me in Western Samoa; by the New Zealand Reparations Estates (Mr. D. R. Eden) and the Department of Agriculture (Mr. Leavasa) of Western Samoa; by the Department of Agriculture of American Samoa (Mr. David Butchart, Mr. Keith Severin); and by the Bernice P. Bishop Museum (Mr. E. H. Bryan, Jr., and Dr. Alexander Spoehr).

I am grateful to Miss Adelina Ramarui for careful assistance in the laboratory at Koror (Palau), to Mrs. Margaret K. Gressitt for drawings made in Palau and Honolulu, to Miss Kimiko Ueki and Mr. Edward Himeno for a few of the drawings, to Mr. James Yamamoto and Dr. E. S. Ross for some of the enlarged photographs of specimens, and to Mr. E. H. Bryan, Jr., for the map of the Palau Islands.

For additional assistance in the Palau Islands I am indebted to Mr. Layton Horner, Mr. Harry Stille, Mr. Mike Sunray, Dr. C. H. Johnston, Mr. Teruo Termeteet and Mr. Adelbai, of Koror; Magistrate Ongelungel of Ngiwal; High Chief Areklai of North Palau; Magistrate Tulap of Angaur; Chief Obok of Peleliu; Chief Rurugodon and Magistrate Mbishuban of Kayangel; Mr. Takeo Melaidao and Mr. Aldbechel of Ngiwal; and Pastor Wilhelm Fey of Koror. For help in Samoa I am also indebted to Dr. J. S. Armstrong, Dr. T. G. Hawley, and Mr. Rasmussen, of Apia, and to former Governor Phelps Phelps, and Mr. Fred A. Bianchi of the Hawaiian Sugar Planters' Association Experiment Station, in American Samoa.

I am indebted also to Mr. G. S. Dun for information on the beetle in New Britain and, for assistance in identification of various invertebrate animals, to Dr. W. L. Brown, Dr. P. J. Darlington, Jr., Dr. A. E. Emerson, Dr. C. H. Edmondson, Dr. A. B. Gurney, Mr. Yoshio Kondo, Mr. R. L. Hoffman, Dr.

M. A. Miller, Dr. R. L. Usinger, and Mr. R. L. Wenzel; for plant identifications, to Dr. F. R. Fosberg and Miss Marie C. Neal. For assistance in connection with literature references, I wish to thank Dr. P. D. Hurd, Dr. E. A. Steinhaus, and Mrs. Aileen Jaffa, of Berkeley, the Hawaiian Sugar Planters' Association Experiment Station, the Museum of Comparative Zoölogy, the Arnold Arboretum, and the Library of the United States Department of Agriculture. For reading the manuscript, or parts thereof, and for suggestions I am grateful to Dr. W. H. Anderson, Mr. Fred A. Bianchi, Mrs. Eloise Christian, Dr. Roderick Craig, Dr. C. E. Pemberton, Dr. E. A. Steinhaus, Miss Amy Suehiro, Dr. L. D. Tuthill, Mr. R. H. Van Zwaluwenburg, and Mr. E. C. Zimmerman.

The printing of this Bulletin was made possible by a generous grant from the United States Trust Territory of the Pacific Islands, and a subsidy from the United States Office of Naval Research paid for the engravings.

J. L. Gressitt

CONTENTS

	Page
Foreword	iii
Preface	v
Introduction	1
Field and laboratory work	3
Methods	3
Spread and control of Oryctes in the Palau Islands	4
Geography and Geology	6
Climate	8
Flora and fauna	9
Ecology of the coconut palm	10
Habitat notes on field headquarters	11
Taxonomy, morphology, and biology	13
Oryctes rhinoceros and its relatives	13
Common names	15
Descriptions of the various stages	15
Morphology	23
Physiology and enteric biota	33
Life cycle	33
Biotic potential	34
Sex ratio	34
Stridulation	35
Larval habits	35
Pupation	38
Adult habits	39
Ecological relationships in the Palau Islands	51
Adult foods	51
Breeding sites (larval hosts)	58
Coconut trunks	58
Coconut logs	62
Coconut stumps	63
Coconut logs used in construction	66
Other palms	66
Miscellaneous wood	66
Ground under old logs	67
Compost	68
Sawdust pits	69
Jungle	69
Other media	70
Feeding experiments	71
Adults	71
Larvae	73
Damage evaluation and population studies	74
Babelthuap Island	74

	Page
Kayangel Atoll	83
Central Palau	84
Limestone islands	85
The southern islands	88
Census summary	93
Invertebrate co-habitants of feeding and breeding sites	93
Coleoptera	95
Blattaria	98
Orthoptera	98
Dermaptera	98
Isoptera	98
Hemiptera	99
Hymenoptera	99
Chilopoda	100
Diplopoda	100
Scorpionida	100
Acarina	100
Crustacea	100
Mollusca	101
Invertebrate parasites and predators	101
Vertebrate relationships	101
Ecological succession in adult hosts	103
Ecological succession in larval hosts	103
Control	105
Biological control	105
Insects	105
Other invertebrates	110
Vertebrates	111
Diseases	112
Cultural control, or sanitation	113
Destruction of dead palms and other trees	113
Proper care of compost and sawdust	114
Trapping	116
Other control methods	118
Caution in planting of coconuts	118
Chemical control	119
Quarantine and legislation	120
The rhinoceros beetle in Samoa	121
The rhinoceros beetle in other countries	124
Conclusions	129
Bibliography	132
Index	149
Figures 1-50	

The Coconut Rhinoceros Beetle

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By J. LINSLEY GRESSITT

INTRODUCTION

The coconut rhinoceros beetle, *Oryctes rhinoceros* (Linnaeus), is one of the most serious pests of the coconut palm. It is presumed to be native to southern India, Ceylon, Burma, Siam, the Malay Peninsula, Indo-China, Hainan Island, southernmost China, Hong Kong, Formosa, the southern Ryukyus, the Philippines, and Indonesia as far east as Celebes, Ceram, and Amboina (Arrow, 9; Leefmans, 183).[1] Arrow (9) reports it from Korea, but this information should be verified. It is also irregularly distributed in the Pacific and has close relatives in Africa and other warm parts of the Old World.

The beetle has been introduced into Samoa, Wallis Island, New Britain, New Ireland, Palau, Tonga, and Fiji. The Palaus are the only islands in Micronesia where it has been found. Other records of coconut beetles in Micronesia apply to the small Saipan, or Mariana, coconut beetle and other species of *Brontispa*, one of which also occurs in Palau. *Oryctes* is rarely found at altitudes higher than 900 meters.

In its native Asiatic home the coconut rhinoceros beetle is more or less controlled by various factors, but introduced into an insular area lacking many of these natural controls, it is a threat to coconut cultivation. In fact it has demonstrated that it may be the most serious pest in the Pacific islands, in many of which the cultivation of coconuts is the primary commercial enterprise. Even in Asia, when breeding materials are abundant, it may do very serious damage. Its economic importance thus varies with the geographical location, faunal and other elements related to the beetle in the region concerned, and abundance of larval breeding media; but in most of the Old World tropics it, or other species of *Oryctes* (Droussie, 85), is considered the most serious pest of coconut palms.

The normal habitat of this beetle is a palm grove or jungle containing palms. It is generally particularly abundant around villages or other places where larval food is plentiful. The larvae develop in dead wood, such as palm trunks, logs and stumps, *Pandanus*, and sawdust pits; in garbage, compost, manure, old latrines, sugar-cane bagasse, rice straw or hulls, thatch roofing, and various other rotting vegetable materials; in soil rich in humus; rarely, in certain living or unhealthy plants and in living roots.

[1] Numbers in parentheses refer to Bibliography, page 132.

Where the beetle is abundant, it causes the death of coconut palms; and where coconut palms are scarce, the beetle kills other palms, sugar cane, pineapple plants, *Pandanus*, or other plants. It is able to vary its habits and choice of food to suit various situations and environments and has demonstrated its power to devastate coconut plantations where it is faced with but slight environmental resistance. The discovery at this late date that the beetle can feed upon *Pandanus* in both adult and larval stages and maintain its population where it has already exterminated the coconut palms, as it has done in the central and southern Palaus, is but one additional example of its powers of adaptation. *O. rhinoceros* has also been reported to spread bud rot on coconut palms (Barrett, 17; Friederichs, 102; and Morstatt, 209). The central spear of an oil palm in Malaya is reported to have collapsed after infection by bud rot which entered at an *Oryctes* feeding tunnel (Corbett, 55). Grubs of an *Oryctes* [?*tarandus*] and *Lachnosterna* were implicated in the transmission of white tannas disease of sugar cane on Mauritius, according to de Charmoy (67), and *Oryctes* was suspected in the transmission of "dead heart" of sugar cane in Burma (Ghosh, 130).

Much has been published about the coconut beetle, but because it is such a serious threat to the growing of coconut palms in the Palaus and other islands where it might be accidentally introduced and because of the great difficulties encountered in attempts to control the beetle in Palau, there is a demand for more information. I have reviewed the literature and other sources of information and attempted to make this study as general and complete as possible with limitation of time and space. Emphasis is on the habits, ecology, and damage done by the beetle in the Palau Islands, with supplementary and comparative information on the beetle in Samoa and a summary of information on biology and control from all available sources. Unless otherwise stated, the information presented is based on my study in the Palau Islands and the Samoan Islands. Statements refer to Palau unless Samoa is specified. The ecological relationships of the beetle are much more complex in Asia, and many questions remain unanswered. Further study will be necessary before the beetle can be adequately understood and controlled.

Hosts, or adult food plants, are the following: *Cocos nucifera* (coconut palm), *Arecastrum plumosa, Phoenix sylvestris* (wild date palm), *Phoenix dactylifera* (date palm), *Elaeis guineensis* (oil palm), *Areca cathecu* (betel-nut palm), *Acanthophoenix rubra, Metroxylon sagu* (sago palm), *Nypa fruticans* (nipa palm), *Borassus flabellifer* (Palmyra palm), *Arenga pinnata* (sugar palm), *Livistona chinensis* (fan palm), *Latania* sp., *Aiphanes caryotifolia, Dypsis gracilis, Verschaffeltia splendida, Dictyosperma album* (red palm), *Raphia vinifera, Mascarena lagenicaulis* (bottle palm), *Corypha elata* (Serdang palm), *Corypha umbraculifera* (talipot palm), *Caryota urens* (toddy or fish-tail palm), *Roystonea elata* (*Oreodoxa regia*, royal palm), *Stevensonia* sp.,

Oncosperma sp., *Pritchardia* (*Eupritchardia*) *pacifica* (Fiji fan palm), *Cyphokentia samoensis, Coelococcus carolinensis* (Caroline ivory-nut palm), *Heterospathe elata* var. *palauensis, Gulubiopsis palauensis, Pseudopinanga insignis* (*Pinanga micronesica*), *Pinanga* spp., *Agave sisalana, A. americana, Pandanus tectorius* (*P. odoratissimus*), *Saccharum* (sugar cane), *Ananas* (pineapple), *Cyathea* sp. (tree fern), *Musa* (banana) and possibly *Colocasia* (taro) and its relatives. Palms of the genera *Normanbya* and *Thrinax* and additional species of some of the above genera were reported to Friederichs (109) as having been attacked at Saigon.

FIELD AND LABORATORY WORK

I spent from July 10 to December 3, 1951, in the Palaus, with field headquarters at Ngiwal on the east coast of Babelthuap, making visits to Koror and the islands having coconut palms. Thirty-three islands of the Palaus were visited. January 1952 was spent in Western Samoa and American Samoa in company with Mr. R. P. Owen, and with Mr. H. W. Simmonds in Western Samoa. The four largest Samoan Islands and one small one were visited. Much of the laboratory work was done in Mr. Owen's laboratory in Koror with the assistance of Miss Ramarui.

The Palaus were revisited during December 4 to 24, 1952, and I stopped briefly at 11 islands and at four municipalities on Babelthuap, including Ngiwal.

METHODS

To determine the duration of life stages, considerable rearing was carried out in the Koror laboratory. This was done largely by isolating larvae in individual containers and supplying them with chips from coconut logs or, for young larvae, with coconut-wood sawdust. Other foods were also tested. The containers used were glass jars, ranging in size from one ounce to one quart, and tin cans of approximately one-pint size, according to the size of the larvae. Rain water was added daily by means of a medicine dropper.

At Ngiwal, the field headquarters, the above rearing methods were duplicated on a small scale as a check, but emphasis was placed on observation in natural environments. Small transparent containers were ideal for close observation but retarded growth and encouraged mold because of the unnatural environment, particularly the humidity. To obtain life-cycle data in the natural environment, coconut stumps were examined and the *Oryctes* of various stages removed, counted larvae of the same age were inserted, and 16-mesh wire screen was nailed over the opening. This was done for a number of stumps with larvae of different ages, including newly hatched larvae, since there was insufficient time to follow individual beetles through their complete life cycles. In addition, coconut logs were taken to Koror, sawed into 30 cm. lengths, and measured larvae inserted into 2 cm. bored holes and each end covered with screening. In Koror some reared larvae were weighed or measured at four- or five-day intervals to observe the rate of growth; others were observed only for molting or metamorphosis; and some were kept in the laboratory hot locker to compare growth at a higher temperature, such as that produced by compost. Others were tested with varying degrees of dampness of food to study moisture tolerance.

To observe the habits of the adults, beetles taken from coconut palms were kept in observation cages of various sizes. These included field cages—6 inch cubes with wood frames and bottoms and 16-mesh screen sides—and boxes of 2 to 4 cubic feet with screen top which were used both at Koror and Ngiwal. The principal observations of the beetles in captivity were made in two large cages, one in Koror and the other at Ngiwal. The Koror cage was 7 feet wide, 15 feet long, and 10 feet high, with soil bottom and screened top partly under a level concrete roof ledge. Two sides were cement wall with two large windows opening into a roofless room; and the other two sides and windows were 16-mesh brass screening extending 25 cm. into the soil, providing ample light and partial protection from the elements. Inside were planted three one-year-old coconut palms, one taro, and one banana plant. On the ground were placed three sections of coconut logs, a fourth log upright against the wall, and separate piles of coconut chips, coconut fronds, and leaves and weeds. The cage at Ngiwal which was in a corner of a porch, partly walled and partly screened, was not successful, presumably because the young palms were in kegs instead of in the ground. Adults put into both cages were marked by rings of fine brass wire around one or two tibiae in different combinations.

SPREAD AND CONTROL OF ORYCTES IN THE PALAU ISLANDS

This beetle is presumed to have been introduced during 1942 into Koror Island in the central Palaus by Japanese shipping from Singapore or Java, or possibly from the Philippines, Indo-China, or Formosa. During the war it spread rapidly, and by 1945 was more than half way to the north end of Babelthuap Island; by 1947 it had reached the north end. By 1947 or early 1948 it had reached Kayangel Atoll, though it did not appear on the main island until 1949 or 1950. It reached Peleliu and Angaur Islands about 1945 or 1946.

The beetle is conspicuously abundant in and around villages and other places which were machine-gunned or bombed during the war, for palms killed by gunfire provided abundant breeding sites for the larvae. Furthermore, damaged palms were more readily killed by the feeding of the adult beetle, thus providing additional breeding sources. In most villages all or most of the bearing coconut palms have been attacked to some degree by the adult beetles.

Pastor W. Fey noticed many dead palms in Koror in December 1945 and noted that by January 1946 there were almost no coconuts on the palms in Koror. He had not noticed the beetle at Ngkeklau, Babelthuap, before leaving there in September 1945.

In the summer of 1946 Richard G. Oakley and Henry K. Townes made an entomological survey of the Marshall, Caroline, and Mariana Islands for the U. S. Commercial Company's economic survey. Oakley (214, p. 30) states that *Oryctes* was abundant on Koror, where it was killing most of the coconut palms, and on southernmost Babelthuap; newly arrived at Ngatpang; and found on Peleliu. He remarks that it was introduced to the Palaus five or six years earlier, in 1940 or 1941. He summarizes (214, p. 65) a few records from other countries, but states that he observed the coconut palm to be the only one affected in Palau. Oakley observed that southern Babelthuap and Koror would serve as a focus of infection for the other parts of the Palaus and suggested the use of compost traps, *Scolia* wasps, and quarantine measures. Townes (282, p. 9) suggested that *Scolia ruficornis* should be better adapted to the Palau climate than *S. oryctophaga* and that *Scolia* is not an aggressive human stinger.

After the organization of the Insect Control Committee for Micronesia (now the Invertebrate Consultants Committee for the Pacific), plans for control efforts were made (1947). As a result, Harold Compere, of the University of California, shipped *Scolia ruficornis* from East Africa. Sixty females reached Airai, Babelthuap, alive in December 1947; F. X. Williams delivered 50 more in June 1948; and T. R. Gardner (118-120) imported 110 female *Scolia patricialis* var. *plebeja* to Koror from Malaya. Another 36 *S. ruficornis* were shipped from Zanzibar by R. T. Abbott in 1950. In late 1951 more than 100 *S. ruficornis* were released at Airai from shipments obtained at Zanzibar by N. L. H. Krauss (175). I observed no wasps in December 1952, but villagers reported to me that a boy had seen a live one about September.

In the spring of 1949 P. J. R. Hill (Pacific War Memorial) made a survey on Koror Island (147). He counted only 285 coconut palms, of which 45 percent had been attacked. Only 11 were over 15 feet tall, and all of these were damaged by the beetle. He states that 24 of 50 oil palms were affected and mentions reports that banana, sugar cane, and betel palm plants had been attacked.

Early efforts at control were ineffective because dead palms which were not completely destroyed provided breeding material for the beetle. Early in 1950 R. P. Owen, Entomologist for the Trust Territory, issued a comprehensive report (216) on the beetle situation, recommending vigorous control, primarily through destruction of breeding sites. This was approved and the control program was started in late 1950. At the beginning of 1953 it was still in progress, the control crew having covered almost one-half of the Palaus in two years. The crew, with the aid of the local inhabitants, fells the dead trunks, and the logs are dragged to water by carabao. Owen mentions in his reports (216-218) that Palauans had informed him that the beetle fed on native palm, sugar cane, and *Pandanus* and that it bred in nests of megapode birds and was preyed upon by monitor lizards.

Autumn of 1951 found all but the very young palms of Angaur Island exterminated, with the beetle breeding in *Pandanus,* and most of the palms gone from Peleliu and the islands between it and Koror, except for groves largely intact in the Ngemelis Islands. On Koror, Malakal, and Arakabesan most of the coconut palms had been exterminated, but some other palms remained. On southern Babelthuap many groves had been exterminated and the beetle was breeding in *Pandanus,* though on the rest of the island many fine groves were only slightly affected, except in and near villages where damage was severe. On Kayangel Atoll the beetle was spreading into the best groves. By December 1952 the population was much reduced, but with destruction more complete on the southern islands, reduced on Babelthuap, and slightly increased on Kayangel.

GEOGRAPHY AND GEOLOGY

The Palaus, part of the western Caroline Islands, extend from 6° 50′ to 8° 12′ north latitude and 134° 07′ to 134° 44′ east longitude, lying in a somewhat southwest-northeast direction. Their area is about 487 square kilometers (188 square miles). They are the result of a combination of volcanic and coral development and are almost entirely surrounded by wide reefs contiguous to, or separate from, the shore, or both. Only Angaur, the southernmost, is entirely outside the main reef, and it has very little reef of its own. To the north of the main islands are several more or less isolated reefs and Kayangel Atoll, the only atoll in the group. Babelthuap, the largest, and northernmost of the main islands, is about 35 kilometers north and south, and up to 12 kilometers across. (See map, figure 1.) It is largely of volcanic origin, with some small coralline islets along its southeastern corner. Its highest altitude, the highest of the Palaus, is 250 meters.

To the south are Koror, Arakabesan, and Malakal, rather small and low, mostly under 100 meters in altitude, and largely volcanic in origin. Southeastern Koror (fig. 2, *a*) and Auluptagel, Ngargol, Urukthapel, Eilmalk, and many islets to their west are narrow, high, steep-sided, and generally undercut islands of raised coral rock which support practically no coconut palms. Peleliu, at the south end of the reefs, and Ngedebus, Ngergoi, and the Ngemelis Islands are largely flat and entirely coralline. Angaur Island is flat but slightly raised, entirely coral or coral transformed by phosphoric acid to calcium phosphate by the action of rain seeping through guano, or phosphatic remains of marine life, into the coral. Much of the coastline, particularly of Babelthuap, is edged with mangrove swamps.

There are 109 principal islands or islets in the Palau group, or 343 including the smallest.

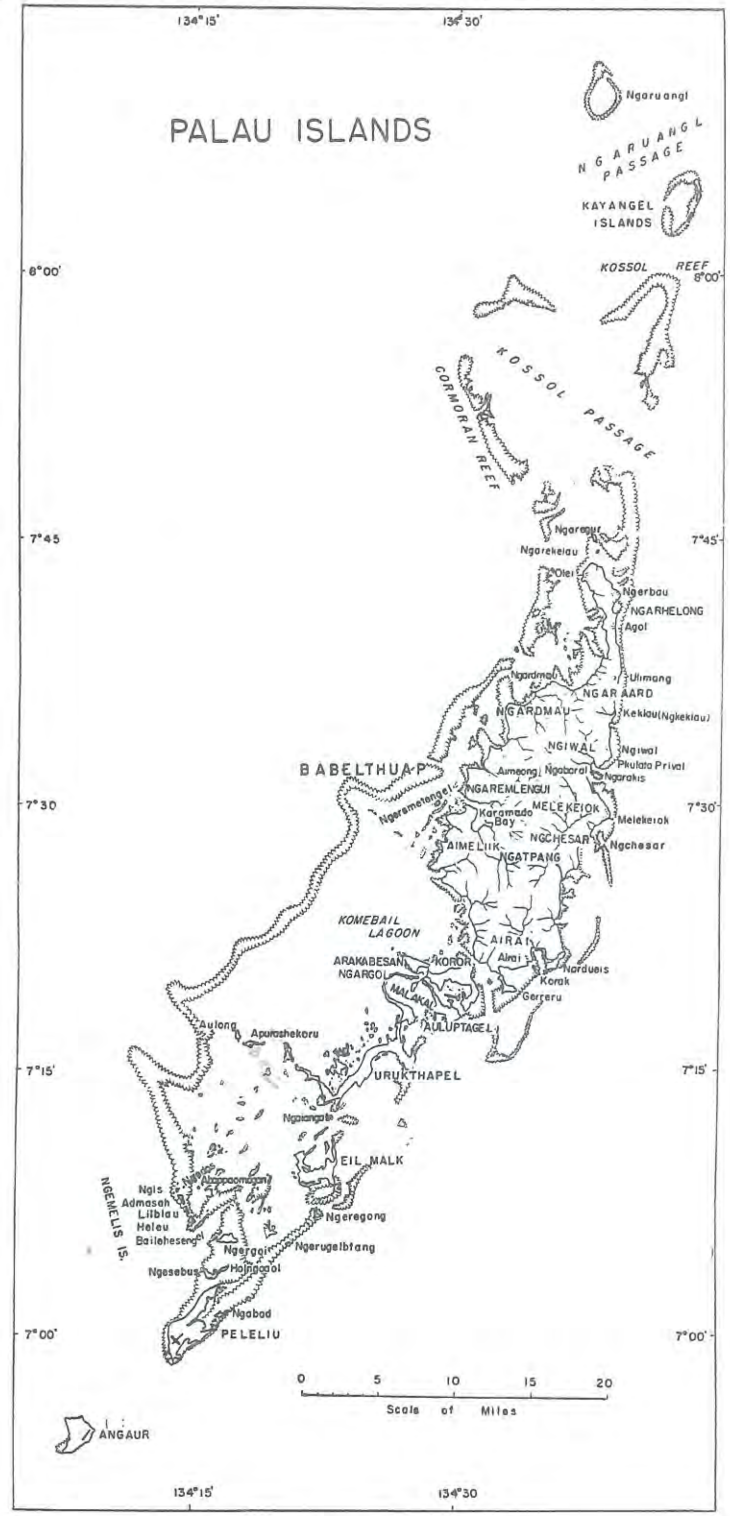

FIGURE 1.—Map of Palau Islands.

CLIMATE

The Palau Islands, six to eight degrees north of the equator and in the warm sea current flowing from the southeast, have a truly tropical climate. There is rather little seasonal variation, and that is largely limited to wind and rainfall.

The minimum temperature ranges from 70° to 74° F., and the maximum temperature from 87° to 91° (rarely 93°) F. There is no seasonal correlation with this slight variation, and the coolest and warmest weather may occur in the same month. The mean monthly temperature ranges from 80° to 82° F., and the mean diurnal range is 9.6° F. The averages and extremes at Koror for the period of this study are shown in table 1. At Ngiwal the exact maximums and minimums were not recorded, but daily records showed the maximums to be slightly lower and the minimums slightly higher than at Koror's weather station, which is on a hill and less enclosed by vegetation.

Table 1

	Average		Extremes	
	Min.	Max.	Min.	Max.
July	75	88	72	93
August	75	86	70	91
September	75	86	73	90
October	76	89	73	91
November	76	88	74	91

The total annual rainfall for 1950 in Koror was 148 inches. The average total for a nine-year period was 137 inches; and for the same period the monthly averages were: January, 8.76; February, 7.18; March, 7.87; April, 6.82; May, 11.68; June, 12.03; July, 18.24; August, 15.44; September, 11.04; October, 9.72; November, 13.08; and December, 15.29. The total number of inches of rainfall during the period of this study is shown in table 2.

Table 2

	Monthly Totals		Highest 24 Hour Rain	
	Koror	Ngiwal	Koror	Ngiwal
July	9.61	....	1.11	......
August	20.42	16.46	4.16	1.73
September	8.57	14.22	2.21	2.00
October	5.42	6.96	1.78	1.61
November	10.74	9.67	1.73	1.70

The average wind is from the northeast or east from November to May, and from the south or southwest from June to October. The strongest winds are generally from the south-southwest from September to November and from the east from December to February.

The relative humidity ranges from 62 to 99 percent and varies as much as 62 to 97 percent within a 24-hour period (July). The monthly figures for the period of this study are shown in table 3.

Table 3

	Koror (for 9 A.M.)		Ngiwal (for 7:30 A.M.)	
	Average	Extremes	Average	Extremes
July	85	62-98	....	....
August	80	67-99	91	....
September	82	64-97	88	77-96
October	77	64-97	79	78-98
November	84	70-97	90	83-98

Babelthuap, on which Ngiwal is located, is the largest land mass and has the heaviest rainfall. Peleliu and Angaur, being smaller and more isolated, have less precipitation than Koror, which is adjacent to southern Babelthuap. There is little annual variation in the length of day and, generally, little variation in atmospheric pressure. The above statistics are for Koror and for 1950 and 1951, unless otherwise indicated.

It is assumed that there are no seasonal or geographical differences in the habits of the beetle, within the Palaus. In islands such as Mauritius and Formosa, where there are marked seasons, there is but one generation of *Oryctes* per year. In the Palaus the generations are continuous and overlapping, with about three generations completed in any 12 months.

FLORA AND FAUNA

The Palaus are true oceanic islands with no evidence of ever having been connected with any continent, hence the species of plants and terrestrial animals are limited in number.

Land vertebrates include only rats, bats, a feral pig, an introduced monkey, some 30 kinds of birds, five snakes, several lizards, and two amphibians (one introduced). The insect fauna is limited, perhaps numbering three or four thousand species. However, the marine animal life is extremely rich.

The plants are relatively richer in species because of the greater ease with which they are transported over the ocean. Fairly rich variety exists in the jungle on both the volcanic and limestone islands. Angaur and Peleliu lost much of their native vegetation during the war and now have dense second growth of pan-tropical or widely distributed Pacific plants, such as *Casuarina, Cassia, Crotalaria, Mimosa, Euphorbia, Sida, Eugenia, Hibiscus, Cordia* (food-plant of adult *Scolia* wasps on Mauritius) and others, mixed with *Ficus, Barringtonia, Calophyllum,* papaya, *Pandanus,* and other introduced or native plants. *Terminalia* is a conspicuous tree on Koror and some of the limestone islands. *Bikkia* and *Dracaena* are abundant on the limestone islands. *Morinda, Codiaeum,* and *Polyscias* are common on Koror and near the villages. *Pandanus* is extremely abundant on all the islands. Along the sand beaches are found *Scaevola, Hernandia, Thespesia,* and *Messerschmidia,* as well as *Barringtonia* and *Calophyllum.*

The coconut palm (*Cocos nucifera*) is probably still the most numerous palm in the Palaus, though it seems safe to assume that it is not native. Next most conspicuous in villages is the betel-nut palm (*Areca cathecu*), which is also introduced. More numerous than the betel-nut palm, at least on Babelthuap Island, is a native jungle palm similar in appearance, *Pseudopinanga insignis* (*Pinanga micronesica*), or *akaboek,* which has smaller red fruit. On the high coral islets of the central Palaus the also somewhat similar, slender, native *Gulubiopsis palauensis* (*asbo, abo*) is conspicuous because it is often taller than the surrounding vegetation and tends to grow on the ridges. The third native palm, also in the Babelthuap jungles, is *Heterospathe elata* var. *palauensis,* which is tall, larger than *Pseudopinanga insignis,* with whitish green flowers on a branching, non-pendulous inflorescence, and with green fruit. The other native palm is *Ponapea palauensis.*

The nipa palm (*Nypa fruticans*) grows near the mouths of the streams by the villages or behind the mangrove swamps just above or at the edge of the brackish water zone. The true sago palm (*Metroxylon*) grows in swamps at Ngiwal, Melekeiok, Ngchesar, and Aimeliik. Introduced palms, mostly on Koror and south Babelthuap, include the fish-tail palm, a fan palm, the bamboo palm (*Chrysalidocarpus*), the oil palm, the royal palm, the sugar palm, and the Caroline ivory-nut palm. Most of the present coconut groves of the Palaus were planted during the period of German government (1899-1918), with nuts brought from New Guinea, but many were planted during the Japanese period (1919-1945). A few, other than self-seeded palms, have been planted since the American-United Nations Trusteeship started following American occupation in 1944-1945. Apparently no great effort was made to plant coconuts during the Spanish regime (1686-1899).

Ecology of the Coconut Palm

The coconut palm is by nature a plant of the ocean shores. It grows at or near the edges of many islands or continents in the tropics, though it may be cultivated far inland. The native home has been debated, but it may have come from South America. The large seed, or coconut, may be carried a long distance by ocean currents, then germinate and grow where washed ashore (Edmondson, 94). The average habitat is sandy flat land behind beaches. Considerable salinity is tolerated in soil and in wind and spray. Sometimes the palm grows in mud or swampy land almost as wet and tidal as the habitat of the nipa palm. In the Palaus coconuts generally grow just behind the narrower mangrove swamps or the beaches, but may be planted on the hillsides sloping toward the sea. The palms require considerable moisture and grow best on alluvial soils deposited on sand, where soil is rich and drainage is good, as well as in volcanic soil.

The life of the coconut palm is about 80 to 100 years. At five years, the diameter of the bole is that of the mature palm, and the height may be 2 to 5 m. to the growing point. Nut production commences by the fifth to seventh year. The final height attained is about 25 m. and the diameter about 50 cm. at two meters above the ground. The bole may be almost 1 m. in diameter. The roots stretch out from the base of the bole leaving a woody cavity inside. The fronds have a very short basal sheath, and are 3 to 5 m. long. The palms are generally planted in rows spaced about 4 m. apart in the Palaus.

On the average, about 12 to 16 new fronds and about 60 coconuts (extremes 20 to 600) are produced per year. A healthy palm may display 25 to 35 fronds and more than 75 nuts of different sizes at one time. The nuts grow to full size in six months and ripen in 13 months (Copeland, 46). The innermost new leaves grow at the rate of 2 cm. per day, making adult beetles in the center of a crown difficult to extract by hooked wires or rods (Friederichs, 113). The fronds on a palm at a given time represent about two years' growth, a new frond emerging in two to three weeks, so damage to a palm may be dated by observing the location on the crown of damaged fronds. The growing portion of the crown contains about five fronds at one time. The palm undergoes no appreciable seasonal cycle during the year in the Palaus.

A variety of the coconut palm, plentiful on some atolls of the western Carolines, grows only to a height of about 2 m. at the base of the crown, producing nuts within easy reach of the arm. Some growing on Kayangel Atoll were not observed to be affected by *Oryctes.* Extraction of adult beetles from the crowns should be simple in this type of palm.

Habitat Notes on Field Headquarters

Ngiwal, selected for field headquarters, is a village with a population of 280 and is the seat of the municipality of the same name. It is located on the east coast of Babelthuap Island, just north of the middle, on flat sandy land just behind a sand beach which stretches the whole length of the village and farther to the north. There is no mangrove swamp along the beach, except at the north end some distance from the village, and a very little near the mouth of the stream. There is a hill and rocky promontory (Pkulata Prival) at the southern end of the village, separating it from another beach backed by a long coconut grove bordered behind by a low forested hill. This latter beach and coconut grove end at the deep-water Ngiwal pier at the northern outlet of the large Namai Bay with its Ngarakis Island and extensive mangrove swamps. At the base of this pier is the Ngiwal sawmill discussed elsewhere.

The north end of the Ngiwal beach ends in a mangrove swamp and then a hill, behind which is a nipa palm swamp. Beyond the hill is an extensive mangrove swamp. A small stream which drains the amphitheatre behind the village (fig. 2, *b*) enters the sea on the north side of the shallow-water Ngiwal pier. Near the mouth of the slow-moving stream is a small nipa palm swamp edged with coconut palms growing in a semi-swampy land. The village ends just north of the stream. The village is on sand, at an altitude of less than 1 m. at high tide.

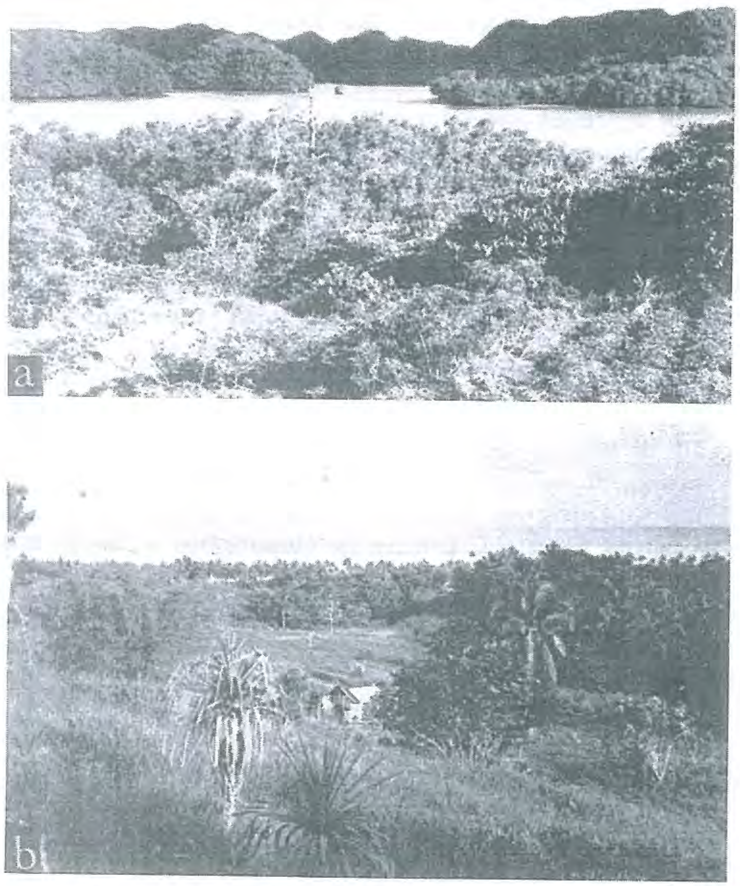

FIGURE 2.—Palau Islands: **a**, view from volcanic portion of Koror showing undercut limestone islands, eastern Koror and Auluptagel in background; **b**, view from grassy amphitheatre behind Ngiwal village, which is at extreme right background.

The reef is one kilometer from the shore with much of the intervening sand exposed at low tide.

Behind the village are the taro fields, on low, wet, mucky black swampland, with sugar cane and *Cordyline* growing along some of the paths through them. The cassava (tapioca) and pineapple fields are on the slopes of the amphitheatre, which otherwise are mostly grassy with scattered *Pandanus tectorius* but with some jungle. The soil there is red and clay-like and allied with bauxite. On the tops or far slopes of most of the hills is jungle. The coconuts which originally grew throughout the village area, among the taro fields, and on the slopes of the amphitheatre have been killed. Betel-nut palms, breadfruit trees, banana and papaya plants, several kinds of *Citrus, Annona squamosa* and *A. muricata,* guava, kapok, *Calophyllum inophyllum,* and some native trees and plants grow in the village area, and four oil palms grow behind a house near the middle of the village. The sago palm grows in a part of the swamp. Two other palms, *Pseudopinanga insignis* and *Heterospathe elata* var. *palauensis,* grow in the nearby jungle. Three ecological types of *Pandanus* grow in the vicinity.

Ngiwal was chosen for headquarters because it had a high population of the rhinoceros beetle and many dead palms but with the majority still living. It was also considered to be typical of coconut-growing communities of the Palaus.

The giant toad (*Bufo marinus*) is not found at Ngiwal, though it is found farther north and farther south on the east coast of Babelthuap. However, monitor lizards (*Varanus indicus*), which die from feeding on the toad, do not seem to be abundant at Ngiwal. Monitor lizards are reported to be common around Ngkeklau, which is only a few kilometers north of Ngiwal. The giant African snail (*Achatina fulica*) is also apparently lacking or almost absent at Ngiwal. A few of their shells are seen being utilized as homes by hermit crabs between Ngiwal village and the Ngiwal sawmill and pier. The villagers say the snails are rare because the hermit crabs kill them for their shells.

TAXONOMY, MORPHOLOGY, AND BIOLOGY

ORYCTES RHINOCEROS AND ITS RELATIVES

The coconut beetle belongs to the genus *Oryctes* (single unbranched horn on head and contouring or very short horns on thorax) of the subfamily Dynastinae (body large, tibiae strongly spined; head, and often prothorax, horned) of the family Scarabaeidae (antennal segments strongly flattened, mandibles short) of the suborder Lamellicornia (antennae geniculate and lamellate). The classification may be summarized as follows:

Order Coleoptera: beetles
Suborder Lamellicornia: stag-beetles, passalids, scarabaeids
Family Scarabaeidae: scarabs, dung beetles, june beetles, etc.
Subfamily Dynastinae: rhinoceros, muck, and cane beetles
Tribe Oryctini: true rhinoceros beetles
Genus Oryctes: palm rhinoceros beetles
Oryctes rhinoceros (Linnaeus): coconut rhinoceros beetle.

The species was originally described by Linnaeus (Syst. Nat. ed. 10, 1:346, 1758) as *Scarabaeus rhinoceros*.

The genus *Oryctes* contains about 42 species, most of which attack palms and most of which occur in Africa, Madagascar, and nearby islands (Arrow, 11; Bertin, 20; and Lepesme, 190). Four are found in southeast Asia or New Guinea; one in southern Europe and Asia Minor; three additional species in western Asia or Asia Minor (Semenov-Tian-Shanskiĭ and Medvedev, 245), and one, doubtfully an *Oryctes*, on Woodlark Island east of New Guinea. Of the 42 species, 15 are found in Africa, 14 in Madagascar (two of them in common), two on Mauritius, and one each in Reunion (and Bourbon), São Thomé Island, Comoro Island, Socotra Island, Rodriguez Island, and the Canary Islands. One is distributed from south Asia to the south Pacific (*rhinoceros*), another distributed in New Guinea and the New Hebrides (*centaurus* Sternberg). *Oryctes ngu* Mohnike (*trituberculatus*) is found in western Indonesia, in addition to *O. rhinoceros*. *Oryctes nudicauda* Arrow, of unknown host, is recorded from Minhla, Burma.

Of 25 species which attack palms, 15 attack coconut; and four other species probably do (Lepesme, 190). One species attacks *Phoenix* palms alone, and two are recorded only from *Elaeis*. *O. rhinoceros* has 29 host genera; *O. monoceros* has 12 hosts; one species has five, one three, one two, 13 have a single host genus recorded, and three have no definite record but doubtless attack the coconut or some other palm. Several attack sugar cane.

The more serious pests of coconut palms in Africa include *O. monoceros* (Olivier), *O. gigas* Castelnau, *O. boas* (Fabricius), and *O. owariensis* Beauvois. *O. tarandus* (Olivier) and *O. chevrolati* Guérin are pests of coconut on Mauritius and Reunion; *O. latecavatus* Fairmaire, on São Thomé; and *O. pyrrhus* Burmeister, *O. ranavalo* Coquerel, and *O. simiar* Coquerel, among others, on Madagascar.

Oryctes nasicornis (Linnaeus) is a pest of grape vines and grafted slips of grape in Italy (De Stefani, 80; Ferraris, 99), and of crucifers (Schøyen, 244). *O. nasicornis grypus* Illiger attacks *Phoenix* palms in the western basin of the Mediterranean. It was implicated in the spread of the Baioudh disease of the date palm, but the role is reported as secondary by Surcouf (273) and Vayssière (295).

COMMON NAMES

Oryctes rhinoceros has frequently been called the rhinoceros beetle or the coconut rhinoceros beetle. It has also been termed the palm rhinoceros beetle (Essig, 97), the rhinoceros palm beetle (Froggatt, 116), the Asiatic rhinoceros beetle (Simmonds, 254), the coconut palm beetle (Cherian, 40), and such names as the black beetle and the coconut beetle. Unquestionably the first few names have been applied to other members of the genus *Oryctes*, probably all of which attack palms and most of which attack the coconut palm. However, since *O. rhinoceros* was the earliest named according to the accepted system of zoological nomenclature; since it is the most widely distributed and most economically important member of the genus; and since it is one of the most important pests of the coconut palm, which it prefers as adult and larval host, it seems logical that it should be called the coconut rhinoceros beetle. "Asiatic rhinoceros beetle" is technically appropriate, but this name is confusing because of the beetle's role in Oceania. On the other hand, another member of the same subfamily—*Strategus quadrifoveatus* (Palisot de Beauvois) of Puerto Rico and certain other islands of the West Indies—attacks the coconut palm and is called the coconut rhinoceros beetle (Plank, 227).

Common names in other languages include the following. *Arm-ar-alius* (Palauan): "bird (animal) of the coconut palm," *yashi-no-kabutomushi* (Japanese in Palau): "coconut helmet insect" (rhinoceros beetle), *taiwan-kabutomushi* (Japanese): "Formosan helmet insect" (rhinoceros beetle), *manu-i-niu* (Samoan): "insect of coconut," *avi'i-vi'i* (Samoan): "a big beetle," *uang* (Tagalog, Bikol, Hiligaynon, Pampangan): "beetle, especially coconut beetle," *kumbang badak, kumbang kelapa* (Malay): "rhinoceros coconut beetle, coconut beetle," *Klappertor* (Dutch): "coconut beetle," *indischer Nashornkäfer* (German): "Indian rhinoceros beetle," *Oryctes du cocotier* (French): "*Oryctes* of the coconut palm."

DESCRIPTIONS OF THE VARIOUS STAGES

Egg

The egg (fig. 3): Measures 2.3-3.7 × 3.2-4.0 mm. Slightly longer than broad: rounded oval, but not ovate. Clear white, minutely granulated, sometimes becoming yellowish brown before hatching. Fairly hard-shelled.

When first laid the eggs are smaller and somewhat cylindrical, about 2.3 × 3.5 mm., but they gradually absorb moisture during development until they become about 3.7 × 4.0 mm., and nearly round.

Larva

The larva, or grub (fig. 4): The skin is fairly thin, but the head capsule is hard, dark reddish brown, and the mandibles are very strong and capable of biting through human skin. The body is long and somewhat cylindrical, but strongly arched, convexly above and concavely beneath, so that the head may touch the caudal end of the body, forming a ring. The diameter of the body is about one-fifth of its length. The larva appears white where muscles or fat lie beneath the exoskeleton, but the latter is actually transparent, and at least in the posterior part of the body, the blackish, partly digested wood in the alimentary canal shows through, except near molting time or metamorphosis.

FIGURE 3.—Ovaries, eggs, and newly hatched larva.

Larvae of the three respective instars may be distinguished by the size of their head capsules more readily than by their relative body size, as the body grows more or less regularly throughout the larval period, from about 8 mm. long to about 100 mm. The head capsule, or cranium, changes suddenly in size twice with the molting of the exoskeleton from the first to the second instar and from the second to the third. Head capsules of the three larval instars are shown in figure 4, *b*. There is some overlap of size between the instars because considerable waste material is voided before molting and quite a bit of tissue is torn down by katabolism preceding and during the molting process. The measurements of the head capsules and the rough body measurements of the three larval instars are given in table 4.

Table 4.—Larval instar measurements (in millimeters)

	FIRST INSTAR	SECOND INSTAR	THIRD INSTAR
Width of head capsule	2.5-3.1	5-6	9.5-11.2
Length of head to tips of closed mandibles	2.8-3.3	5.1-6.8	11-12.5
Length of body, stretched out	7.6-25	22-65	60-105
Width of body	2.5-7	6-12	10-20

Larval instars: The newly hatched first instar larva (fig. 3) has a head greater in diameter than the body, and the abdomen tapers distinctly toward the posterior end. When newly emerged the head capsule is white like the body, but gradually turns reddish brown during the first 24 hours, during which no food is taken. The head capsule (fig. 4, *b*) is in the form of a broad, slightly convex disk forming, roughly, three-fifths of a circle, truncate anteriorly, with the mouthparts projecting forward in a rounded triangular form. The head capsule, as well as the clypeus and the labrum, is almost entirely covered with moderately close distinct punctures, which are finer on the occiput. The epicranial suture is visible only on the posterior portion of the occiput. The antennae arise from the front margin of the head capsule beside the bases of the mandibles. They are slightly shorter than the mandibles, and have four swollen-cylindrical segments, the last one longer and acute, with about 15 pale sensory spots. The mandibles are longer than their width at base, tapering, but with a large internal tooth some distance from apex, forming a sinuate oblique cutting edge which is about one-fourth the mandible length in the left mandible

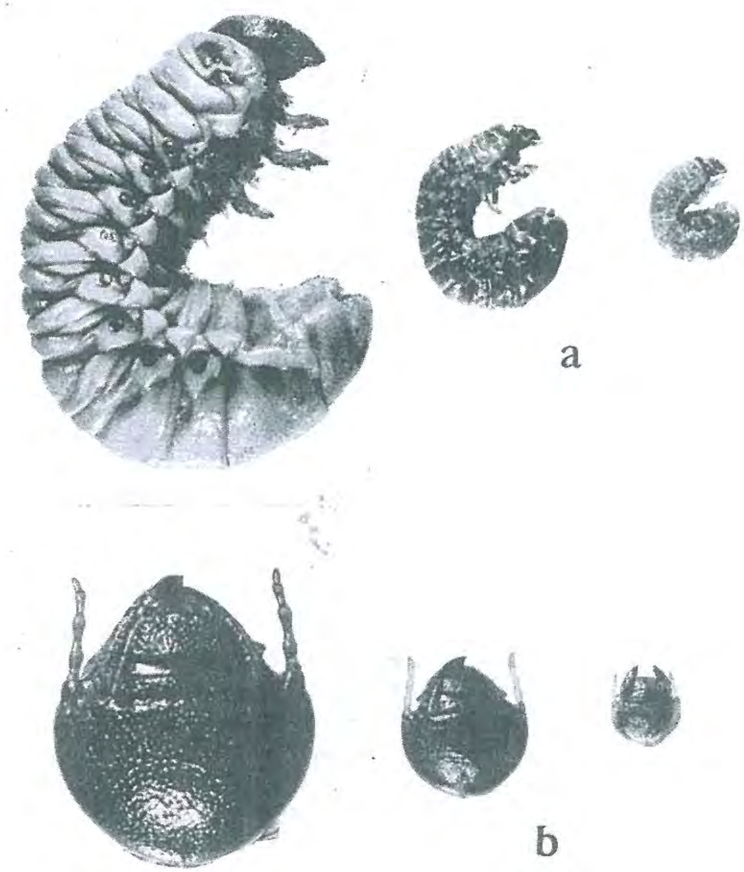

FIGURE 4.—Larvae: **a**, mature third instar, two-thirds grown second instar, and two-thirds grown first instar; **b**, head capsule of third instar, of second instar, and of first instar.

and about one-fifth the length in the right mandible. In addition there is a slightly complex molar area projecting inward near the base, and on the pale portion of the ventral surface a broadly oval stridulatory zone with more than 15 transverse striae, which become finer anteriorly. The labrum is nearly twice as long, in the longitudinal sense, as the clypeus. The frons is very sparsely clothed with erect pale hairs of moderate length. The clypeus and labrum have the hairs much more dense. The maxillae are fairly narrow, and have moderately long three-segmented palpi similar in form to the antennae. The lacinia and the galea are similar and both acuminate, the latter with some added spines. There are five isolated obtuse stridulatory teeth placed sub-obliquely along the dorsal face of the stipes near the external border. The labium is small and bears a pair of two-segmented palpi which are much shorter than the maxillary palpi. The epipharynx (inner surface of labrum) is slightly convex, roughened and asymmetrical. The hypopharynx (near labium) has two heavily sclerotized black asymmetrical grinding structures. Pronotum with about

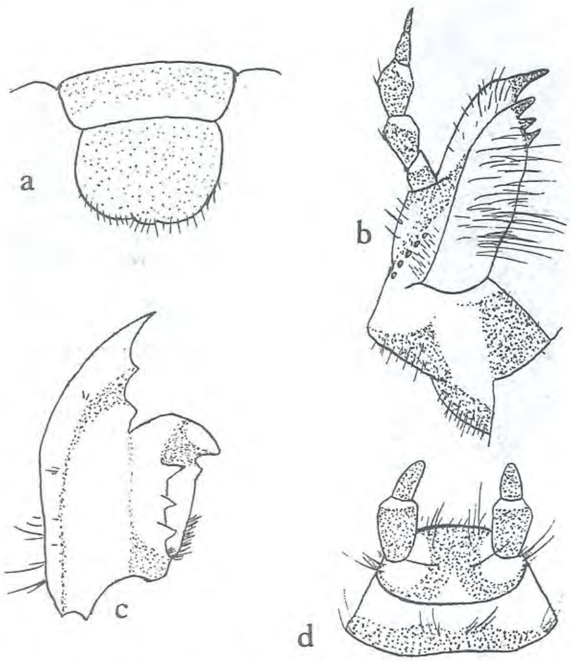

FIGURE 5.—Larval mouthparts: a, clypeus and labrum; b, left mandible, dorsal view; c, left maxilla, dorsal view; d, labium, ventral view.

15 fairly long hairs and some shorter ones on each side. Abdominal tergites each with a similar number of longish hairs, and numerous very short ones on the raised areas. Thoracic spiracle twice as high as wide, subreniform with a narrow, shallow emargination at middle of posterior portion. Abdominal spiracles less than twice as high as wide, more evenly oval; posterior ones broader and slightly emarginate on middle of anterior margin. Anus transverse, terminal and subventral, bordered beneath with a row of numerous long hairs. Other rather long hairs on sides of posterior abdominal segments. The above mentioned structures are not modified by growth during the instar. The body simply increases in size by the adding of body cells which stretches out the folds between the sclerites of the body segments. Legs shiny, with setae more numerous beyond middle. Fore pair shorter,

and hind pair longer, than middle pair. Coxa about as long as trochanter and femur combined; tibiotarsus about as long as trochanter, with a stout claw.

The second instar larva (fig. 4, *a*) differs from the first in size and in having the head capsule more closely punctured and the epicranial suture more distinct; the last antennal segment relatively shorter, less acute; the left mandible having the node near the middle of the inner edge forming a distinct tooth, and that of the opposite side moderately distinct; the thoracic spiracle broader, more oblong-oval, with a slight posterior emargination and with an oval slightly raised bulla just anterior to center; the posterior abdominal spiracles likewise more rounded, but otherwise similar, with the emargination anterior.

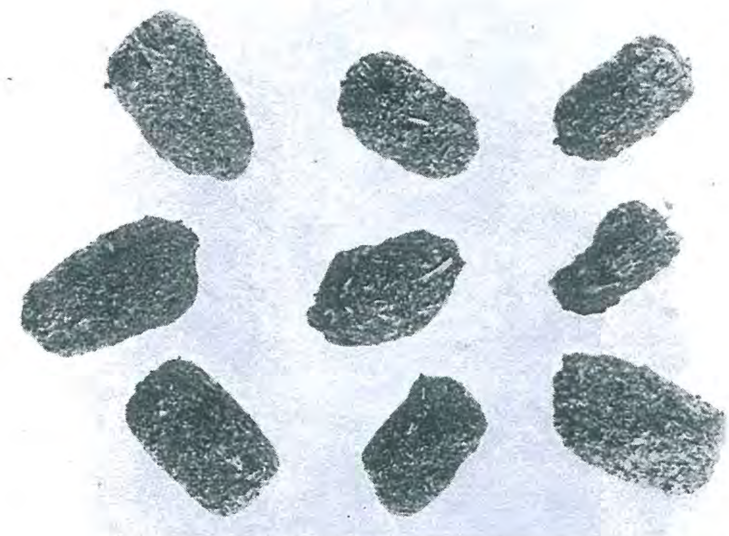

FIGURE 6.—Dried fecal pellets of third instar larvae.

The third instar larva (fig. 4, *a*) has the head capsule still darker; the last antennal segment relatively still shorter and, as in the second instar, with a blunt tip and with about 17 sensory spots; the mandibles (fig. 5, *b*) with more complex molar areas; the pronotum with a large reddish-brown, sclerotized, subpentagonal area on each side just above and anterior to spiracle, with 18 dorsal, and about 50 lateral, bristles on each side. The fifth abdominal tergite has over 250 bristles on each side, many of them very short. The spiracles are much larger than in the preceding instars, relatively more sclerotized, more distinct, more rounded and with the central raised bulla more rounded, and the respiratory plate flat. The dorsum is largely covered with short, not very dense bristles, in addition to the sparse long hairs. The grub is shiny blue-gray, more whitish at sides, until the third week. Then it becomes whiter until it stops feeding, finally becoming cream-colored and somewhat translucent appearing as it shrinks in preparation for pupation.

The feces of the mature larva (fig. 6) are formed in black flattened-elliptical pellets measuring 6.7-9 $\times$ 4-5 $\times$ 3-4.4 mm.

Oryctes grubs may be distinguished from similar (lamellicorn) grubs in Palau and Samoa by the closely and evenly punctured head, the fairly dark cranium, the indistinct epicranial suture, the lack of a pair of conspicuous swellings at tip of posterior end of the body, and the fact that the body hairs are not very conspicuous.

Pupa

The color is somewhat yellowish brown and the body has a somewhat rubbery appearance. Most of the external adult structures can be detected (fig. 7). The sex can generally be determined by the length of the cephalic horn: In the female just once or twice as long as broad; in the male three or more times as long as broad.

The pupa ranges from 39.4 to 51.5 mm. long, 19-23.6 wide, and 16 to 19.4 deep.

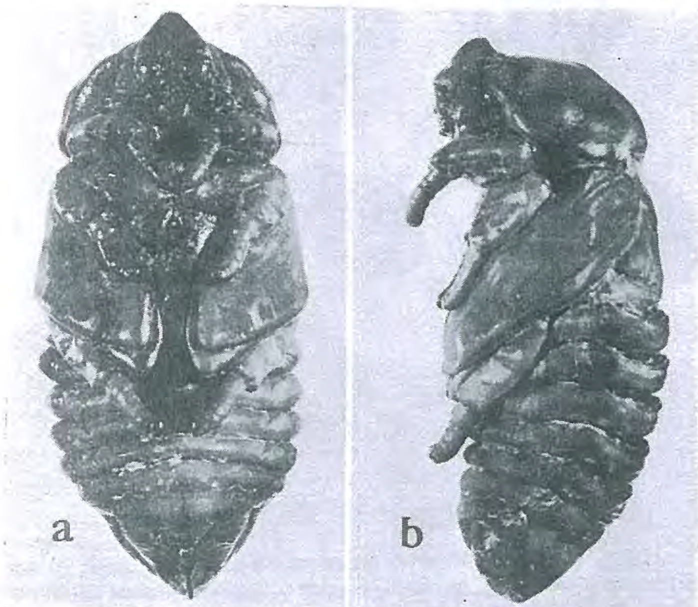

FIGURE 7.—Pupa: a, ventral view; b, lateral view.

Adult

The color is dark reddish brown to black. The surface is rather smooth and shiny, with minute punctures or bristles in part. The ventral surfaces and legs bear distinct reddish bristles. The sclerotization of the exoskeleton is highly developed, and the beetle is extremely strong. The sides of the mandibles and parts of the legs and ventral surfaces of the body are clothed with bright reddish brown hairs.

Male (figs. 9, *a*; 10, *a*): Black to dark reddish brown above and on tibiae and tarsi; reddish brown on thoracic sterna and femora, darker brown on abdomen. Clothed with dense orange-red to purplish red erect hairs on labrum, sides of mandibles, ventral surfaces of prothorax and mesothorax, extreme base of abdomen, and a few beside anus; pygidium shiny and naked.

Body depressed-cylindrical; elytra slightly broader than prothorax, and widest just behind middle; broadly rounded posteriorly. Head small, bearing a large, erect, slightly curved, tapering horn two and one-half to four times as long as its width at base, and rather blunt distally. Prothorax broader than long, widest behind center, tapering anteriorly; anterior concave area largely sculptured in a transverse fashion and top of declivity slightly projecting at center; each side with a depressed crescentic punctured area lateral and on each side posterior to anterior concavity; an additional concave punctured area on each side adjacent to anterolateral angle; posterior portion of disk convex, smooth and only microscopically punctulate except along a groove adjacent to basal margin. Scutellum triangular, blunt behind, finely punctured. Each elytron smooth on humerus and feebly punctured apically, with seven regular rows of punctures; one parasutural and the others in three pairs on disk, the sutural stripe, paired stripes and margin each separated by four or five subregular rows of fine punctures, or by irregular punctures. Pygidium glabrous and minutely punctured; a row of stiff hairs along extreme ventral margin. Length 30 to 57 mm.

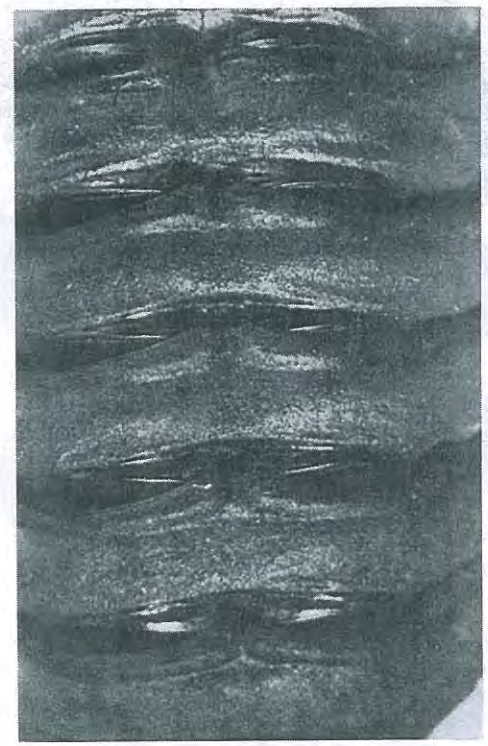

FIGURE 8.—Pupa: dorsal surface of abdomen showing stridulatory structures.

Female (figs. 9, *b*; 10, *b*): Similar to male in structure, but usually with a shorter and relatively stouter cephalic horn. However, this character is not always reliable. For certain determination, attention must be paid to the pygidium, which is entirely clothed with the long, erect, reddish hairs, in contrast to the shiny, glabrous pygidium of the male. Length 29 to 51 mm.

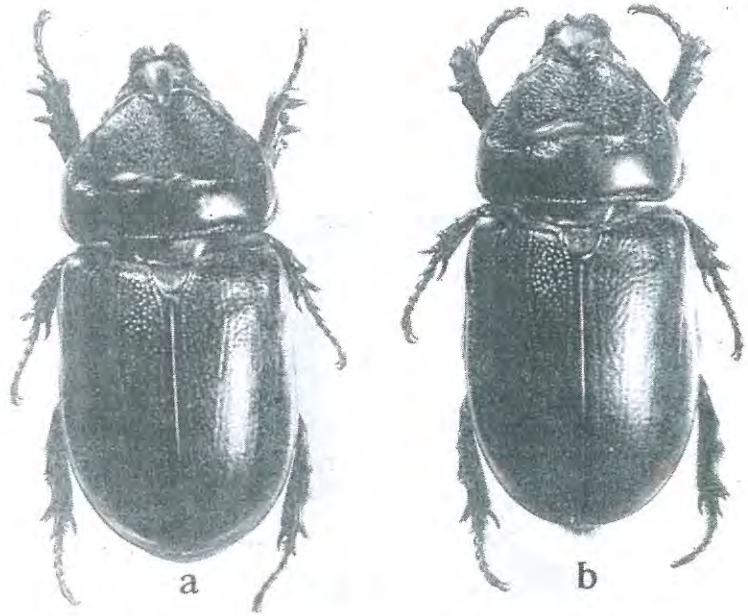

FIGURE 9.—Adults, dorsal view: a, male; b, female.

In both males and females there is considerable variation in size of body and, particularly, in length of the cephalic horn. This is correlated with the environment of the larva. For instance, a larva of either sex in an unfavorable environment—one in which the wood or other food is too dry, too wet, too decomposed, too hard, or a species of plant other than a preferred type, infested with fungus, or otherwise unfavorable—will develop into an adult with an undersized body and very short horn. Or a further extreme may result in deformation or failure to transform satisfactorily from the pupal stage. Under very favorable conditions, a female may develop a horn as long as those of almost the largest males; and conversely, a male may have an almost vestigial horn. Dwarfed, or "minor" individuals, frequently developed from larvae reared in the laboratory, where conditions of the environment were unfavorable. It was particularly difficult to keep the food uniformly damp in the small containers adapted to frequent observation.

Adult *Oryctes* have a slightly unpleasant, weak musky odor. The newly emerged adults have a different, quite strong odor, presumably that of the molting fluid. The pupae also have a characteristic odor.

MORPHOLOGY

This beetle is highly sclerotized, with hard exoskeleton, sharp spines on tibiae, and powerful muscles. The compound eyes are covered with a thick transparent layer of

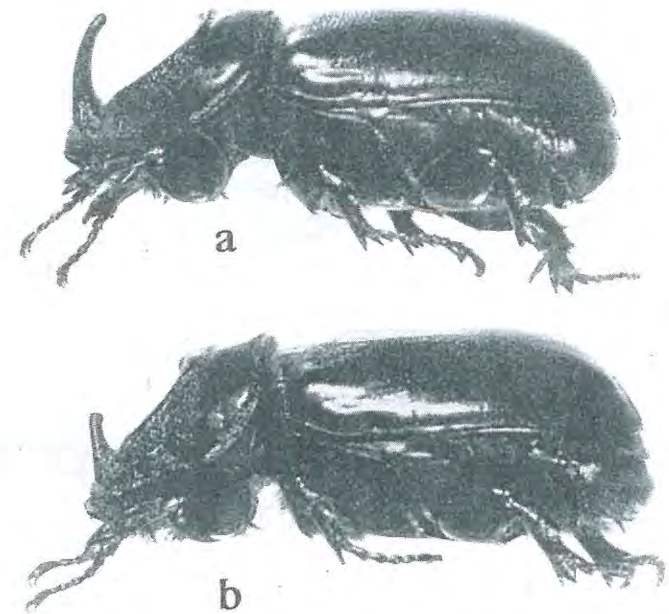

FIGURE 10.—Adults, lateral view: a, male; b, female.

cuticle, with facets distinguishable beneath. A narrow posteriorly projecting flange from base of horn protects central portion of eye. The gular area is in form of a large smoothed ridge which is received in a longitudinal groove in prosternum, serving to keep head from turning to either side when mandibles are used for gouging or horn is used as a lever or pincher. The postocciput is deeply emarginate at each side of center. The antennal club is formed of three rather thick lamellae and is no larger in male than in female. The mandible (fig. 11, *a*) is stout, short, without a straight cutting edge, but with a short, curved blade on lower inner side which operates as a chisel by means of a scraping motion. The maxilla (fig. 11, *b*) has stiff hairs and a four-segmented palpus. Labium (fig. 11, *c*) is long, convex, with many long hairs and three-segmented palpi. The tentorium is in lower portion of head, attached to sides of large convex gular area, in cross section appearing somewhat in form of a broad "H."

The cervix consists of a pair of heavily sclerotized, somewhat compressed and sinuate pieces in the sides of the neck. The mesoscutum is large, broadly trapeziform, the scutellum narrowed and rounded posteriorly, and the metascutum large, hairy, divided into two by the narrow and posteriorly tapering postscutellum. The wing (fig. 12) has nine veins reaching, or nearly reaching, the posterior border. The coxal cavities are large, extending across a large part of each thoracic sternum. First six abdominal tergites smooth, glabrous, yellowish brown to pale chestnut brown. Seventh tergite heavily sclerotized and pigmented, serving as a stridulatory area in producing sound by friction against hind elytral borders. The spiracles are of two types. Each of first four abdominal spiracles large, narrowly elliptical and vertical, with a large, very slightly arcuate opening for almost entire length. The last three are each much smaller, broadly oval, with a subcircular opening. The basal spiracles (fig. 13, *a, b*) are on the pale, feebly sclerotized upper portion of the pleuron, hidden by the elytron, whereas the three hind spiracles are on the lower, heavily sclerotized and pigmented exposed portions.

Internal Anatomy of Third Instar Larva

Digestive system: The alimentary canal (fig. 14) is only a little longer than the body in the larva. From the mouth through the thorax it consists of a straight, slender oesophagus. The posterior end of the foregut is retracted (fig. 14, *c*) to form a valve-like structure just before the actual cardiac valve, where the midgut starts and the canal suddenly increases several times in diameter. The posterior portion of the cardiac valve may fold inward to close the opening, through which the food, surrounded by the peri-

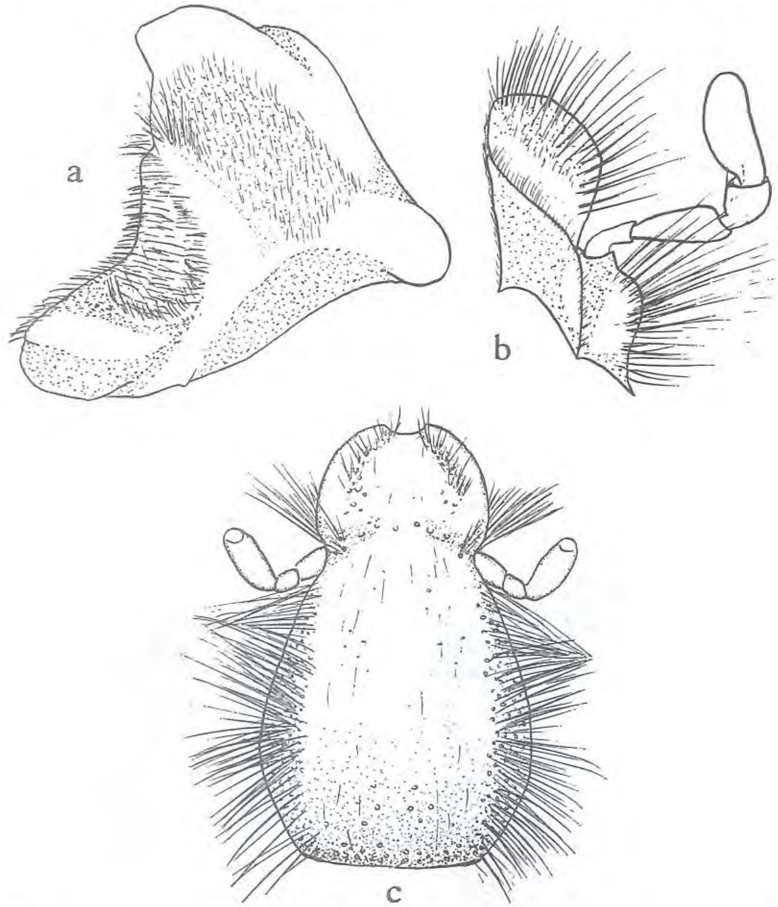

Figure 11.—Adult mouthparts: **a**, left mandible, medial view; **b**, left maxilla, ventral view; **c**, labium, ventral view.

trophic membrane, passes. The midgut (fig. 14, *a*, 4-8) is very large, is always full in feeding larvae, and may be more than one-half as long as the body and more than one-half as great in diameter as the abdomen, but it may be reduced to less than one-third the diameter of the body as metamorphosis approaches and the body cavity becomes crowded with fat storage. It is more or less cylindrical, tapering slightly at the posterior end before meeting the small intestine, which tapers still more. The midgut has a large number

Figure 12.—Hind wing.

of narrow papillae-like coeca at the anterior end, pointing anteriorly and folding over the anterior end. These are followed by a broad band of dense circular muscles on the anterior sixth or so. Just behind this band is a continuous ring of about 20 moderately large coeca, pointing backward along the gut and each tapering to a point. Following these, the central portion, about three-fourths of the length of the midgut, is thin-walled, with the muscles very thin, except for four long strips of longitudinal muscles extending the entire length, one on each side and each consisting of two large muscle strands, besides some shorter, more slender longitudinal strands near the posterior end. A short distance anterior to the

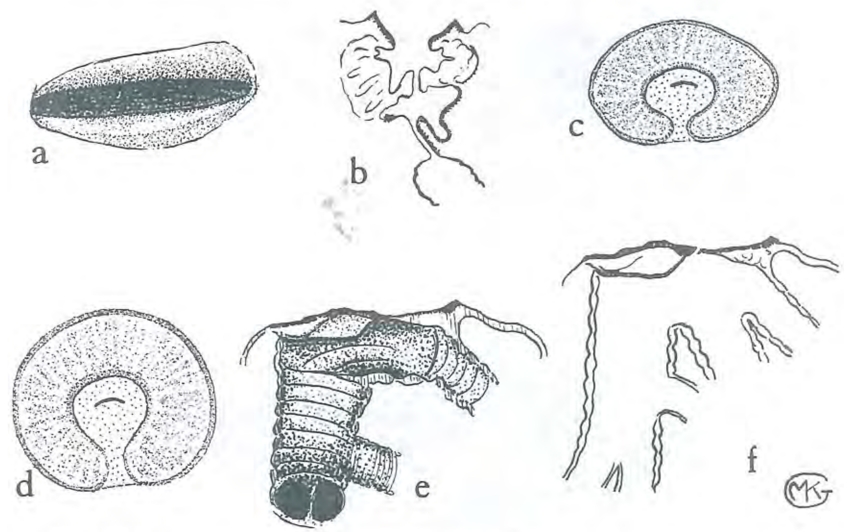

Figure 13.—Spiracles: **a**, adult spiracle, third abdominal segment; **b**, transverse section of same showing trachea below; **c**, thoracic spiracle of larva; **d**, eighth abdominal spiracle of larva; **e**, transverse section of fifth abdominal spiracle of larva; **f**, diagrammatic section of same.

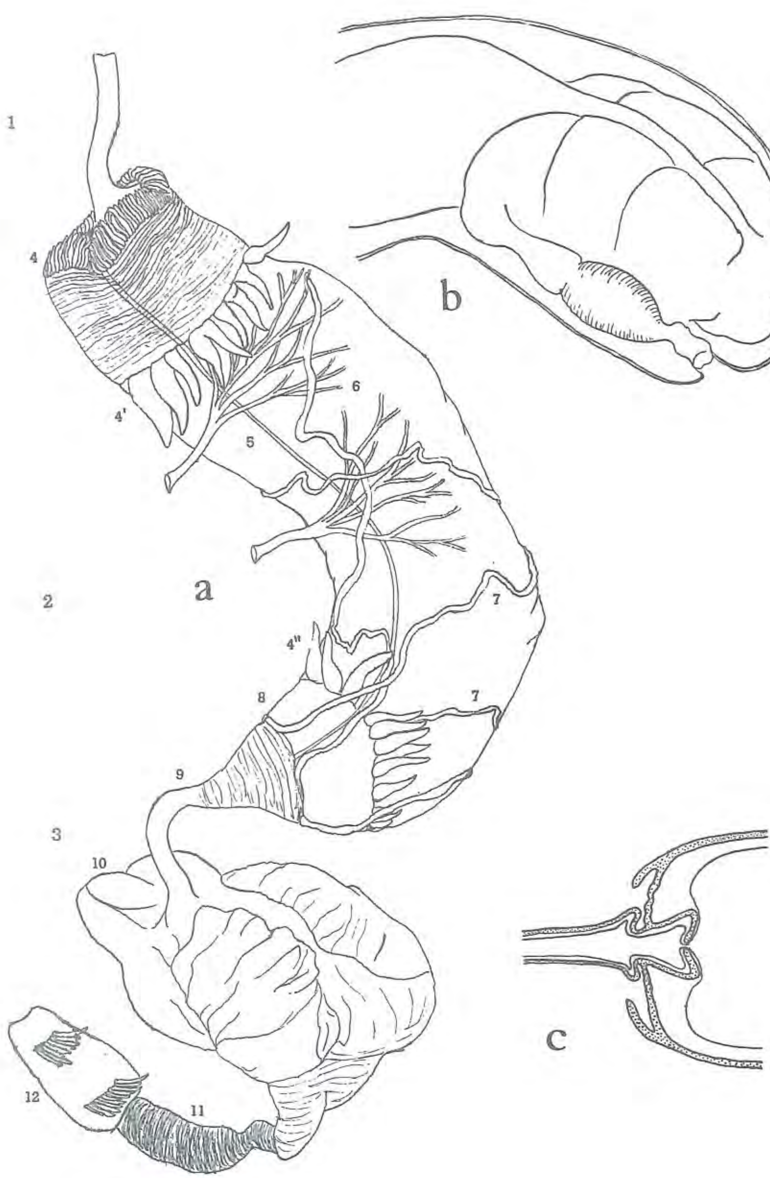

FIGURE 14.—Digestive system of larva: a, alimentary canal; b, posterior two-fifths of abdomen showing folding of hind gut, with beginning of colon situated posteriorly and end situated anteriorly; c, longitudinal diagram of cardiac valve at anterior end of midgut. 1, foregut; 2, midgut, from 4 to 8; 3, hind gut, from 8 to 12; 4, 4', 4", three sets of coeca; 5, lateral side of midgut; 6, tracheae on surface of midgut; 7, Malpighian tubules; 8, termination of Malpighian tubules between midgut and hind gut; 9, ileum; 10, colon; 11, rectum; 12, rectal sac.

posterior end of the midgut is another band of gastric coeca, similar to the preceding group, but directed anteriorly.

The division between the midgut and hindgut is marked by a strong ring of circular muscle and the attachment of the four Malpighian tubules (fig. 14, *a*, 7), one pair attached adjacent to each other, the other pair widely spaced, on the other side. The anterior end of the ileum (fig. 14, *a*, 9) tapers strongly to a cylindrical slender tube for a short distance. The hindgut then suddenly enlarges, forming the colon (fig. 14, *a*, 10), which is swollen, irregular in shape though roughly ovate, and may be even larger in diameter than the midgut, and as much as 15 mm. wide. It is covered with circular muscle strands, with longitudinal muscles external to them in two wide strips, and has some irregularities in surface contour. The colon is only a little longer than broad, and ends suddenly, changing to the moderately slender rectum. The rectum (fig. 14, *a*, 11) is at first approximately 5 mm. in diameter and very muscular, with groups of longitudinal muscles both internal and external to the close circular muscles. It then becomes more slender and is more or less cylindrical with the circular muscles external for a distance of more than 15 mm., when it finally meets the rectal sac. These portions of the hindgut are somewhat folded on themselves (fig. 14, *b*). The rectal sac is the terminal portion of the alimentary canal and is

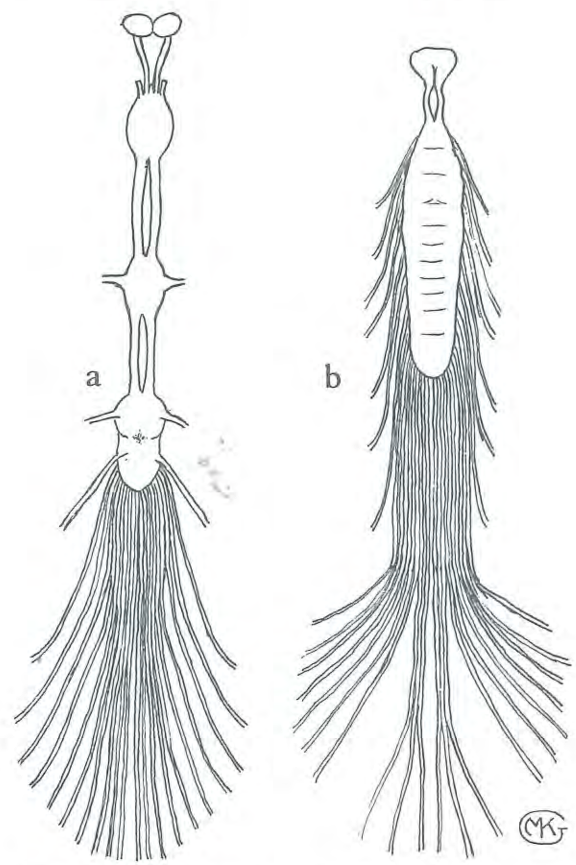

FIGURE 15.—Central nervous system: a, larva; b, adult.

thin-walled, without distinct muscle strands. The outer surface bears three pairs of isolated groups of papillae appearing like very small coecae, one of each pair before the middle and the other beyond the middle. This sac ends with the transverse anus.

The lining of the foregut has many longitudinal ridges or folds, that of the midgut is macroscopically rather smooth, that of the ileum is folded when empty, and that of the colon is irregularly corrugated to nodose or papillose, in part with short hairlike processes. The lining of the rectum is moderately smooth to slightly wrinkled and that of the rectal sac is quite smooth.

Excretory system: There are four Malpighian tubules (fig. 14, *a*, 7), attached to the gut in one adjacent pair and one widely spaced pair. The tubules are very long and for the most part lie in a sinuous fashion on the wall of the midgut, extending forward from its posterior end.

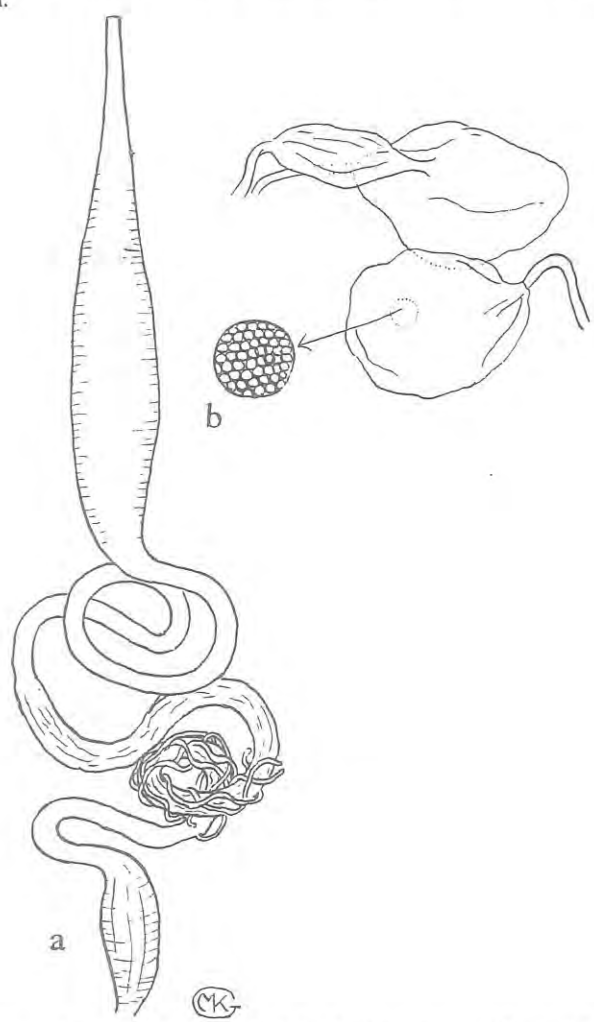

FIGURE 16.—a, Digestive system of adult; b, air sacs in abdomen of adult, showing enlargement of surface of sac.

Respiratory system: The larval tracheal system consists principally of a very large main trunk on each side of the body, connecting with the spiracles and branching to all parts of the body. The spiracles have a cavity beneath each which passes directly into three to 10 tracheae of different sizes, the largest going direct to the main lateral trunk, the others to neighboring areas.

Muscular system: The head and neck are well equipped with muscles for moving the mandibles and other mouthparts, as well as the head. The thorax has much less of a concentration of muscles than in the adult, because of the lesser function of the legs, and lack of wings. The dorsal and ventral muscles are largely thin and flat, and are both longitudinal and obliquely longitudinal. They may be in more than one layer near the hind borders of the segments or where oblique, but they do not cover the entire inner surface of the dorsum and sternum posteriorly. In the sides of the segments the muscles are more numerous and thicker, a few of them almost cylindrical, and are most numerous in the neighborhood of the pleural lobes on the sides, which function somewhat like prolegs in locomotion, as do the terga and sterna.

Circulatory system: The heart is a very thin-walled, flattish tube running along the mid-dorsal wall of the abdomen. "Wing" muscles between the segments force the blood forward through the thorax.

Nervous system (fig. 15, *a*): The brain is small, with a pair of cerebral and optic lobes. The suboesophageal ganglion is well developed, but simple. The prothoracic ganglion is similar to the suboesophageal, but a little larger. The mesothoracic ganglion is partially fused with the common metathoracic-abdominal ganglion, the combined structure being located at the border of mesothorax and metathorax.

Internal Anatomy of Adult

Digestive system: The alimentary canal (fig. 16, *a*) consists of a slender tube, about three times the length of the body. It extends in a straight line just above the ventral nerve cord from the neck through the thorax. In the abdomen it curves back and forth many times, particularly in the dorsal half of the abdomen, above the reproductive organs and below the heart and air sacs. It appears to be of fairly uniform thickness almost throughout, with numerous slight swellings or irregularities, except after feeding, and with subdivisions not very distinctly demarked. The midgut is long and slender, but may be as much as 4.5 mm. in diameter when engorged. Coeca are lacking or minute. There is a slight swelling just before the constriction between midgut and hindgut, where the four slender Malpighian tubules are attached. The hindgut, for a length of about 1 cm. before reaching the anus, becoming the rectum, increases in diameter and has thinner, less spongy walls, with the circular muscles fairly close and the longitudinal, outer muscles widely spaced. The rectum passes dorsal to the reproductive structures and descends to the anal opening closely adjacent to the inner wall of the pygidium.

Excretory system: Four slender Malpighian tubules wind along the midgut and empty into the gut at the commencement of the hindgut.

Respiratory system: Along each side of the body cavity is a large tracheal trunk, besides some accessory ones, with connections to the spiracles and organs. There are one pair of thoracic spiracles and eight pairs of abdominal spiracles (fig. 13, *a*). There are relatively few air sacs in the thorax, and most of them are in the ventral portion above and on each side of the oesophagus. Air sacs are numerous in the dorsal portion of the abdomen (fig. 16, *b*) being crowded above and between the upper folds of the alimentary canal; most of them 1.2 to 1.6 mm. long. There are about 600 in the abdomen.

Muscular system: The most extensive muscular development is in the thorax, where the muscles are principally involved in flying, walking, and in moving the head and horn in relation to the prothorax. The muscles in the head are concerned with the mandibles and other mouthparts and antennae. In the prothorax the muscles in the dorsal portion partly extend horizontally for its entire length, some of them being attached to the inner

FIGURE 17.—a, Reproductive system of adult male: 1, testes; 2, *vas deferens;* 3, accessory glands; 4, ejaculatory duct; 5, aedeagus. b, end view of parameres of aedeagus.

surface of the cavity forming the emargination in the exoskeleton on each side of the middle of the postocciput, for pulling the horn backward. Others extend obliquely forward and downward from the mesoscutum, connecting below the middle with the phragma anterior to the thoracic spiracle, and more or less continuous with the episternal-epimeral suture in the prothoracic acetabulum, with other muscles continuing from the anterior face of the phragma to the inner end of the cervical sclerite. In the central portion of the metathorax, the longitudinal muscles extend from the dorsal wall almost to the ventral wall of the body. Anteriorly they attach to a phragma of the anterior border of the mesothorax, which is nearly 5 mm. in height. On each side of this large central area are the extensive tergosternal muscles.

In the abdomen the longitudinal tergal muscles are in a thin layer adjacent to the dorsal wall stretching from anterior to posterior margin of each segment. These muscles are absent along the central portion where the dorsal blood vessel runs. There are no

longitudinal muscles on the ventral wall of the third to fifth sternites. Muscles concerned with moving the terminal portion of the abdomen in mating or oviposition are attached to the sides of the inner wall of the pygidium, but not along the middle of the inner face of the pygidium, where the rectum descends.

Circulatory system: The heart or dorsal aorta runs along the dorsal wall of the abdomen adjacent to the exoskeleton. It contains seven chambers, each tapering laterad for some distance from the aorta along the intersegmental line. The blood appears to pass through the thorax along an ill-defined break in the longitudinal muscles through the upper central portion of the thorax.

Nervous system: The central nervous system (fig. 15, *b*) is much abbreviated with the concentration of the ganglia in only two units. The first is the brain, which consists essentially of two principal lobes, with several pairs of small branch nerves. The brain connects by means of the circumoesophageal connectives with the combined suboesophageal, thoracic, and abdominal ganglia. This structure, which is about 3 mm. long and runs the length of the prothorax beneath, and just anterior to, the front end of the midgut, is shaped like a miniature of the entire body, as far as relative length of the subdivisions is concerned. The portions representing the different segments of the thorax and the abdomen may be distinguished, and each has at least one large pair of nerves originating from its side. The last division has at least two pairs. The nerves to the thorax branch out into the respective segments, and those for the abdomen extend posteriorly in a single layer forming a wide median strip of adjacent nerves, separating posteriorly. Seven pairs of nerves pass beyond the third abdominal segment.

Male reproductive system (fig. 17): The testes are 12 large, distinct structures located laterally in the lower hind portion of the abdominal cavity. Each is almost round, compressed, nearly one-half as thick as wide, slightly concave on each side, but more so on the side where the very slender, separate sperm tube is attached in the central concavity. The opposite side has a central ring with a translucent, thinner-walled center. Each testis is nearly 4 mm. in diameter. The *vasa deferentia* are at first slender, sinuous and confused with branching accessory glands before thickening considerably, and then becoming more slender before joining with the outlets to the accessory glands to form the ejaculatory duct, which is relatively short and strongly thickened till it meets the aedeagus.

The aedeagus is a large, heavily sclerotized structure entirely retracted within the body when copulation is not taking place. It measures 10 mm. or more in length and consists of a large, less pigmented bulbous portion occupying nearly two-fifths of the total length, and a terminal, red to blackish smooth portion with a strong, paired hooklike structure, directed slightly backward, at the end, consisting of the forceps. The central portion has a deep groove along each side, and the apex articulates slightly with the terminal portion.

Female reproductive system (fig. 18): The ovaries are of the polytrophic type. Each pair consists of six ovarioles and each ovariole may contain at least six developing ova. Thus a total of at least 72 eggs may be developing at one time. Since these are laid at the rate of about 10 or more per day during an egg-laying period, and since a female may live a few months, well over 100 eggs might be laid during the normal life of a female. The spermatheca is oval, thick-walled and several millimeters long. The colleterial glands are slender, long, and sinuous, opening into the vagina near the union of the spermathecal tube and the common oviduct.

The female genitalic structures (fig. 18, *b*, 9) consist of a pair of broad, two-segmented lobes, lying on each side of the entrance to the vagina. The basal segment is broad, almost square, and slightly pigmented, the terminal segment more sclerotized, setose, and rounded in distal outline. In addition, there are two pairs of sclerotizations at the union of the rectum with the vagina, the inner pair narrow and oblique, the outer wider and transverse.

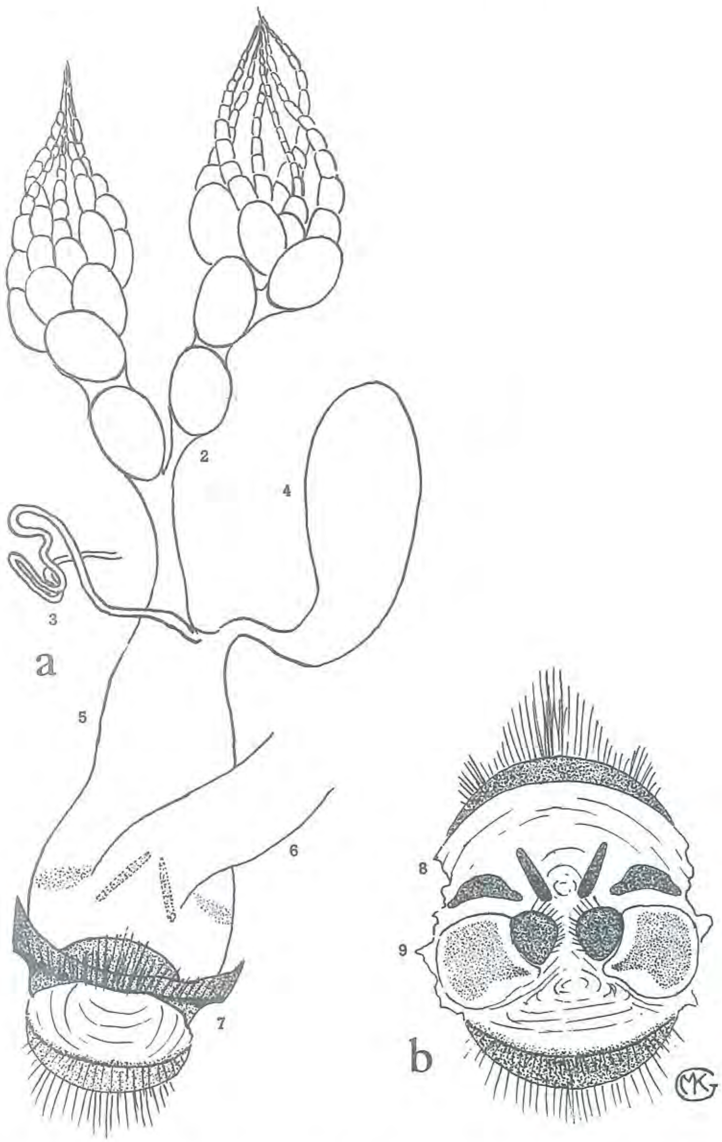

FIGURE 18.—a, Reproductive system of adult female: 1, ovaries; 2, oviduct; 3, accessory canal; 4, spermatheca; 5, vagina; 6, rectum; 7, anus. b, posterior view of anal opening: 8, intestine opening between oblique sclerotizations; 9, vestigial valvifers and valvulae of ninth abdominal segment of each side of opening of vagina.

PHYSIOLOGY AND ENTERIC BIOTA

Since the food of the larva, decaying wood or other rotting vegetable materials, is relatively low in nutritive value, large quantities of food must be eaten. Correlated with these feeding habits is a large alimentary canal, which is nearly a centimeter in diameter, and large quantities of common types of bacteria which assist in breaking down the materials to be digested. Stained microscope slide smears from the inner walls of larval midguts were made in Palau and Samoa, and were examined by Steinhaus. They demonstrated that the bacteria were not specific, but were common types and that there were apparently no protozoans present.

Since this is a large-bodied insect, the tracheal system is highly developed, with large spiracles, many branched tracheae, some of the main trunks nearly 2 mm. in diameter, and numerous air sacs, particularly in the adult. The relatively weak flight of the adult is undoubtedly correlated with its large body in the physiological, as well as the aerostatic, sense. The movements of the larvae are likewise slow. The larvae can thrive under high temperatures in compost or other decomposing materials. A temperature of 39° C. was measured adjacent to larvae, and situations still hotter were found, where the grubs were very warm to the touch.

LIFE CYCLE

Metamorphosis is complete, with four stages: egg, larva, pupa, and adult. The egg stage lasts about 11-13 days, under optimum tropical conditions, but has been reported as lasting 8 to 18 days. It took 22 eggs laid on October 1, 12 days to hatch. The eggs change from the cylindrical to the rounded form about five days after being laid. The larva hatches from the egg by splitting the egg shell in a somewhat irregular fashion.

The larval period is divided into three stadia separated by molts. A short resting period precedes each molt, during which the body weight decreases. The length of a larval period is about two to three months. The range in reared specimens was 80 to more than 130 days. From marked groups of larvae of the same age kept outdoors in normal circumstances, the normal average for the Palaus is considered to be about 72 days. Since there are no discernible climatic seasons in the Palaus, this is considered to be true for any time of year, varying only under abnormal or unfavorable conditions such as insufficient or excess moisture, rotting, and fermentation or other transformation of the food material. The average duration of the first stadium is assumed to be about 19 days; of the second, about 21 days; and of the third, about 32 days. The last includes a pre-pupal resting period of about 7 days (average for 30, 6.7 days) during which time no food is taken, the body loses weight, and the skin shrinks and becomes a creamy or pinkish white.

The pupal stage lasts 16 to 24 days, generally 18 to 21 (average for 41 was 19.6 days). This is a period of resting and transformation from larva to adult and no food is taken. The adult remains in the pupal cell 17 to 22 days after transformation. The length of the adult stage ranges from two to four months or more. I assume the normal averages to be about 90 days for males and 100 days for females. Labitte (182) records 37.5 and 55.5 day averages for *Oryctes nasicornis*. Leefmans (183) records four to four and one-half months for *rhinoceros* adults in captivity.

The total life span in Palau may range from 150 to about 270 days, and I assume the average under normal conditions to be about 200 days. The pre-incubation period is about 12 to 20 days. The period from the laying of an egg to the first egg of the next generation may be as little as 115 days. Thus, given favorable circumstances, more than three generations may develop in one year.

In Palau, development is apparently even and continuous throughout the year, hence individuals of all stages exist together. In Indo-China (Caresche, 35) the life cycle may occupy three to nine months, according to the time of year in which the egg is laid, which may be throughout the year. Lepesme (190) states that in New Guinea *O. rhinoceros* lays only at the beginning of the rains, but this probably refers to *O. centaurus*. In Madagascar and Mauritius other species of *Oryctes* have a single generation per year, correlated with contrasted seasons.

BIOTIC POTENTIAL

A female beetle lays 70 to more than 100 eggs in its lifetime. Taking 90 as the average number of eggs laid by one female and assuming the sex ratio to be one female to one male with an average life cycle of four months (to middle of egg-laying period of each female), the theoretical figure of 186,390 progeny per original female during one year (16,995,293,890 by the end of two years) is obtained. This explains the rapidity with which the coconut palms were exterminated on Koror, Arakabesan, Angaur, and Malakal Islands and the almost complete extermination on Peleliu and southernmost Babelthuap. That extermination of the host plant has not taken place elsewhere is assumed to be the result of limitations of suitable breeding media and environmental resistance. The introduction of a few grubs in Samoa in 1909 resulted in the collecting of some 7,000,000 grubs and 240,000 adults within three years (Burkill, 29), without stopping its spread.

SEX RATIO

Of 282 specimens examined from Palau and Samoa, 142 were males and 140 were females. This suggests a ratio of about 1.014 males to one female. The 282 specimens included a large proportion reared or collected in the field from pupal cells, so should be a reasonably fair sampling. Other workers have indicated males and females to be about equal in number (Friederichs, 109).

STRIDULATION

The adult male *Oryctes* produces a distinct stridulation by the friction of the dorsal surface of the last abdominal segment against the posterior borders of the elytra (Gravely, 135). The sound—a low, somewhat grinding, squeak-like call which is seldom uttered—appears to be a sign of annoyance, but may be a mating call, as it is produced only by males. Sound is produced by friction in back and forth motions, the double stridulation being repeated in fairly rapid succession about four times. The series is often repeated at intervals of about one minute or more by a single individual, even in cages containing several males.

The pupa also makes a faint stridulatory sound, more continuous but slower and much fainter than the stridulation of the adult. This sound is made by friction of the dorsal sclerotization of the abdominal segments (fig. 8) produced in rotating slightly the end of the abdomen (the only pupal movement). It is felt as a distinct vibration when the pupa is held in the hand. The paired structures occur between each two segments from first to sixth with a rudimentary pair between the sixth and seventh. The anterior edge of the posterior segment scrapes over the fine, oblique ridges on the segment anterior to it, and the cavity beneath provides resonance.

The larva is able to make some sounds by scraping the teeth on the upper portion of the stipes of each maxilla against the ridged stridulatory area on the under side of the respective mandible. One evening in the laboratory a rapid, high-pitched, vibrational sound was heard from some mature larvae in a tin can. Possibly the sound was amplified by contact of the mandibles with the can, as it has been stated that the sound may not be audible to human ears (Gardner, 109; Gravely, 135).

LARVAL HABITS

Not all dead wood is satisfactory for oviposition or development, nor is any type of compost. Wood that is too hard, or too wet, or hardened by having been soaked in water is not suitable. However, the wood may range in consistency from fairly solid and moderately dry through mealy or pulverized to almost soggy. Coconut is preferred. Other types most frequently attacked are *Pandanus*, breadfruit (*Artocarpus*), *Calophyllum inophyllum*, and mango (*Mangifera*). In general, either the wood must be soft enough for the adult female to bore its way in for egg laying, or there must be some hole, injury, crack, or softer part (such as the center of the top of a coconut trunk) for the beetle to make a start and lay a few eggs. Compost containing banana stalks appears to be particularly favorable. There is no clear evidence that the larvae will feed on coconut roots, though they eat wood closely adjacent to the roots and are found in soil mixed with coconut trunk chips around the root stumps. It is assumed that the roots are too hard or contain some chemical which is unfavorable for the physiology of the larvae. It has been stated by some that larvae will not eat coconut husks. However, Cherian and Anantanarayanan (40) and Mackie (202) record rotting husks (coir refuse) as a host, and when husks are mixed with other material in compost piles, larvae may at least be present near them. Some other beetles (tenebrionids and weevils?) feed in the rotting husks, which are left in large piles in many coconut groves after copra has been extracted. As shown by the food tests recorded below, larvae are able to live upon husks.

Farm manure and old latrines also serve as breeding places for the grubs. In these situations moisture and respiratory requirements are significant factors, and the grubs are mostly around the outer edges of dung heaps (Kunhi Kannan, 181).

The larvae are normally scavengers but may feed in the trunks of living palms (Hobley, 148) when the tree is seriously injured by adult feeding, by some injury to the palm which causes local rotting, or by the accumulation of debris among petiole bases of fronds which are delayed in falling. Several such scarred palms, probably attacked after war damage, were observed at Airai, Babelthuap.

Larvae of *O. rhinoceros* have been recorded from living stems of sugar cane by Muir (212); and both larvae and adults of *O. monoceros* have been reported in sugar cane, and once in sisal in Zanzibar (Aders, 1). *O. nasicornis* is said to feed on roots of fruit trees as larvae (Plotnikov, 228), and larvae of other *Oryctes* to feed on roots of sugar cane (de Charmoy, 66) or other roots (Aders, 1). Larval damage by *O. rhinoceros* to young teak seedlings in a nursery in India is reported by Chatterjee (39).

The newly hatched larva generally finds some sawdust left by the parent female in her boring for oviposition (fig. 19, *a*) on which to start feeding before commencing on more solid wood. The movement of the larva may vary with the hardness of the wood, or with dampness, rotting, density of larvae, or competition. Normally, a number of larvae are found close together, and the distance traveled by a single larva may be as little as a few centimeters. The volume of wood consumed by one larva during its entire development is estimated at about 500 cubic cm. As many as 150 larvae have been found in one coconut trunk (1.8 m. high) at one time, and presumably 1,000 beetles could develop from one palm within a few months.

It is believed that the larvae in compost travel considerably more than those in wood. The larva is generally found in the soil or rich compost at the lower

level of rotting vegetable matter, such as banana stalks, breadfruit leaves, papaya skins, taro remains, and miscellaneous garbage. This material may contain old coconuts or coconut husks in various conditions. The larvae may travel more widely in sawdust and are apt to be farther apart than in wood. They may be found far below the surface.

A young larva moves in an exposed situation by walking with its thoracic legs, with the end of the abdomen curved to one side (generally the left). Some-

FIGURE 19.—a, Old coconut log showing nearly mature larva in pale wood at upper left, some eggs in center behind adult female at end of exposed oviposition tunnel; b, fragment of old coconut trunk with several pupal cells and three pupae in their cells.

times it may nearly straighten out. A mature larva on a flat surface may walk in a manner similar to a young larva; stretched nearly straight, walking on the ventral surface using the legs; or on the back, moving the segments by contraction and expansion as does an earthworm. In wood, larvae are in the natural curved attitude, and move about largely by means of expansion and contraction of the abdominal segments, both longitudinally and transversely, making use of the swellings on the sides of the segments. Larvae have been found under charred bark of a trunk which had been partly burned. Larvae may be found in wood in close proximity to nests of ants or termites with no apparent friction between them, but the ants attack the *Oryctes* larvae when the latter are exposed. Large numbers of *Anoplolepis longipes* may band together and carry off first or second instar grubs.

Apparently the larvae are cannibalistic when circumstances demand. A small larva kept in close confinement with a larger one was partly eaten when suitable food was exhausted.

In molting from the first instar to the second or from second to third the grub first becomes somewhat sickly and pearly and semi-translucent in appearance as it rests in preparation. It also appears to be more hairy than the full-fed mature grub, as the body has shrunken in the period between the last feeding and the molt. The more hairy-appearing character is also true of newly molted grubs, since they have the full complement of setae for the instar, but grow with feedings by stretching the folded portions of the sclerites. The molting process consists visibly of a swelling in the thoracic area, and by this time the new spiracles of the next instar can be seen through the skin about to be shed. With the pressure from the fluid between the new and old skin, aided by muscular action, the old exoskeleton splits, while the suddenly enlarging new head capsule continues to press against the old capsule for leverage until the body is more than one-half free. The process to this point takes about eight minutes, but the freeing of the posterior portion of the body requires only one minute. As the body emerges quite a bit of colorless fluid is released. When newly emerged, the larva is white with only the tips of the mandibles blackish and the spiracles and the setae very pale reddish. An hour later the head, legs, and spiracles are pale pinkish amber, and two hours after molting these are reddish brown but still pale. Pigmentation is not complete for nearly 24 hours. The larva defecates a single pellet some minutes after the molt. The exuviae are white and pliable except for the head, legs, and setae.

Pupation

When the larva has finished its feeding, it prepares a place for its transformation to the adult stage. If in a standing trunk, it may bore inward into solid wood and not remain in the hollowed region under the bark (fig. 19, *b*).

It then makes an oval cell measuring about 55 × 35 × 33 mm. in size, and the entrance is stopped up with sawdust, frass, or feces. If the surroundings have been completely pulverized, it uses semi-liquid excrement to help construct a cell wall more stable than the loose sawdust and old feces pellets. Often in the soil, beneath decomposed logs, or beneath compost, a rather large cell may be constructed with walls as much as an inch thick, of fibers, debris, or mud. Pupation has been observed about 15 cm. deep in ground beneath manure heaps (Coleman, 44) and at similar depths under compost; and in sawdust it may occur a meter or more beneath the surface.

Figure 20.—Pupal cell, in longitudinal section, from which adult emerged at upper end, made of stringy fibers from top center of a dead coconut trunk; larval and pupal skins in bottom of cavity.

When the metamorphosis from larval to pupal stage takes place, the larval skin splits down the back as in a larval molt and the old skin is pushed backward and becomes pressed against the wall of the bottom of the cell (fig. 20), leaving the fresh pupa.

Adult Habits

When the beetle metamorphoses from the pupal to the adult stage, the pupal skin is shed somewhat irregularly in pieces or sheets, but generally with the skin of the dorsal surface remaining intact and that of the legs, wings, and abdominal sternum detaching separately or remaining partly attached. The new adult remains in the pupal cell for 17 to 22 days, until it is fully sclerotized and ready to chew its way to the outside, if necessary. When it first emerges the adult is nearly white, soon becoming reddish brown. After about 12 hours it is nearly fully pigmented, except for the elytra which are still pale red-brown. In 24 hours pigmentation is almost complete. The adult emerges in the evening and proceeds to fly, looking for a feeding site and then for a mate.

Mating takes place at night, but also in daytime in such protected situations as a standing or felled trunk and in cages. In copulation the body of the male is at right angles to that of the female.

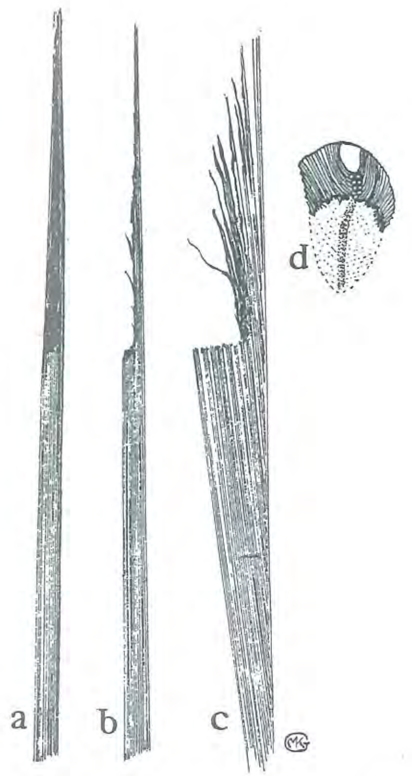

FIGURE 21.—Central developing frond of coconut-palm crown tunneled by adult beetle: **a**, front view; **b**, side view, unopened; **c**, leaflets partly expanded; **d**, cross section with eaten portion dotted.

The feeding habits (figs. 21, 22) of the adult *Oryctes* make it the serious pest that it is. The adult beetle flies at night from its place of emergence in a rotten log, stump, trunk, or compost heap to the top of a living coconut palm. It then enters the side of an upper or middle frond near the growing point by crawling down the upper surface of the petiole, crowding its way down between that and the one inward from it. It then bores inward (figs. 23, 24) to, or

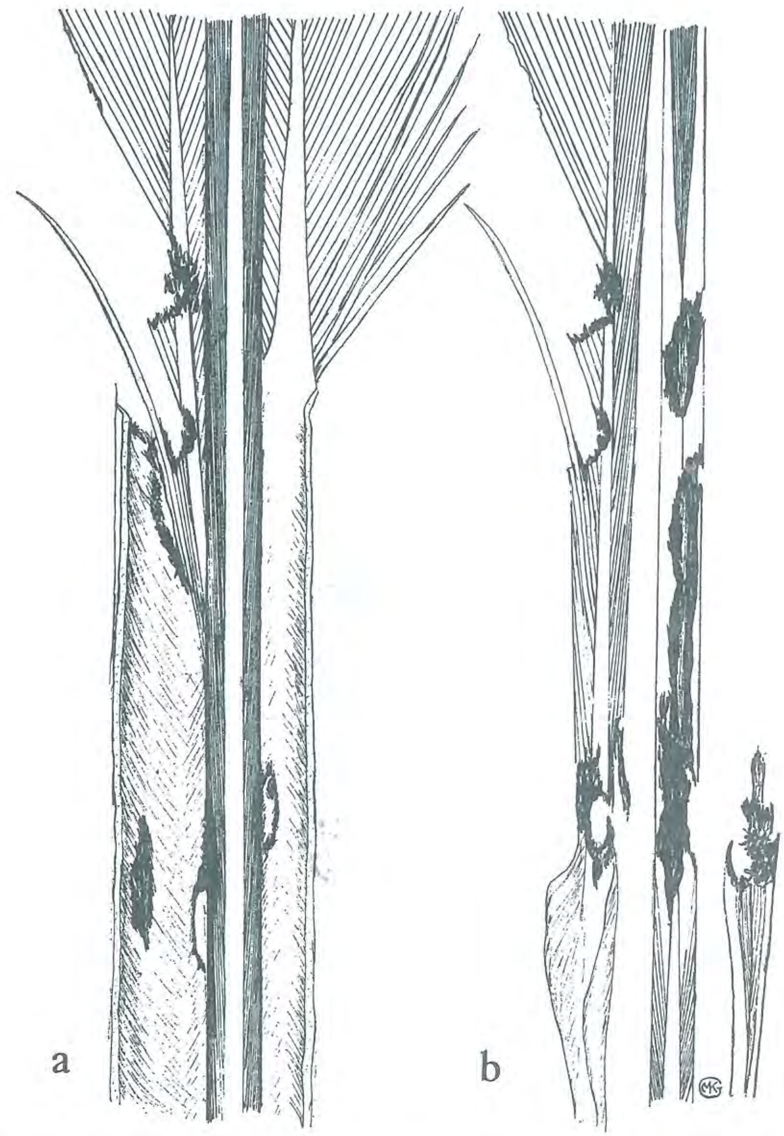

FIGURE 22.—Work of two adults in crown of young coconut palm: **a**, partially opened crown; **b**, three inner fronds separated, showing frond at right severed and one at left nearly so.

near to, the center of the crown above the growing point and digs its way downward through the white center consisting of the new fronds or inflorescences which are soft and compactly folded as long, vertical semicylinders. It sometimes bores upward (fig. 27), contrary to Friederichs statement (113), though not frequently, since the inner fronds of the crown grow faster than the outer ones. The beetle does not ingest the solid plant material, but sucks

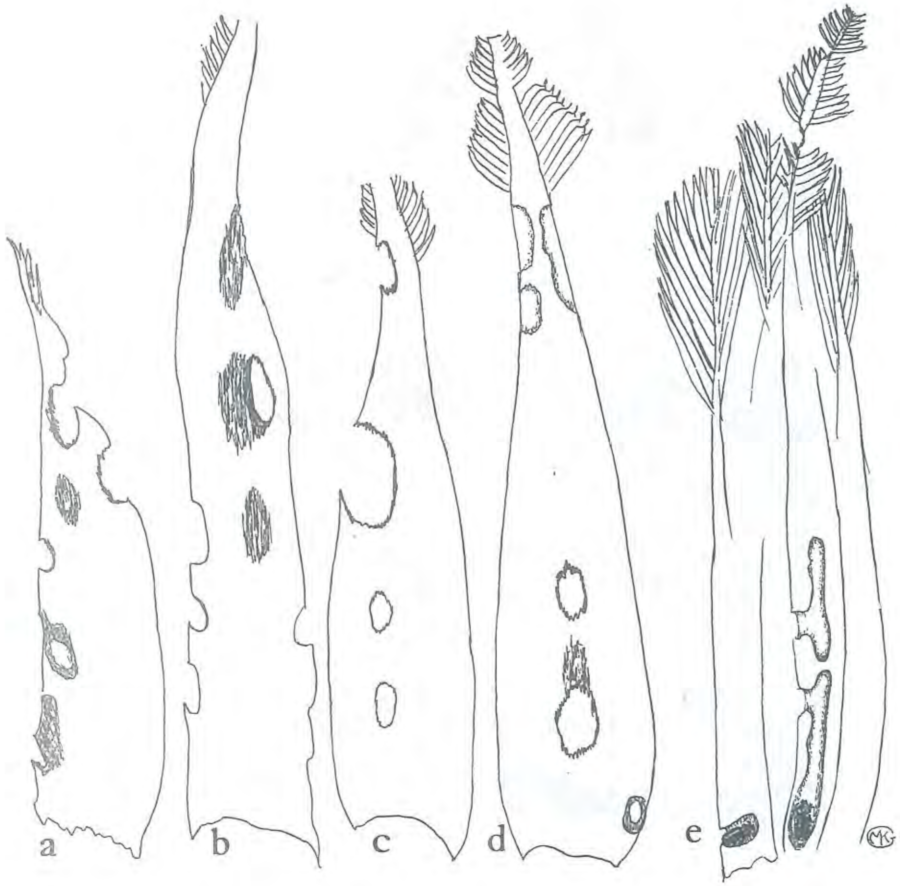

FIGURE 23.—Dissection of crown of recently killed mature coconut palm, showing work of six or more adults: **a-d**, outer four fronds, removed. **e**, inner fronds in sagittal section, showing three tunnels containing two adults; female in lower center tunnel had finished feeding and was ready to exit or was reversed during felling of palm, male in feeding position in new tunnel entered through hole in lower right corner of *d;* entrances to two central tunnels pass through centers of fronds *c* and *d* and through sides of fronds *a* and *b*.

the juices that flow upward from the macerated cell tracts. It chisels with its mandibles by up and down motions of the head, rather than by chewing. In boring it also uses its clypeus, horn, and fore tibiae. The beetle thus generally bores holes through the bases of two or more fronds. It may bore downward 5 to 30 cm. into the softer cabbage, backing out or turning around in the soft interior.

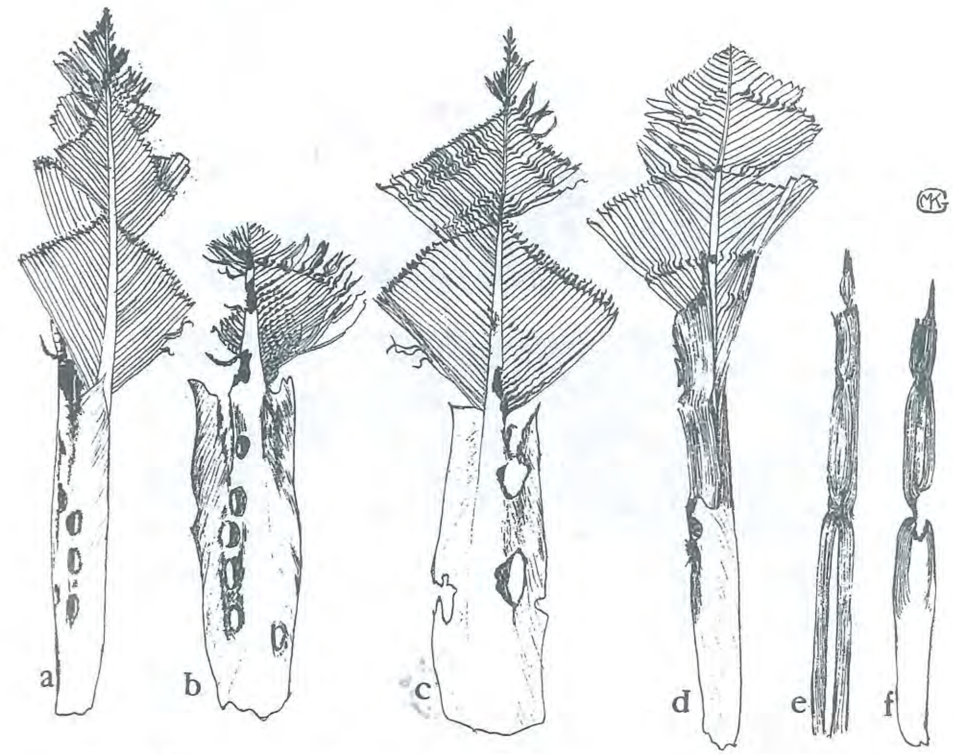

FIGURE 24.—Dissection of crown of recently killed mature coconut palm, showing partial evidence of work of at least nine adults over a period of time: **a**, central portion of crown, undissected; **b**, outermost frond of *a;* **c**, next frond; **d**, third and inner fronds together; **e**, fifth and sixth fronds, growth stopped; **f**, fourth frond, severed

The boring cuts off a frond (fig. 25), or it leaves large angular symmetrical gaps in the leaflets of one or more fronds (figs. 23, 29), where the inner portion of the unopened frond is chewed, leaving the midrib. Or, the terminal portion of a frond may be left hanging from a partly severed midrib. Frequent attack by a number of adults results in the death of the palm. As many as three or four adults may feed in the crown of one palm at the same time. In addition, holes are left in the petioles through which the beetle enters (figs. 24-26). Rarely, adults bore into partly grown nuts causing them to drop from the palms, and into date palm inflorescences tapped for toddy (Friederichs, 109).

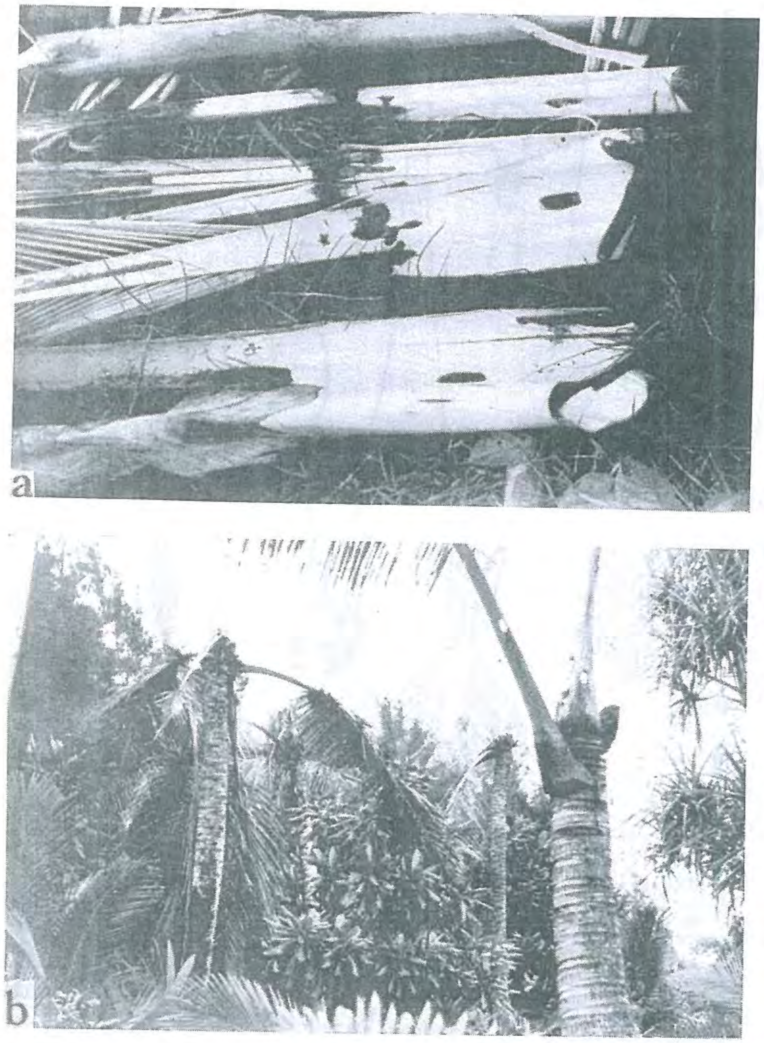

FIGURE 25.—a, Dissection of crown of a probably killed three year old coconut palm, Peleliu, showing feeding tunnels of three adults, the middle tunnel having severed innermost fronds (upper center). b, four half-grown killed coconut palms on east coast of Peleliu, palm at right showing entrance holes of four or five adults in the two persisting petioles; *Pandanus* at right probably attacked by adults.

In sugar-cane stalks the beetle bores upward in the stem from the bottom, entering from the ground at the roots (Van Deventer, 287). Rarely, according to Friederichs (109), the beetle may bore into the husk of a green coconut. Feeding takes place day and night and may continue for two or three days.

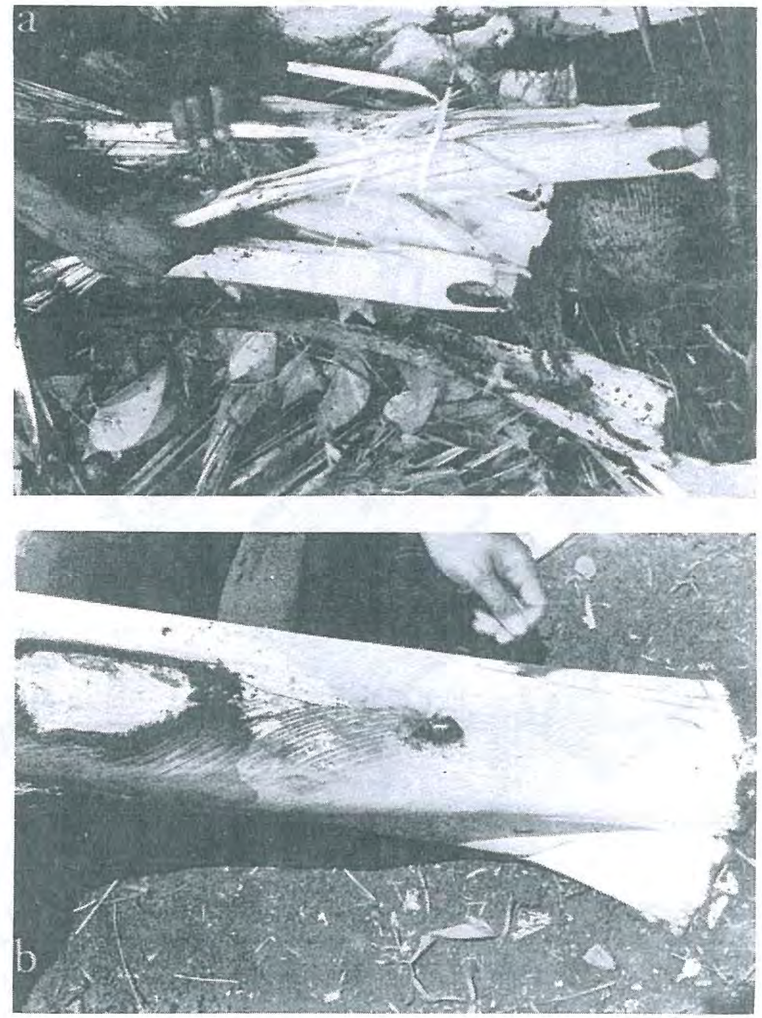

FIGURE 26.—Adults in coconut palm crowns: a, adult in tunnel in upper portion of crown of grown palm; b, crown of mature palm with outer fronds removed, showing adult entering new tunnel, old scar at left.

Of two adults found when a dying palm was felled, one remained in the severed crown for more than 48 hours, moving a total of 30 cm. down the center of the crown toward the growing point. It had entered the crown 1 m. above the growing point instead of at the very top of the crown (fig. 28, *b*). Table 6 and two detailed palm analyses (pp. 52, 61) record information on adult feeding habits.

FIGURE 27.—Adults boring upward in coconut palm crowns: **a**, adult reaching center of crown of six-year old palm; **b**, adult tunneling straight up center of crown of three-year old palm.

The adult beetles appear to have a gregarious instinct which tends to cause more than one individual to attack a palm at the same time, whereas a neighboring palm may be unattacked. This habit may be partly correlated with the meeting of the sexes in the tops of palms for mating, followed by feeding in the same palm, but the following experiment suggests that other factors are involved.

FIGURE 28.—Adults in coconut palm crowns: **a**, adult tunneling downward from top of crown, Babelthuap; **b**, adult nearing center of crown of five-year old palm, Tutuila.

In the outdoor cage at Koror seven adults were admitted on August 23, four more were added during the following week, and others later. Several adults attacked one of the three similar one-year-old palms more or less simultaneously, and within a week at least two adults had bored into the center of the palm by entering at the base of one of the few slender fronds (fig. 30, *b*). Since there was room for only one burrow down the center of the plant, it was not unusual to find two or three adults in the same burrow at once. Three openings were noticed after a few days, presumably because of overcrowding, and then some tunnels into the ground were found near the base of the palm.

On September 6 two males and two females were inside the palm. An adult was once found several inches below the surface of the ground in one of the tunnels. The ground was hard and full of pieces of broken glass and concrete. About three weeks after the first feeding was noticed the palm was completely hollowed and the center of the crown had collapsed, being severed at the base and leaving only the drooping outer fronds. At this stage it resembled the palms less than one year killed in northern Peleliu (fig. 43, *a, b*).

FIGURE 29.—Adult feeding in young coconut palms: **a**, tunnel near top of crown of three-year old palm, Ngiwal; **b**, scars of two previous feedings on stunted four-year old palm, and two scars on frond at left, Peleliu.

I noticed that from time to time a feeding adult backed up in its burrow and pushed the frass resulting from its feeding out of the entrance with its hind legs and body. One adult was seen to back up to the opening of the burrow and a considerable amount of fluid appeared to pour out from under its elytra, after which the beetle again descended into the tunnel. This fluid is assumed to have been a mixture of excess palm sap, rain water, and liquid beetle excrement which accumulated in the burrow and found its way under the elytra by means of surface tension or the creation of a vacuum under liquid surroundings (fig. 30, *b*). It is apparent that the beetles are accustomed to wet surroundings, as attested by the fact that adults can feed in the generally submerged crown of the nipa palm. That the environment in the cage was not

ideal was evidenced by the fact that most of the adults confined in the cage for long periods became moderately infested with mites.

The second of the three palms in the cage was not attacked until two weeks after the first palm was killed, or six weeks after the experiment started. Feeding was commenced by a female which had emerged from the pupal stage 26 days before. Within a few days other adults were feeding in the same palm, which died in two weeks. The third palm and a new one substituted for the first were not fed upon during the three months of the experiment. These results seem to suggest that adults may prefer to feed in a tunnel bored into a coconut crown by another adult, but two or three adults may be found in individual burrows in one palm crown at the same time.

The first four eggs were found in the cage 13 days after the first adults were admitted and about a week after the first feeding was observed. These were laid by a female removed from its pupal cell 29 days earlier in a somewhat teneral state. The next eggs were found 18 days after the experiment started, also in a log (fig. 30, *a*), and laid by another female from the same source, and thus about 35 days old from the time of metamorphosis. On October 25, a female 38 days old (from metamorphosis) was found to have laid 18 eggs in a log. All these eggs hatched. Adults were frequently found resting in the pile of coconut-wood chips, and some overlooked eggs were found to have hatched into larvae at various times. Sometimes a male and female adult were found together inside a log. One female was found burrowing in the ground underneath a log. Some adults burrowed into the ground at or near the edge of the cage and even though the screening was sunk about 25 cm. into the ground, some escaped by digging beneath the screen. In small cages, adults forced their way directly through brass screening, using horn, clypeus, and fore tibiae. An adult female may feed for several days in a palm, during the 10 to 20 day pre-incubation period, before searching out a place in which to lay its eggs. After laying a series of some 20 to 40 or more eggs during a period of three or more days, the female probably leaves the larval habitat and proceeds to a palm to feed again for a few days, while further eggs mature in the ovaries. Past workers have reported 50 to 71 eggs (Leefmans, 183) or fewer, except for Cherian, who reported 140 eggs (40). Friederichs assumed that there was a single egg-laying period (113). The adult females generally die in the situations in which they lay their last eggs.

Arrow (12) states that from the leg structure it would appear that the two sexes of species of *Oryctes* work together as in *Strategus*. However, I fail to detect dimorphism in the legs of *O. rhinoceros*. Banks (14) assumes that males might dig egg tunnels for the females, but I have found no such evidence. I often found females tunneling alone in wood for egg laying. The females definitely make their own feeding tunnels in the palm crowns. In nature, no more than one adult was found in a single feeding tunnel, even when more than one adult occurred in the same crown.

FIGURE 30.—Outdoor observation cage, Koror: a, two adults on section of coconut log: male, above, disturbed; female in oviposition tunnel at center. b, one-year old palm fed upon by several adults; one adult backed to opening of tunnel (upper left center), voiding liquid excrement and accumulated fluid from beneath elytra.

The adult beetles, being nocturnal in habit, are attracted to artificial lights at night. However, the attraction is apparently not very strong. Most records obtained of beetles entering houses have been between 8:00 and 8:45 p.m. (See table 5.) J. S. Armstrong informed me that in Apia he observed them

attracted up to 9:00 p.m. Some have stated that the beetles are not, or only rarely, attracted to light. Pastor Fey told me that while he lived in tents just after his return to Koror from Babelthuap in the fall of 1945, two or three adults were attracted every night. This is apparently an index of a very dense population in view of the accumulated records. One adult was observed flying about a lime tree and a breadfruit tree at 5:00 o'clock on a dull rainy afternoon (October 9) in Ngiwal. Flight in cages was noticed at 5:20 p.m. A female has been seen to move its head rapidly up and down just before taking to flight.

Table 5.—Flight of adult beetles to light at night

Aug. 1, Koror, female	Sept. 21, Koror, 8: 45
Aug. 10, Koror, 8: 15, male	Sept. 21, Koror, 8: 45
Aug. 16, Koror, 8: 30	Sept. 22, Koror, 7: 45
Aug. 16, Koror, 8: 30	Sept. 27, Ngiwal, 7: 45, female
Aug. 17, Koror, 9: 00	Sept. 28, Ngiwal, male
Aug. 18, Koror, 8: 30, female	Oct. 6, Koror, 8: 15, female
Aug. 22, Ngiwal, 7: 50, female	Oct. 9, Ngiwal, 7: 45, male
Aug. 23, Ngiwal, 8: 30, female	Oct. 12, Koror, 8: 50, male
Aug. 23, Ngiwal, 8: 30, female	Oct. 13, Koror, 8: 50, female
Aug. 23, Ngiwal, male	Oct. 29, Koror, 6: 20, female
Aug. 25, Ngiwal, 7: 50, male	Nov. 12, Koror, 8: 12, male
Sept. 3, Peleliu, 8: 45, male	Nov. 13, Ngiwal, 8: 25, female
Sept. 8, Koror, 8: 40, female	

According to an anonymous author (7) *Oryctes* adults may attach themselves to trunks by means of their horns. Lepesme (190) states that Ghesquiere saw *O. owariensis* use its horn in making its feeding gallery in an oil palm crown. Doane (83) also describes the beetle's use of its horn. From handling many adult *O. rhinoceros,* I found that the horn is frequently used as a tool for exerting leverage, particularly in helping to force its way through a small opening, in removing obstacles, in gaining purchase, and by operating against the pronotal ridge as a pincer, possibly both for protection and for attachment. On a smooth level substrate a beetle is unable to right itself. One adult can easily push a weight of 500 grams when the weight is placed on a container covering the beetle on a table top.

ECOLOGICAL RELATIONSHIPS IN THE PALAU ISLANDS

ADULT FOODS

The coconut palm is the favorite and principal food of the adult *Oryctes rhinoceros*. Mature palms are preferred, but when they are lacking, even year-old palms may be attacked. A palm analyzed at Ngiwal (Oct. 17, 1951) was 22 m. tall and 25 cm. in diameter, nearly dead, bore no coconuts, and had only a few green fronds left, most of them dwarfed, distorted, or truncated. Its condition was attributed solely to *Oryctes* attack. The temperature inside the crown was 29° C., one degree below air temperature at the time of felling (10:30 a.m.). A single adult *Oryctes* had just bored downward about 8 cm. from the top of the center of the crown, where it had entered, chewing parts of the newest emerging fronds. Earlier attacks may have fatally damaged the palm. The contents of the crown included one adult male *Oryctes;* a small calandrine weevil in tip of crown; a dead, medium-sized histerid beetle between petiole bases; earwigs; black cockroach nymphs; a centipede; a millipede; a small gecko; and sowbugs. A newly killed palm (Ngiwal, Nov. 10, 1951) had been attacked almost simultaneously by four or more adult *Oryctes* (fig. 24) one or two weeks previously, as well as by additional ones earlier. In all, probably 10 to 15 adults had attacked the palm within the preceding few months. The larger unopened fronds had been severed some distance from their ends, and rotting had commenced at this point. The growing point did not appear to have been touched. The wood of the trunk was somewhat hardened. Animals present were an earwig, a few large red ants, parasitized red coconut scale scattered on lower fronds, a *Lithobius,* several *Porcellio,* and a short earthworm. Some abstracted notes of adult feeding in coconut are presented in table 6.

Table 6.—Adult feeding in living coconut palms

Locality, Month	Adults	Sexes	Notes
Ngiwal, Aug.	2	male, female	Palm dying; fronds dropping; female tunneled 30 cm.
Ngiwal, Aug.			33 cuts in fronds leaflets; 15 holes in petioles; almost no nuts.
Ngiwal, Aug.	1	female	Adult dead; center of crown fallen, top rotting; fly larvae and earthworms in smelly top.
Ngiwal, Aug.	2	male, female	Dying; 20 cuts in remaining fronds; male in upper mid-crown; female near top.
Peleliu, Sept.	2	male, female	Top malformed; attacked many times; one nut.
Ngiwal, Sept.	2	male, female	Dying; newest fronds very short; malformed; female in center, male going into side; both near base of crown.
Airai, Oct.	2	male, female	One in center, one in top of crown.
Airai, Oct.	1	female	Young palm.
Ngiwal, Nov.	1	female	Palm dying; all fronds affected. Brontispa, earthworms, cockroaches, isopods found.

In *Pandanus tectorius,* the adult beetle bores into the area of the growing point at the tip of the crown by crawling in between bases of terminal leaves and chewing its way inside, perforating the bases of several leaves as it goes to the center. (See figures 37, 38.) The result is an irregular chewing off of the terminal halves or more of several new leaves, or the destruction of some leaves, in addition to the making of the holes forming the entrance tunnel

through the bases of a few leaves. The tunnel may continue downward for some 12 cm. and come out on the side of the stem (fig. 37, *c*). Frass may be left at the point of entry, as in coconut. The plant or branch is doubtless killed when the growing point is chewed, when more than one adult attack at once, or when rotting sets in following the feeding by an adult. However, feeding by an adult does not necessarily kill the plant. Sometimes a few new leaves may be sent up before the plant dies (fig. 38, *a*). One plant appeared to have died when new, malformed leaves were caught in a hole made in an older leaf by an *Oryctes* adult.

This widely distributed and common plant of the tropics is found not only on the coasts, but in swamps and jungle and on open ridges and slopes. It perhaps used to grow in much of the area now planted to coconuts, but still covers a large area in the Palaus. The Palauan species are *P. tectorius, P. dubius,* and one other. Only the first was found infested (figs. 37, 38), but it is by far the most common on all the islands. Both ecological forms of this dominant *Pandanus* are attacked: the large, erect, generally unbranched swamp-inhabiting form and the branching, treelike form found on level mixed-forest land, coastal strips, grassy ridges and slopes, and high or low coral islands.

Ample evidence of adult feeding in *Pandanus* plants was observed in inland Aimeliik municipality on October 19, 1951, where more than 125 plants of the erect swamp-inhabiting form had been killed by *Oryctes* (fig. 38, *b*) and others were being attacked. At the southern end of Angaur Island much evidence of adult feeding in living *Pandanus* was observed on October 22 and on December 1 to 3, 1951, when in a small area near the extreme southern tip almost every one of more than 50 plants of the branching form was affected by recent adult feeding, many of them being dead. Many dead plants or dead branches or plants with holes and cavities are seen in the main Palau village on Angaur. Evidence of attack was seen on a number of other islands, mostly those just north of Peleliu, and on some of the high limestone islands.

This plant has not been recorded as a host from other countries. Oakley (214) mentions that he and Townes found *Oryctes* only in coconut in the Palaus, but Owen (216) quotes Palauans on Angaur as saying that *Pandanus* was attacked. Palauans in several localities have noticed it was attacked, but many are not aware of such attacks. This new host record for both adults and larvae poses a serious question in regard to the control of *Oryctes* by coconut grove "sanitation," the present control program in the Palaus. *Pandanus* is probably not fed upon by *Oryctes* where coconut palms are abundant, though it can serve as a reservoir host in areas where mature palms have been exterminated. Whether it might serve as larval food in areas where mature palms remain is somewhat doubtful, since adult *Oryctes* prefer coconut. Apparently *Pandanus* is preferred to very young palms, as it was being fed upon extensively on Angaur where many young coconut palms remained. *Pandanus* cannot support as large a population as the coconut palm because it is a less favored host and may be scattered in dense vegetation which is unfavorable to the beetle's dispersal. Most attacks were noted in solid stands of the plant, or plants in clearings.

On the sugar palm (*Arenga pinnata*) the effects of adult *Oryctes* feeding on the fronds are less distinct and less symmetrical (fig. 32, *a*) than on the coconut palm. Some of the fronds may be largely intact, as far as the midrib is concerned, but with the leaflets largely eaten off in an irregular manner; and other fronds may be missing. On the road from Airai to Ngatpang, just inside of Aimeliik municipality, a stand of 25 sugar palms was found on October 19, 1951. All were killed by *Oryctes* except three very young ones and three older ones each of which had only one or two fronds left. *Oryctes* was breeding in the dead trunks. Two other palms of this species were seen on the same road in Airai municipality, one of them nearly dead.

The effect of adult *Oryctes* feeding on the sago palm (*Metroxylon sagu*) is similar to that on the coconut palm. A single living palm, attacked by the adult, was seen in Aimeliik municipality, on the Airai-Ngatpang road, near the border of Airai municipality, on October 19, 1951. The palm was growing on a bank, above a small stream on the hillside, near the road.

There are several oral reports that adult *Oryctes* has fed upon the betel-nut palm (*Areca cathecu*) in the Palaus. Harold Mayo, an agriculturist of the Trust Territory, states that he has observed its attack in Aimeliik municipality, southwest Babelthuap. Sangdei, Owen's beetle control program foreman, reports having seen two betel-nut palms attacked in the same municipality. I saw some at Ngardmau which were probably attacked, but they were not felled. Many *Areca* palms were killed by *Oryctes* on Koror after coconut palms became scarce.

The nipa palm (*Nypa fruticans*) which is moderately common in the Palaus, is a recorded host in other countries, but no clear evidence of attack on it by adult *Oryctes* has been noted in the Palaus.

The effect of adult feeding on the native palm *Heterospathe elata* var. *palauensis* appears to be similar to that on the coconut palm, with obtusely truncate fronds. One attacked palm of this species was noticed in the jungle behind Ngiwal village on November 5, 1951. Two fronds were affected, presumably by a single feeding (fig. 32, *c*). Another affected palm was seen between Ngarhelong and Agol on November 25 (fig. 31, *a*).

The native palms *Pseudopinanga insignis* and *Gulubiopsis palauensis* are also apparently fed upon by the adult beetles, though I did not personally observe this.

Adult feeding on the fan palm (*Livistona chinensis*) results in fronds with the ends somewhat arcuately truncate (fig. 31, *b*). An affected palm on Koror was seen on November 16.

Mayo states that he saw two affected royal palms (*Roystonea elata*) in Ngatpang municipality in 1949.

The effect of feeding on the oil palm (*Elaeis guineensis*) is both a truncating and tapering of the frond (fig. 32, *b*). One affected palm of this species was seen on Koror on November 16.

FIGURE 31.—Effect of adult feeding on palms: a, *Heterospathe elata* var. *palauensis*, between Ngarhelong and Agol; b, *Livistona chinensis*, Koror.

The adult beetle tunnels in sugar cane (*Saccharum officinarum*), hollowing it out while pushing the solid plant material out of the entrance hole. Fey noticed sugar cane hollowed out by adult *Oryctes* in Koror in 1946 when coconut palms on the island were nearly exterminated. Some Palauans in various places have noticed that *Oryctes* attack sugar cane, and I observed probable attack on cane on Eilmalk Island. In the Palaus, sugar cane is grown

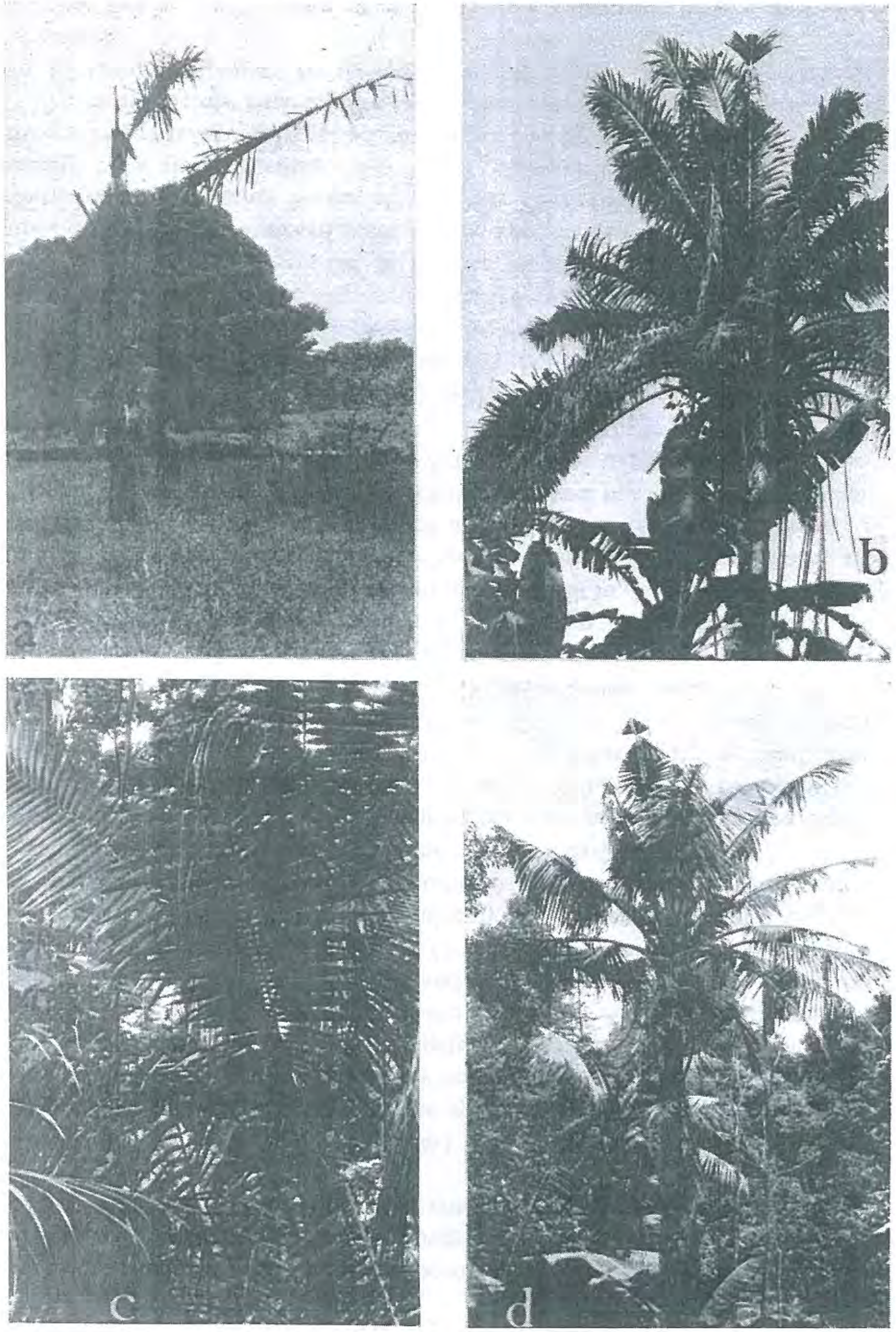

FIGURE 32.—Effect of adult feeding on palms: **a**, *Arenga pinnata*, Airai-Aimeliik; **b**, *Elaeis guineensis*, Koror; **c**, *Heterospathe elata* var. *palauensis*, near Ngiwal; **d**, *Cocos nucifera*, one of few remaining coconut palms on Eilmalk.

principally in small patches in yards or in single rows along paths or edges of taro fields.

The adult *Oryctes* bores into the center of the pineapple (*Ananas comosus*) plant from between the bases of the leaves. A farmer at Melekeiok reported observing *Oryctes* attack in his pineapple plants in 1950, but most Palauans are unaware that this plant is attacked by the beetle.

There have been several oral reports that *Oryctes* attacks banana (*Musa* spp.) in the Palaus (Hill, 147). Magistrate Tulap of Angaur showed Owen a hole in a banana plant which in the latter's judgment might have been caused either by *Oryctes* or by the giant African snail.

Several Palauans have stated that *Oryctes* attacks taro (*Colocasia*) and related plants (*Cyrtosperma, Alocasia, Xanthosoma*). These reports have been from places such as parts of Peleliu where coconut palms had already been killed off by the beetle.

Rough estimates of the numbers of the various adult *Oryctes* food plants in the Palau Islands are presented in table 7. Those listed as introduced palms include the following (symbols refer to footnotes to table): **Metroxylon*, 40 on Babelthuap; **Livistona*, 2 on Koror; **Elaeis*, 10 each on Babelthuap and Koror; **Arenga*, 10 on Babelthuap; †*Roystonea*, 2 on Babelthuap; **Coelococcus*, 1 on Babelthuap; *Caryota*, 15 on Koror; and *Chrysalidocarpus*, 3 on Koror.

Table 7.—Estimates of populations of probable Oryctes hosts in the Palaus

Host	Kayangel	Babelthuap‡	Koror Arakabesan Malakal	Limestone Islands and E. Koror	Peleliu Ngemelis and islets	Angaur	Total
*Cocos mature	12,950	90,000	10	100	2,800	....	105,860
young	5,000	180,000	1,000	3,000	5,000	500	194,500
*Areca	50	6,000	30	....	200	25	6,305
Nypa	....	9,000	200	....	1,000	20	10,220
*Introduced palms	....	70	40	....	....	....	110
*Heterospathe	....	4,500	300	....	....	....	4,800
*Gulubiopsis	....	....	....	220,000	....	....	220,000
*Pseudopinanga	....	300,000	....	....	....	....	300,000
*Pandanus tectorius	2,000	750,000	45,000	300,000	30,000	10,000	1,137,000
Rhoeo	....	50	80	....	50	50	230
Agave	....	....	20	....	....	....	20
*Saccharum	400	30,000	10,000	50	1,200	1,000	42,650
*Ananas	....	10,000	6,000	....	....	....	16,000
*Musa	800	20,000	2,000	100	2,000	1,000	25,900
†Colocasia	15,000	400,000	60,000	200	100,000	50,000	625,200
Totals	36,200	1,799,620	124,650	523,450	141,250	62,595	2,692,795

* Observed to be fed upon in the Palaus.
† Reported orally as fed upon in the Palaus, but not observed by writer.
‡ There are many young coconut palms on Babelthuap because the nuts were not all used during the war, and mature palms are abundant.

BREEDING SITES (LARVAL HOSTS)

Coconut Trunks

The most prolific breeding source of *Oryctes* in Palau is the standing dead trunks of the coconut palm killed by the feeding of the adult beetle (figs.

Figure 33.—a, Mature larvae in top of felled dead coconut trunk, adult and pupa at left; b, mature larva in compost, Ngiwal.

33, *a*; 34; 42). During the period when the beetle was increasing and extending its range throughout most of the islands, this was augmented by gun fire, providing an almost unlimited breeding medium and allowing the beetle to attain a very high population level. This population decreased in some areas

only when most or all of the coconut palms were destroyed. In some areas the population is still high. In others, where war damage was less or where the beetle did not spread until well after the end of the war, the beetle has never attained so dense a population, and the coconut palms have not been exterminated. Various arresting influences, as well as more limited larval food supply, are assumed to have retarded increase of the beetle to the point where extermination of the host was impossible or unlikely.

Attack by the beetle upon trunks of killed coconut palms commences at the top even, as a rule, when there may be holes or other severe injury to some part of the trunk. Eggs are laid by the female beetle in the top of a palm within about two months after the crown has fallen to the ground. The hardened woody portion of the trunk still has its full height. The young larvae commence feeding in the tunnel filled with sawdust bored by the parent female while ovipositing, or in the loose stringy top center portion of the trunk. Soon the larvae may migrate outward and feed gradually downward under the bark (fig. 34, *a*) for a short distance, as the woody material is consumed. The bark is left intact by the larvae, and often also part of the center of the trunk. Or both the center and the subsurface area may be consumed, leaving a portion of the wood between. This, however, may be penetrated by the mature larvae for construction of the pupal cells, or it may be entirely consumed and pupation may take place in cells made in the pulverized wood and excrement. The population of larvae may be quite dense, up to 80 or more occurring in the top meter or two of a trunk. As the wood is thus nearly or completely consumed, the remaining bark enclosing the sawdust and other remains may be blown loose and fall to the ground. Generally before this occurs this portion comes to be inhabited by cockroaches, and often geckos. Sometimes seeds of trees deposited by birds take root, and may help to keep the top attached to the rest longer than would otherwise be the case.

The above process continues as a cycle, with the top portion falling down at intervals depending largely on the density of beetle larvae. It is not a strict cycle repeated by generations of young beetles, but is continuous in that generally different ages of larvae are concurrently in the same trunk. Sometimes all stages of the beetle may be found in close proximity. Adult female beetles so found may be either those which have flown to the trunk and entered it from the top for oviposition or mating, or those in the pupal cells, having just transformed to the adult stage. Males may also fly there for mating.

The length of time required for the complete destruction of the trunk depends on various factors besides the height of the original trunk. Some trunks are more favorable for the breeding of the beetle than others. Nearly all dead trunks seem to be attacked, though some are also attacked by other insects or by fungi before the major part of the trunk has been consumed. Various beetles —passalids, lucanids, tenebrionids, rhipicerids, and elaterids—come to bore in wood, the first two and part of the third family feeding largely under the bark. Sometimes these larvae are found quite close to those of *Oryctes;* but except for the more rapid consumption of the wood, no serious competition has been noticed. At any rate, the *Oryctes* larvae, if more than one-half grown, are larger than any of the others, and stronger. The rhipicerid larvae are more heavily sclerotized, but usually attack wood at a later stage of rotting than is preferred by *Oryctes*. Termites and ants are often present.

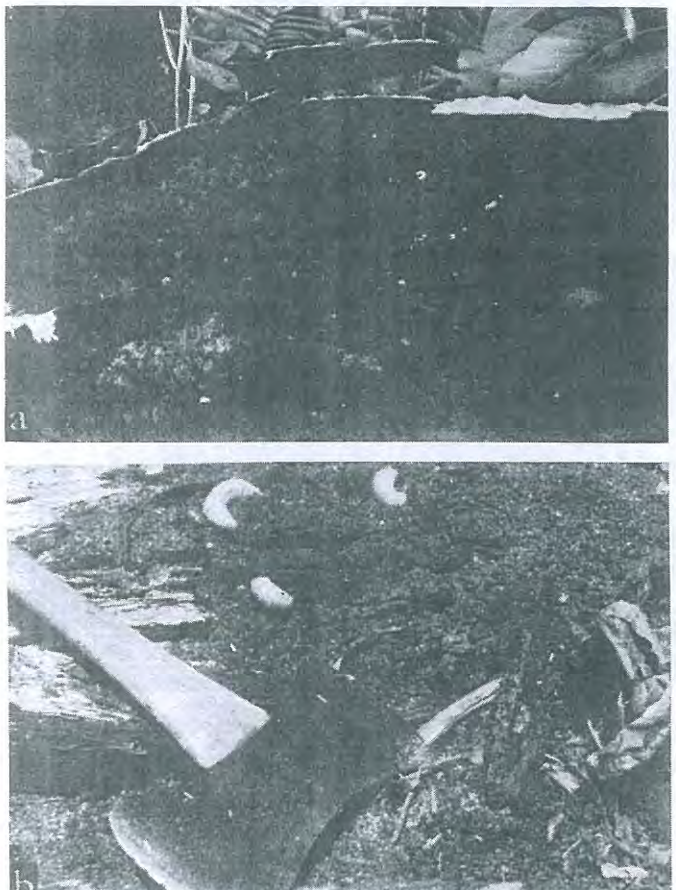

FIGURE 34.—Larvae in coconut trunks and logs: **a,** first instar larvae and young second instar larvae under bark of felled dead trunk; **b,** mature larvae in old log, millipede at left.

When the top portion of a trunk is blown over by wind, some larvae or other stages may be carried to the ground with it. However, probably not many are killed in the fall, as they are most apt to be strong, full-grown larvae preparing their pupal cells and are cushioned by the sawdust and feces inside the bark. If the fallen portion is shattered, the mature larvae may enter the ground and construct their pupal cells. Data from collections are presented in the following analyses and in table 8.

An analysis was made of a standing dead coconut trunk in Ngiwal village (Nov. 3, 1951) which was presumed to have died nearly one year earlier. It was heavily infested with fungus in the lower half, having a strong fungus odor and bearing several large shelf fungi 4 to 6 m. from the ground. The height was 16.5 m. and the diameter was 32 cm. The following *Oryctes* were found: 68 submature first instar and 54 young second instar larvae mostly from 1.1 to 4.4 m. from top; two adults (male, female), 3 m. from top; four dead adults, two of them males, about 2 m. from top. Other inhabitants included 12 adult and 18 larval *Gonatas*, one *Toxicum*, one *Callirhipis* larva, one *Pediris* larva, an adult *Amarygmus*, a black cockroach, two *Spirostrophus,* three *Trigoniulus,* one *Thereuonema,* one slender centipede, six *Cubaris,* one *Porcellio*, all near top; a large *Nasutitermes* colony and a small *Neotermes* colony near middle. The top meter was dry and pithy; the next 4.4 m. damp and completely eaten around just under the bark. Hermit crabs came on the scene within five minutes after felling.

Another trunk at Ngiwal, dead fully a year and eaten more than half way down and partly hollowed, contained nearly as many larvae, including larger ones, and three male and four female adults. It also contained ?*Oxycetonia* larvae, one *Alaus* larva, a dascillid larva, an adult *Figulus,* some adult and larval *Amarygmus*, small cockroach nymphs, *Nasutitermes* and *Glyptotermes,* a moth larva, two adult *Scolopendra*, and two *Thereuonema*. A third trunk, examined at Ngiwal five days after it fell in a storm, was taller, partly infested by fungus, and contained fewer grubs, a mating pair of adults (11:00 a.m.) and another adult female. There were 51 eggs in the tunnel just behind the latter female, and two groups of six and three eggs, respectively, in two other tunnels. Other inhabitants included larval and adult *Gonatas,* a *Figulus,* a *Pediris*, *Anoplolepis, Odontomachus* and other black ants, slugs, *Nasutitermes, Chelisoches*, a small cricket, *Amarygmus*, beetle larvae, a snail, one *Hormurus,* earthworms, amphipods, two *Scolopendra*, and many millipedes of three species.

Table 8.—Collections from standing dead coconut trunks

Locality; date	Eggs	Larvae* L_1	L_2	L_3	Pupae	Adults	Notes
Ngiwal, Aug.	32	....	....	34	....	3	10 m. high; lucanids, passalids present
Peleliu, east coast Sept.	....	8	8	16	1	1	7 m. high; adult in pupal cell
Peleliu (islet) Sept.	....	45	36	2	3	14	4.5 m. high; old, 2 males, 12 females
Peleliu (islet) Sept.	3	....	....	10	10	7	2.8 m. high; old, 5 males, 2 females
Peleliu (Ngabad I.) Sept.	....	15	5	130	....	1	1.8 m. high; mold; maggots of Pseudeuxesta prima
Ngiwal, Sept.	4	2	2	11	....	6	4 male, 2 female, all in broken hollow middle; 16 m. high; termites
Ngiwal, Oct.	49	11	12	16	....	5	3 male, 2 female; Figulus; Setenis; other tenebrionids
Ngiwal, Oct.	146	12	1	....	....	13	8 male, 5 female; also 4 dead adults; 14 m. high; upper half hollowed
Ngiwal, Nov.	23	12	15	28	....	8	5 male, 3 female; 20 m. high in taro swamp, count incomplete

* L_1, L_2, L_3, indicate first, second, and third instar larvae.

The records for 55 standing trunks, from which the samples in the above table were selected, gave the following averages: nine and one-half eggs, seven first instar larvae, seven second instar larvae, 21 third instar larvae, one-half pupae and two and one-half adults (not counting dead adults) per trunk. Of 106 of the adults, 49 were male and 57 were female. The number of eggs, first and second instar larvae, and pupae are lower than they should be because pupae are overlooked in solid portions of trunk and many of the others are lost in the undergrowth, or burrow into the ground when the trunk is fractured as it falls.

Coconut Logs

The situation in regard to coconut logs (fig. 34, *b*) is similar to that in standing trunks, but the moisture content is apt to be much higher because the horizontal surface exposed to rain is much greater and the contact with the substrate offers opportunity for moisture absorption. If the substrate is damp soil and if the log is largely in contact with it, the wood may harden from excessive exposure to water and soon become unfit for larval *Oryctes*. If the substrate is sand, the moisture may not be sufficient to harden the wood, unless the location is near the level of a stream or the water table. At Ngiwal many logs lying on sand less than 1 m. above high tide level contained *Oryctes* larvae. If a log lies partly on rocks, coral, or debris that elevate it slightly above the substrate, it is usually quite suitable for breeding the beetle.

The damper environment in logs, as compared with dead trunks, means, as a rule, a large variety of scavengers, together with their natural enemies. Thus there are more types of beetles, such as tenebrionids and elaterids; other scavengers, such as cockroaches, millipedes, sowbugs, amphipods, slugs, and hermit crabs; and predators, such as carabids, centipedes, and *Alaus*. Some collections from logs are listed in table 9.

An analysis was made of a coconut log lying on the low sand between Ngiwal village and its beach. It was partly opened on September 26, when 12 second and third instar larvae of *Oryctes* were removed. It was chopped up on October 15, disclosing the following: seven mature *Oryctes* larvae, 25 *Pycnoscelus*, 25 *Trigoniulus*, five small millipedes, three larval *Gonatas*, a moth larva in dry portion under bark, five amphipods, two slugs, a slender centipede, a *Toxicum*, two *Callirhipis* larvae, and two *Leptochirus*. The log was about 15 m. long. The terminal portion located in the shade of young trees, was wet and soggy, containing no insects. The remainder, containing most of the above listed, was slightly damp, not very hard, and only starting to become infested with fungus, though it was probably more than one year old.

Table 9.—Collections from coconut logs

Locality; date	Eggs	Larvae L_1	L_2	L_3	Pupae	Adults	Notes
Ngiwal, Aug.	....	....	....	....	2	8	adults in pupal cells
Olei, Aug.	9	11	3	8	....	....	on low wet ground
Ngiwal, Sept.	16	34	15	8	1	7	2 males, 5 females; 5 in pupal cells
Ngiwal, Sept.	4	1	....	3	....	2	male, female; log, old, rotten
Ngiwal, Sept.	....	2	....	2	....	3	1 male; 2 females; old, rotten

Coconut Stumps

The coconut stump (fig. 35) habitat is apparently even less favorable for the breeding of *Oryctes* than is the coconut log. The open top of the stump collects rain and stores water, hence the soaked wood may become too hard for the breeding of the beetle. However, if the stump is cracked or perforated so that most of the water can seep out, or cut or broken off so that it sheds water, over-soaking may not occur. The difference in this effect of water catchment between a stump and a dead standing trunk is that the area of the opening at the top of the trunk is much less than that of the cut stump and there is a much greater depth for drainage. Also, there is greater surface area for evaporation with the trunk than with the stump.

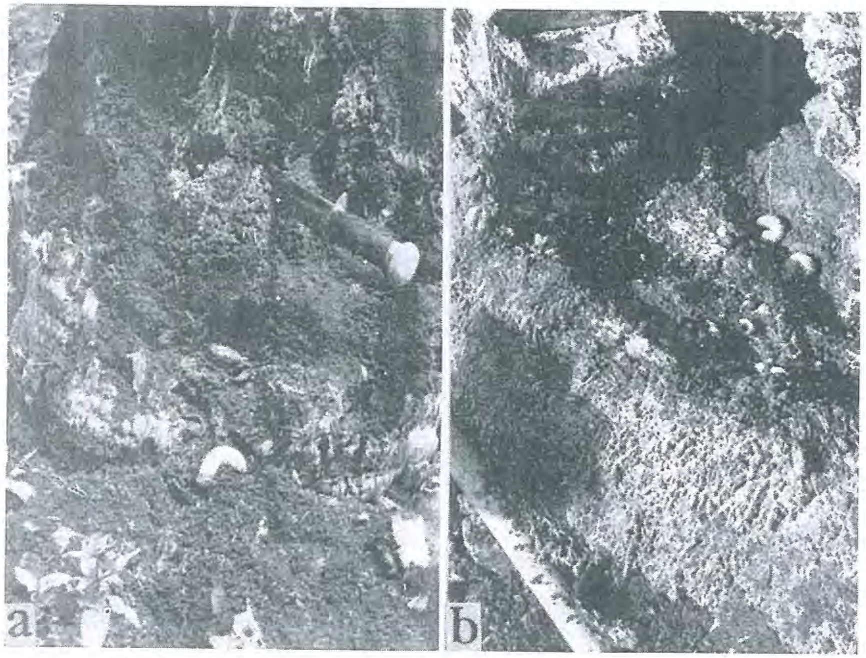

FIGURE 35.—Coconut stumps: a, adult to left of knife, pupa in center, mature larva below; Angaur Island. b, adult in upper center of stump, larvae of all three instars below; Ngiwal.

Stumps are apt to last longer than logs because of their greater diameter and hardening by soaking. The numerous hard roots also serve as protection from various forces, besides providing firm attachment to the substrate. Quite often the stump is eaten completely down to the base of this cavity lining the area of root attachment. In one stump (Koror) this region was below the surface of the ground (perhaps graded soil, as it was in a cassava field on a slope) and larvae, pupae, and adults in pupal cells were found in the very bottom, 50 cm. below the ground level. The inside of a stump may, after some lapse of time, become quite soft and spongy but still support *Oryctes*, as well as other animals. Co-habitants of *Oryctes* in coconut stumps include *Callirhipis*, millipedes, termites, ants, various beetles, hermit crabs, toads, and rats.

An analysis was made of a coconut stump at Ngiwal (Nov. 3, 1951) which was probably more than a year old and considerably eaten. It stood 1 m. high

and was 70 cm. wide at the top. It contained 10 first instar *Oryctes* larvae under bark and three second instar larvae in the top center, and also 43 larval and seven pupal *Callirhipis;* 24 *Uloma* larvae; three *Amarygmus* larvae; two small ant colonies; a small pale cricket; an earwig; a small colony of *Nasutitermes;* eight *Spirostrophus;* a *Trigoniulus;* two kinds of small earthworms; a scorpion; and a *Pupina.* Though old and damp, and with some of the bark already detached, this stump still consisted largely of solid whitish wood, except that the top center and the sides beneath the bark were pulverized and blackish.

A newer coconut stump at Ngiwal (Nov. 5, 1951) was presumed to have been six or eight months old when examined, though it was relatively untouched. It stood 1.1 m. high and was only 22 cm. wide at the top. The bark was partly detached. On one side was a colony of *Nasutitermes.* Two recent holes made by female *Oryctes* from the outside were on the surface: one near the center of the sawed-off top of the stump, the other on one side 12 cm.

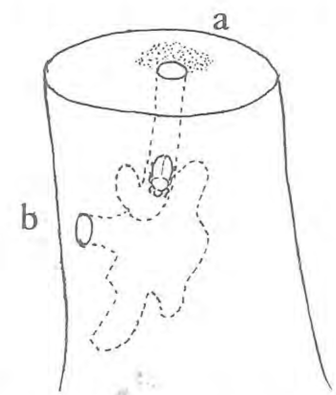

FIGURE 36.—Adjoining oviposition tunnels of two female *Oryctes:* a, newer tunnel, containing female, with new sawdust around opening on top of stump; b, older tunnel, entrance at side.

below the top. Both holes had been made within a few days, and the one at the top of the stump (fig. 36, *a*) had evidently been made the evening before. The female beetle was only about 10 cm. from the top in its sawdust-filled tunnel, in which it had already laid six eggs. The tunnel made by this female was short, joined that made by the other, and had only one short side tunnel. The tunnel made by the earlier female (fig. 36, *b*) was more extensive, with several short branch tunnels, but it did not extend more than 24 cm. from the top of the stump, and the beetle was gone. Its tunnels contained 42 eggs, which had already grown to full size with sub-rounded shape. (See table 10 and figure 35.)

Table 10.—Collections from coconut stumps

Locality; date	Eggs	Larvae L_1	Larvae L_2	Larvae L_3	Pupae	Adults	Notes
Peleliu, July	....	....	....	24	4	....	largely eaten
Ulimang, Aug.	12	....	2	4	....	1	old
Angaur, Aug.	....	1	....	39	3	1	12 of L_3 about to pupate
Airai, Oct.	....	....	2	3	....	....	very old; many toads in stump
Koror, Oct.	....	4	2	2	1	2	male, female; pupal cells
Melekeiok, Oct.	5	1	....	3	....	2	2 females; old stump

Coconut Logs Used in Construction

Coconut logs not treated chemically or soaked for a long period in water before use are subject to attack by *Oryctes*. Those used as vertical posts for house supports or other structures are particularly vulnerable, as they provide a situation rather similar to that of a standing dead palm. The coconut logs used in bridges, even simple ones of a few horizontal logs over a very small stream, are, if not frequently wet, likewise suitable hosts. Collections from this habitat include larvae from school porch posts and sawmill posts at Ngiwal and bridges of different sizes at Ngiwal, Melekeiok, and Aimeliik.

Other Palms

The standing dead trunks and logs and stumps of other palms may serve as larval hosts, even trunks much less solid and woody than coconut trunks. Collections from this source include second instar larvae in a standing dead betel palm and second and third instar larvae in a betel palm stump at Ngiwal, eggs in a fallen dead betel palm at Airai, and boring evidence in *Arenga* at Aimeliik. In a dead stump and log of *Heterospathe elata* var. *palauensis* at Ngiwal were found an *Amarygmus* pupa, a moth larva, a centipede, a weevil cocoon, and two small snails; and in the crown were found more weevil cocoons, termites, earwigs, maggots, and *Leptochirus*. Evidence of *Oryctes* work was not certain.

Miscellaneous Wood

Presumably larvae may be found in almost any kind of dead wood providing certain conditions are fulfilled. The trunks, stumps, or logs must be fairly large and must be old enough to have at least partially rotted to a rather soft state. Furthermore, they must not be too dry, or excessively wet. (See table 11.) An old kapok stump at Ngiwal, 1.7 m. high and 60 cm. in diameter contained two *Oryctes* second instar larvae; 22 larvae, one pupa, and one adult of *Olethrius*; dascillid larvae; large red ants; small black ants; medium black ants; *Coptotermes*; red *Collembola*; *Lithobius*; and *Thereuonema*.

Table 11.—Miscellaneous dead wood

Locality; date	Material	Source
Aimeliik (Owen) 1951	250 larvae	standing dead mango tree
Angaur, July	10 L_1	old fallen Barringtonia log
Ngajangel, Sept.	4 L_1	old fallen Barringtonia log
Airai, Oct.	1 L_3	unidentified old stump
Ngardmau, Oct.	several L_3	dead Calophyllum trunk
Ngiwal, Oct.	1 L_2, 2 L_3, 1 pupa; 3 adults (2 males, 1 female); 1 dead adult female	remainder of old kapok log; also: earthworms, millipedes, cockroaches, hermit crab, rat, much fungus

Plants killed by adult feeding serve as an important larval habitat. Of about 125 *Pandanus* plants killed by *Oryctes* in southwest Babelthuap, nearly all of those examined contained immature stages (fig. 37, *b*). On Angaur Island larval feeding in many *Pandanus* trunks as well as killed branches of still living plants was observed. A number were eaten down into the prop roots. Other animals found in dead *Pandanus* plants were cockroaches, sowbugs, and *Amarygmus*. Living *Pandanus* plants bore many small oval holes in the leaves made by a moth larva. *Nasutitermes* were found in many branches hollowed by *Oryctes* larvae on living plants. (Table 12 presents selected collection data.)

Table 12.—Collections from dead Pandanus trunks

Locality; date	Eggs	Larvae L_1	Larvae L_2	Larvae L_3	Adults	Notes
Aimeliik, Oct.	47	....	....	....	....	top of trunk partly toppled over
Aimeliik, Oct.	....	....	....	11	....	larvae mature
Aimeliik, Oct.	....	....	14	16	....	L_2 mature: L_3 new
Aimeliik, Oct.	....	....	....	....	2	male, female; dead: 1 affected by muscardine fungus
Angaur, Dec.	....	1	....	....	4	3 male, 1 female; probably more L_1 lost

Ground Under Old Logs

Larvae are frequently found under old logs of various sorts, particularly old coconut logs, and this habitat is not always completely distinct from coconut logs and shallow compost piles containing or bordered by coconut logs.

That is, a log may be rotting to the point where larvae may slide beneath the log and feed upon the disintegrating remains. For those under logs in, or closely adjacent to, compost, it may be difficult to judge whether the parent female was attracted to the log or to the compost. Larvae may feed on a log from the underside or on pulverized wood or the rich compost underneath the log. In this situation, and in some types of compost, the larvae appear to feed like earthworms. That is, they feed on large quantities of humus, extracting nutritive material from it as it passes through the digestive tract. Under these conditions the volume of material consumed must be larger than in the case of pure wood. Third instar larvae were found at Ngiwal and Melekeiok under isolated coconut logs or under coconut logs beside which were many coconut husks. They were generally in places where there was humus on top of the sand.

Compost

The villages of Palau contain many compost piles, generally one or more per house. These may be shallow, or on the surface of the ground (fig. 33, *b*). They may cover a number of square meters or be deep and rectangular with vertical sides and measuring 1 to 3 square meters. Both may be used in the same yard for different materials or for different stages of composting. The material from the first type may be shoveled into a deep pit dug beside it after a period of accumulation on the surface. Common ingredients of the pits are banana stalks, fruit stems, coconut husks and shells, coconut frond baskets, fallen breadfruit, breadfruit leaves, other leaves, and garbage. Garbage is mostly vegetable, but includes fishbones and, rarely, bones of chickens, ducks, or pigs. The shallow pits are generally located beside banana plants or are more or less surrounded by them, because the stems of banana plants are hard to move when they are cut and because they are generally grown behind the houses, but principally for the compost to serve as fertilizer for the banana plants. The temperature varies considerably in different types of compost. It may be from just below air temperature to at least 20 degrees higher. Not all compost piles or garbage pits are infested with *Oryctes*. Insufficient woody or leafy plant material or too high a decomposition rate seem to be unfavorable. However, numerous larvae have been found in shallow pits where abundance of dead coconut trunks, stumps, and logs were available and not completely infested. Larvae have been found close to rotting garbage or in pits with leaves only. At Ngiwal larvae were found in about one-half the shallow pits examined (table 13). No larvae were found in compost on Angaur, where five pits were examined. Co-habitants are *Pseudozaena*, earwigs, *Gryllotalpa*, *Acheta*, cockroaches, maggots (*Ophyra*), and millipedes. Some of the deeper pits with damper garbage and much higher temperature contain maggots of *Hermetia*, sowbugs, and millipedes.

Table 13.—Compost collections of Oryctes, Palau, 1951

Locality; date	Nature	Area (sq. meters)	Greatest depth of Oryctes	Larvae L_2	Larvae L_3	Pupae	Adults	Total
Ngiwal, Aug.	shallow much debris	13	35 cm.	2	277	14	19	312
Ngiwal, Aug.	shallow much debris	10	40 cm.	15	67	4	1	87
Kayangel, Sept.	under banana plant	1	2 cm.	4	....	....	....	4
Ngiwal, Sept.	under banana plant	5	8 cm.	....	26	....	....	26
Airai, Oct.	shallow	1	12 cm.	....	3	....	....	3
Airai, Oct.	deep, leaves	2	90 cm.	....	86	1	....	87
Ngiwal, Oct.	moderately deep	1	65 cm.	....	1	....	....	1

Sawdust Pits

Sawdust is an ideal breeding medium for the beetle, as no chewing through solid wood is necessary in order to lay the eggs in suitable situations for the young larvae. A sawdust pit may continue to breed beetles until the sawdust has been entirely digested by the larvae. A large pit at the temporarily abandoned sawmill at the deep-water Ngiwal pier was examined at intervals. In August, 6 square meters were dug up, revealing 10 eggs, 53 first instar larvae, 21 second instar larvae, 127 third instar larvae, 7 pupae and 9 adults, or a total of 227 *Oryctes*. In November, 1 square meter produced 4 eggs, 1 first instar larva, 11 second instar larvae, and 4 third instar larvae, and 3 male adults, a total of 23. The greatest depths at which the insects were found were 60 cm. for eggs and adults, 90 cm. for larvae and 25 cm. for pupae. Other insects found in the pit included a few termites (*Prorhinotermes*), one *Callirhipis* larva, and larvae and pupae of small beetles, possibly of the Dascillidae.

In Koror, four abandoned sawmills and one new one were examined, but no *Oryctes* were found. One mill had not been used since before the war and the sawdust was decomposed or burned; at another the water table was too high; at the third the sawdust was too thin, too oily, and on wet clay; and at the fourth, which seemed favorable, the sawdust was of American coniferous wood.

Jungle

The rhinoceros beetle is quite capable of feeding and breeding in virgin jungle or forest where palms or *Pandanus* are present, as they are in the Palaus. *Pandanus* is found on all the islands, and native palms on most. The lack of native palms on outlying islands does not mean lack of reservoir hosts, because of the abundance of *Pandanus*. Extensive breeding in the jungle has not been observed in Palau except in pure *Pandanus* jungle. Evidence of breeding to a slight degree has been noticed on a few occasions in *Pandanus* or palms near the edge of the jungle on Babelthuap, the limestone islands, and islets north of Peleliu. It is difficult to determine how general this is. I found no larvae in true mixed jungle on Babelthuap, but noted evidence of adult *Oryctes* feeding on the *Heterospathe* palm in jungle behind Ngiwal and between Ngarhelong and Agol. In jungle behind Ngiwal I saw probable evidence of breeding in dead trunks of the *Pseudopinanga* palm, probably killed by the beetle. Records for *Pandanus* breeding are listed under that plant.

It is assumed that there would be more breeding in jungle if dead coconut palms and compost were not so abundant in the Palaus and if there was more cutting and clearing in the jungle. In addition to the correlation between *Oryctes* destruction and war damage to palms, it also appears that the beetle has been more prolific in the areas of less rainfall since overly wet environments are less favorable for breeding. Sunshine entering jungle probably improves the breeding situation. As the village and coconut grove debris is cleaned up in Palau, new breeding situations may be provided as the human population grows and spreads inland on Babelthuap.

Other Media

Manure heaps have been recorded as a breeding media for *Oryctes*, frequently as the favorite habitat, in South India by Cherian and Anantanarayanan (40), Coleman (44), Fletcher (103), and Kunhi Kannan; in Burma by Ghosh (131); in Formosa by Takahashi (278) and Takano and Yanagihara (279); and elsewhere by Corbett (55) and Jepson (159). At present this is not an important breeding source in the Palaus, where cattle are few.

Piles of rotted coconut husks have been recorded as breeding media, but this has not been corroborated in Palau. On Kayangel these piles of husks are commonly burned at intervals. At Ngiwal coconut husks were found which had a slender beetle larva and red millipedes in them. The potash in coconut husks and banana stalks may prevent larval breeding in them. Refuse of the nipa palm has been recorded as a larval breeding medium in Java (Leefmans, 183), but this has not been seen in Palau.

Bagasse is not an important habitat in Palau because so little sugar cane is grown, but if cultivation is increased, attention must be paid to this and to cane leaves and also to pineapple wastes, if the latter crop is grown commercially. Bagasse is important elsewhere (Leefmans, 183; Subramaniam, 272).

Other media, according to Ghosh, are rotten paddy straw and rice husks (131), and grass-thatched roofs (127). Others are cacao refuse (Friederichs, 109), coffee refuse (Fletcher, 103), bark of *Melaleuca* (Corbett, 48), and old sisal plantations (Fletcher, 103; Harris, 143).

FEEDING EXPERIMENTS

Adults

Various foods were tested on adults by confining the two together with no alternative food. For this purpose screen-topped wooden boxes of 1 to 4 cubic feet in volume were used, as well as large glass jars. The following were tried:

Cocos nucifera: Adults in jars readily bored into, or chewed on, sections of coconut crown heart (unopened leaves).

Pandanus tectorius: Two adults caged with a crown with trimmed leaves bored partly into the cut base of the stem overnight (Ngiwal, Nov. 10). Two days later they had bored a tunnel about 9 cm. long into the base and had pushed out quite a bit of frass.

Areca cathecu: The top of one young plant was not fed upon by a caged adult (Ngiwal, Sept.), whereas another adult caged with the cut top portion of a palm (Ngiwal, Nov.) chewed a short distance into each end and also into the base of one petiole on its inner side.

Heterospathe elata var. *palauensis:* One adult confined with the freshly cut top section of a mature palm of this native Palauan species (Ngiwal, Nov.) bored 12 cm. into the base of the section overnight. The heart somewhat resembles that of the coconut palm, but is harder.

Colocasia esculenta: On several occasions (Koror, Oct.; Ngiwal, Nov.) adults in boxes or jars chewed these plants considerably. Some attacked in the normal fashion forcing their way between leaf petioles to their bases and then chewing into the tuber from the top, and others chewed away rootlets and into the tuber from the bottom. On some occasions tubers were hollowed or almost completely consumed. The adults lived for a month or more after feeding on this and the following three plants.

Xanthosoma sagittifolium: An adult confined with a plant of this species (lacking the leaves) chewed into an area of about 25 square cm. and removed about 15 cubic cm. from the bottom of the tuber (Ngiwal, Oct.).

Cyrtosperma chamissonis: One adult confined with a 50 cm. cut basal section of the top of a growing plant (Ngiwal, Nov.) in 10 hours chewed part of the basal end and then entered for twice its body length into the top end of one of the cut leaf stalks. In 24 hours it chewed a few centimeters farther down the same tunnel. A week later it had hollowed a considerable part of the plant.

Alocasia macrorrhiza: Several adults together in one cage fed extensively upon uprooted or chopped-off plants of this species (Koror, Oct.-Nov.). Some chewed into the cut ends of both petioles and tubers, and others bored into the sides of petioles where they separated from other petioles, or into the crotches.

Ananas comosus: One entire pineapple plant from an over-grown ancient part of Ngiwal village was caged with three adults (Nov.). One beetle ate down into the crown from the top, making a tunnel 16 cm. long. The other two chewed into the side of the plant between leaves. In Western Samoa (Jan.) one adult of a pair confined with a ripe pineapple fruit had in two days chewed a tunnel parallel to the axis for almost the length of the fruit. A few days later both adults were in the rotting fruit, much of which had been chewed up.

Saccharum officinarum: An adult confined with two sections of a sugar cane stalk (Ngiwal, Oct.) chewed slightly on the sides of one section and then chewed away the lower end of one section just below the leaves for about one-half its length. A few days later it had hollowed one section for 8 cm. and made an opening on one side of the hollowed portion.

Carica papaya: Two sections, including the terminal portion, of the top of the stem of a freshly cut plant were bored and largely hollowed by a pair of adults (Ngiwal, Sept.). One was hollowed for 25 cm. One adult female beetle was still in a section when the cage was cleaned after four weeks. Two adults confined with a nearly ripe papaya fruit (Ngiwal, Nov.) chewed into the side at several points, once as far as the seeds. A week later the adults were dead, but they were more than two and one-half months old and at least near the end of normal life span. The papaya was by then very moldy.

Musa spp: One adult of several in a cage (Koror, Nov. 8) commenced to bore into the stem of a young banana plant as soon as it was put in the cage and continued to feed for at least several hours, entering the stem from the side. By a week later the plant was almost completely consumed. An adult in another cage (Ngiwal, Nov. 7-9) bored 20 cm. into the cut top of a petiole 3.5 cm. in diameter, from the top of a large banana plant. Another in the same cage chewed slightly into several cut petiole ends and then bored a short distance into a petiole crotch.

Rhoeo discolor: Two adults confined with a trimmed plant of this species (Angaur, Dec. 2) overnight chewed leaf bases and into the side and top of the plant at two points.

Dracaena angustifolia: Two adults confined with a crown of this plant (Ngiwal, Oct. 7-9) each chewed partly through several leaf bases. Another placed in a jar with a section of stem failed to eat. This is not considered a favorable adult food plant because its leaves are too thin and narrow and its stem too slender and too hard and dry.

Cordyline terminalis: This plant is grown along paths in the taro fields, and its leaves are used for wrapping pounded tapioca for carrying on trips. No feeding was observed when an adult was confined for 24 hours with the crown of a plant (Ngiwal, Nov. 5), but slight chewing at leaf bases was observed

after three days. The leaves are considered to be too thin and the stem too slender and dry to serve as suitable food for adult *Oryctes*.

Persea americana: Two adults confined with a nearly ripe avocado fruit (American Samoa, Jan.) chewed through the skin and into the fruit at several points.

Hanguana malayana: This plant has leaves a meter long and 12 cm. wide and a short, stout, fleshy stem and grows in water at or near edges of streams, swamps, or ponds. Adults caged with a cut plant from Ngiwal (Koror, Nov. 16) chewed considerably into the stem from between leaf bases.

Hymenocallis littoralis: Some adults confined with a plant of the spider lily (Koror, Nov. 22) chewed into the center of the plant from between leaf bases near the top.

Tacca leontopetaloides: Some adults confined with an entire mature plant (Koror, Nov. 20) chewed into the stem at two points (one a point where the stem was bent back) and also into the tuber beside the base of the stem.

Sugar water: Cellucotton impregnated with a sugar solution was chewed up promptly when twice used as food for captive adults. Wood soaked with sugar water was also chewed by captive adults.

Table 14.—Longevity of larvae on abnormal food, Ngiwal

Food	Notes	Days
Extra wet coconut wood	too wet	34
Extra dry coconut wood	growth retarded	36
Corrugated cardboard (dampened)	mold; considerable growth	37
Crumpled wrapping paper (dampened)	slight growth	33
Normal coconut wood	growth normal	60+*

* Plus sign indicates that larva was killed to close experiment.

Larvae

A number of materials were tested as larval foods by isolating portions of each kind of food in jars with single larvae of known age. For each experiment, check larvae of the same age were kept in the same type of container and fed upon normal coconut wood. The tests were run in two series, one at Ngiwal, with only one set, and the principal one at Koror, with 15 sets of each test. The former were in large jars, the latter in small jars. The results indicate that the containers in the main test were too small, providing a less natural environment because of excessive evaporation or lack of constant control. Thus the figures are considered low.

The results of the smaller test at Ngiwal are shown in table 14 and those of the larger test in table 15. All larvae used were second instar larvae in their second week.

Table 15.—Longevity of larvae on abnormal food, Koror

Food	Days Av. of 15	Days Maximum
Extra damp new coconut wood	20	61+*
Extra dry coconut wood	24	80+
Damp fungus-infested coconut wood	28	86
Smelly red-rot coconut wood	17	61+
New coconut husk	7	17
Old coconut husk	12	20+
Copra (dried coconut meat)	5	11
Corrugated cardboard	16	66
Damp paper, in small strips	15	85
Tall grass (?Miscanthus)	21	61+
Sawdust I (native Palau woods, oily)	11	30
Sawdust II (American coniferous woods)	5	14

* Plus sign indicates that larva was killed to close experiment.

DAMAGE EVALUATION AND POPULATION STUDIES

In order to evaluate the damage caused by the rhinoceros beetle in the Palaus, a census was taken of the coconut palms, living and dead, in the localities or islands studied. These data, taken in connection with the populations of beetles in the sampled palms and other breeding media, are used in estimating the beetle populations. In explaining the various densities of populations, the availability of suitable breeding situations must be taken into consideration.

Babelthuap Island

Parts of Babelthuap, the largest of the Palau Islands (area 396 square kilometers, or 153 square miles) are seriously affected by *Oryctes*, whereas other parts are only slightly damaged. The differences are correlated with the spread of the beetle northward and also with war damage to palms and other factors. Ngiwal, the field headquarters, is discussed first, then the other municipalities are discussed in clockwise order around the island from Ngiwal.

The immediate village area of Ngiwal was studied in some detail. In general, the severe damage was within the limits of the village (figs. 39, *a;* 40, *a, b*) but also in the scattered palms among the fields behind the village (fig. 2, *b*). Along the coastal strips away from the village, damage was much less severe and few palms were killed, particularly among those adjacent to the beach. At the sawmill by the deep-water pier, however, damage was severe.

Of about 1,250 grown coconut palms in the actual village area of Ngiwal, about 99 percent had been affected by the beetle within the two-year period of growth of the fronds existing at the time of the census (August 1951). The majority of the palms had been fed upon by the adult beetle five to 10 or more

times during that period. About 280 palms (22.4 percent) had been killed since the advent of the beetle, and 55 of these were still standing at the start of the study. Of the 225 stumps, logs remained for 98. In addition, 31 palms were considered to be dying, and many others probably doomed. At the end of the study additional dead palms were found. Over 1,000 young palms were growing within the same area, and of these about 15 percent showed signs of damage by adult beetles. This verifies earlier reports that the beetle prefers to attack grown palms. The population of all stages of *Oryctes* in Ngiwal villages is estimated in table 16. This estimate is for the Ngiwal village area only, excluding outlying groups of palms, adjacent coastal strips, hills, or the sawmill.

Table 16.—Estimates of Oryctes population in Ngiwal Village, 1951

Situation	Eggs	Larvae	Pupae	Adults	Total
Standing dead coconut palms	1,200	2,750	190	190	4,330
Coconut logs	700	1,800	70	70	2,640
Coconut stumps	1,400	3,800	100	100	5,400
Garbage and compost	1,300	3,000	100	100	4,500
Other palms, dead trees (including logs and stumps)	400	1,000	37	40	1,477
Live coconut palms (grown)	....	10	3	2,000	2,013
Live coconut palms (young)	....	....	......	500	500
In pupal cells (all habitats)	....	....	......	400	400
Totals	5,000	12,360	500	3,400	21,260

On the slopes behind the village, and among the farther taro patches are palms not included in the census. They are almost entirely affected, many of them seriously, and some have been killed. Along the coastal strands north and south of the village and on the hill just south of the village, the coconut palms are less affected. On the hill, many have been slightly or moderately affected; but behind the beaches, less than half are affected, except near the Ngiwal sawmill, where all are seriously damaged and nearly 50 have been killed. Damage is worse on the fringes and slight in dense stands of coconut palms because the adult flight is impeded. (See Robin, 241.)

On my visit to Ngiwal in December 1952, after a year's elapse of time, conditions appeared similar to those of 1951, but actually the number of mature living palms was about 6 percent less. The tall standing dead trunks were those which were newly killed or about to die in 1951. This probably involves a slight reduction in population, but not as great a reduction during the year as seen where the beetles had been present longer, as at Peleliu and Airai. A substantial breeding environment of dead trunks and compost was still present.

Ngarakis Islet lies in Namai Bay between Ngiwal and Melekeiok. It is surrounded by mangrove, but in the center has about 18 coconut palms, some dying, others moderately to seriously affected by *Oryctes*. On a broad, low hill just south of Ngabaral hamlet, west of Ngarakis, a large grove of palms appears from the bay to be almost unaffected by the beetle.

Melekeiok municipality is more seriously affected by *Oryctes* than is Ngiwal municipality. The village extends through a considerable part of the coconut groves, so the war damage to the palms was extensive. Many palms had been largely consumed or cleaned up before 1951. In the fall of 1951 about 50 standing dead trunks, 100 stumps, and 50 logs remained, with several hundred palms moderately to seriously affected, about 20 dying, and hundreds not very seriously affected. Over 300 palms had been destroyed. In general, the palms have received more care since the war than those in Ngiwal. Some groves on hillsides behind the village have suffered rather little, but the fringes on the landward side have been more seriously affected (fig. 41, *b*) and some probable evidence of attack on *Pandanus* was noticed just beyond the last palms. Attack on pineapple and *Pandanus* in 1950 was reported. A population of about 25,000 *Oryctes* is estimated for the area, and it is presumed to have been greater a year or so earlier. Melekeiok village is the locality where Steinhaus attempted field infestation of *Oryctes* with the Japanese beetle milky disease (May 1951).

Nghesar (Ngchesar) municipality (Kaisha) was visited briefly on only a few occasions, but most of the coconut groves were seen from the water many times. At a place just north of Nghesar, *Oryctes* was hard to find, even though old coconut logs were present. It is more abundant on the south side of the village. There are still extensive stands of palms remaining in localities along or near the coast, mostly fronted with mangrove swamps. These groves are isolated from Airai to the south of Melekeiok to the north by jungle, and have been less affected than either. A population of 15,000 *Oryctes* for the municipality is the rough estimate. The magistrate states that *Oryctes* arrived there in 1948, but probably 1946 is more nearly correct.

Airai municipality, southeastern Babelthuap, had a large number of coconut palms before the war, and it has suffered the most among the municipalities of Babelthuap. This is attributed primarily to the fact that it was the earliest infested (probably early 1943, or sooner) and that it also suffered extensive war damage because of the presence of the Japanese airport and garrison. Also in some parts of the municipality Japanese soldiers cut down palms for food toward the end of the war. Other palms were probably unnecessarily felled for the dollar bounty during 1948. Most of the remaining coconut palms are in the eastern part, around Airai village. Here there are roughly 1,600 living palms, of which about 600 bear nuts in small quantities, 800 are seriously affected and hardly, or not, bearing, and 200 are dying. There are roughly 120 dead standing trunks and additional logs or stumps remaining. Larvae were found in two of three compost pits examined. A population of 30,000 *Oryctes* in all

stages was estimated for the Airai village area alone. The population in the rest of the municipality is probably low. Between the village and the pier opposite Koror almost no palms remain. From the pier to the west end of the municipality, I noticed only a few affected young coconut palms, no mature palms except betel palms, and one dying *Arenga*. Airai village is the site of most of the *Scolia* liberations.

In December 1952 newly killed or dying palms were seen, but the number of dead trunks had been reduced, and the *Oryctes* population decreased. The easternmost part of Airai municipality, including Iwang and other villages not before visited, had badly damaged palms, but few dead trunks. I saw one *Heterospathe* palm which had been attacked.

Of the Airai Islets, Nardueis has on its southern side about 100 coconut palms, which appear rather slightly affected by *Oryctes*. On a hill just west of the grove is the largest stand of *Heterospathe* palm observed. About 12 coconut palms on the islet northeast of Nardueis also seem little affected. Korak Islet has four standing dead trunks but no living palms. Ngothugothu has five stumps on the small beach. Garreru Islet has three two-year old *Cocos* on one beach and 14 stumps or eaten-down trunks but no living ones on another.

Aimeliik municipality, southwestern Babelthuap, lies between Airai, the most seriously affected area, and Ngatpang, the least affected by *Oryctes*. It is isolated from the latter by jungle, but there is no particular barrier between Aimeliik and Airai except scarcity of palms, of which there were more a few years ago. The largest infestation in *Pandanus* (figs. 37, 38) was seen just inside Aimeliik on the road from Airai (Gressitt, 137). Farther along this road, toward inland Ngatpang municipality, the remains of a few old, dead, eaten coconut trunks were observed, and evidence of *Oryctes* feeding was seen on sago palm, ivory-nut palm, and sugar palm (fig. 32, *a*) with breeding going on in the latter. The main village of Aimeliik (Ngarekeai) was not visited, but had been cleaned up in the control program some months earlier. A considerable number of reasonably healthy palms remain in several groves near the sea. Their condition in December 1952 appeared to be good.

I visited the older village of Aimeliik (Ngchemiangel) farther west on November 1 and traversed the road inland to the former Japanese cacao plantations, now being revived. Though this area was also cleaned up, *Oryctes* damage was in evidence in the few score of remaining palms, which had practically ceased to produce nuts, or were dying or recently killed. Inland from the coconut stands was seen some possible evidence of attack on *Pseudopinanga, Pandanus,* and *?Flagellaria*. A grove of bearing palms grows to the northwest of the village, slightly inland from the coast. A population of 40,000 *Oryctes* is estimated for the municipality.

FIGURE 37.—Adult feeding, and larval breeding, in *Pandanus:* **a**, top of crown newly killed by adult, Angaur; **b**, adult feeding holes in base of crown, Aimeliik; **c**, base of crown, showing old tunnel exposed by falling of leaves; tunnel entrance behind bent leaf, Angaur; **d**, submature larvae under surface of base and stem; others inside stem;

FIGURE 38.—*Pandanus:* **a**, crown tunneled by adult and malformed, new shoot has died, Angaur; **b**, dead plants killed by adults and crumpling from being hollowed by feeding of larvae, Aimeliik.

Ngatpang municipality (Gasupan) is the least affected of all those on Babelthuap, despite the fact that it is only across the southern end of the island from Airai. This may be because it is somewhat isolated by jungle-covered hills from the coconut groves to the east, and by Karamado Bay and mangrove from the north. But perhaps more important reasons are that there was little or no war damage here and that the community cooperated well in the control campaign (fig. 49, *b*). Probably some other natural factors also contributed, because the damage was not serious before the control programs were instituted. This municipality was visited twice, first on October 19 when it was entered over the mountains from the southeast, across upper Aimeliik from Airai. No coconut groves were seen in the interior, except one surrounded by, and being overgrown by, jungle to the northeast of the road toward the border of Aimeliik, and another grove at old Ngatpang. The second visit was to the main village (Mehebehubel) on November 20. Here damage was found to be slight to moderate near the pier and in the village, but lacking to very slight in the groves between the pier and village and around the village. Oakley (214) states that in 1946 the beetle appeared to have just reached Ngatpang.

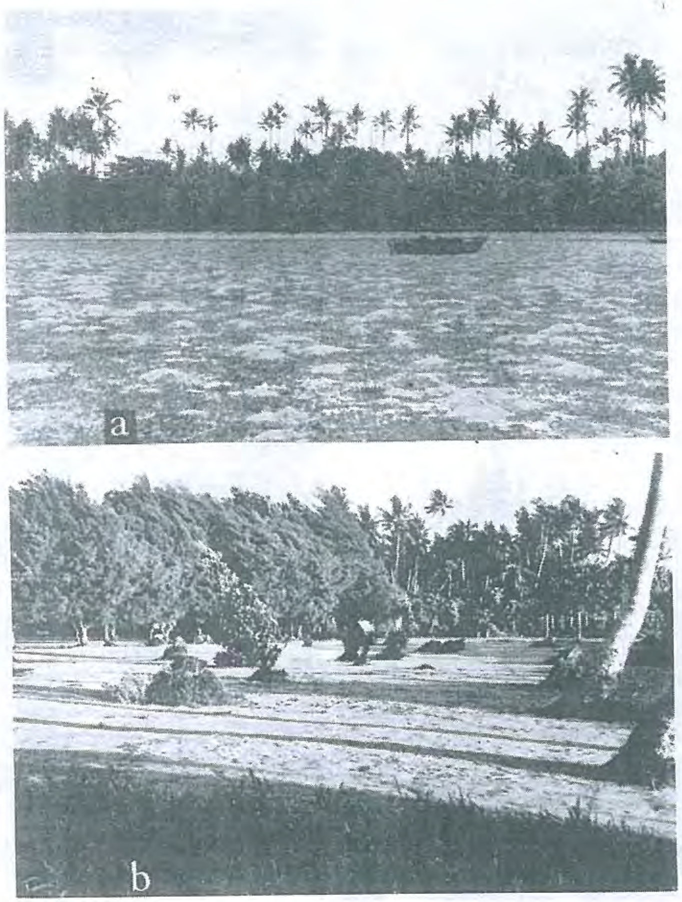

FIGURE 39.—a, Center of Ngiwal village and beach, from inter-tidal zone, showing sparsity and poor condition of coconut palms; b, Ulimang village, near beach and school, showing remains of many coconut stumps.

In December 1952 the old abandoned village of Ngatpang inland from Karamado Bay was visited and moderately severe damage to palms was seen. The coastal groves were still in good condition.

Ngaremlengui municipality was moderately affected by *Oryctes*. The control program was being completed at the time of my 1951 visits. South of Ngeremetengel village (July 24) a moderate number of remaining palms were scattered over the hills. Felled logs had been dragged to the small streams or the edge of the mangrove swamps. On walking across Babelthuap from Ngiwal, after emerging from the jungle-covered interior, some former Japanese clearings now grown with tall grass, were found to have scattered coconut palms affected by the beetle, and a few dead trunks not reached by the control team. Near the former pineapple cannery, inland from Aimeong village, a considerable area of grassy clearings had been planted to new coconuts some months earlier. Aimeong village still had a good stand of coconut palms remaining, as well as many betel-nut and nipa palms. In 1952 the coastal groves appeared to be in good condition.

Ngardmau municipality (Karasumau), northwestern Babelthuap—visited twice (Sept. 21, Oct. 10) at the start of the control work there—is probably the most seriously affected next to Airai, perhaps because the large Japanese settlement, the headquarters of the former bauxite works, was heavily attacked during the war. There are coconut groves in the village and inland from it, but they are isolated by jungle both from Ngaremlengui for a long distance on the south and from Ngaraard-Ngkeklau on the east. In Ngardmau village were seen about 60 standing dead trunks, more than 50 stumps or logs, about 50 dying and many seriously affected palms, besides some probable attack on the betel-nut palm. A population of 50,000 *Oryctes* was estimated at the start of the control program.

In Ngaraard municipality, as elsewhere in northern Babelthuap, damage was moderate to serious (fig. 41, *a*) in the villages and rather slight along the beaches or in large groves. The village of Ngkeklau has suffered rather little from *Oryctes*, and villagers attribute this to the fact that monitor lizards feed on larvae in logs and stumps. I did not make a detailed survey but I saw little evidence of damage while walking through the village and traveling along the coast. Ulimang, the largest village of Ngaraard, has suffered severe damage around the center (fig. 39, *b*). About 150 old stumps, 30 standing dead trunks, 15 dying palms, 80 seriously affected and 1,000 moderately to slightly affected palms were estimated. Alap village just to the north suffered less, and the hamlet near the Ngaraard pier on the west coast is little affected. The east coast groves appeared to be still in good condition in December 1952.

Ngarhelong, the northernmost municipality, suffered quite a bit in the village areas and along the roads but rather little in the groves which stand apart on some of the slopes on either side of the peninsula. Agol village on the east coast had about 15 standing dead trunks, 60 old stumps, 10 logs, 50 seriously affected, and many other moderately affected palms. In Ngarhelong village, 25 standing dead trunks, 80 stumps, five logs, and 60 seriously affected palms were observed. At Olei village 12 standing dead trunks, 40 stumps, 10 logs, and 40 seriously affected palms were seen. Between Ngarhelong and Olei probable evidence of adult attack on *Pandanus* was noticed. Between Agol and Ngarhelong two damaged *Heterospathe* palms were noticed (fig. 31, *a*). The control crew cleaned up the area in the winter of 1952-1953.

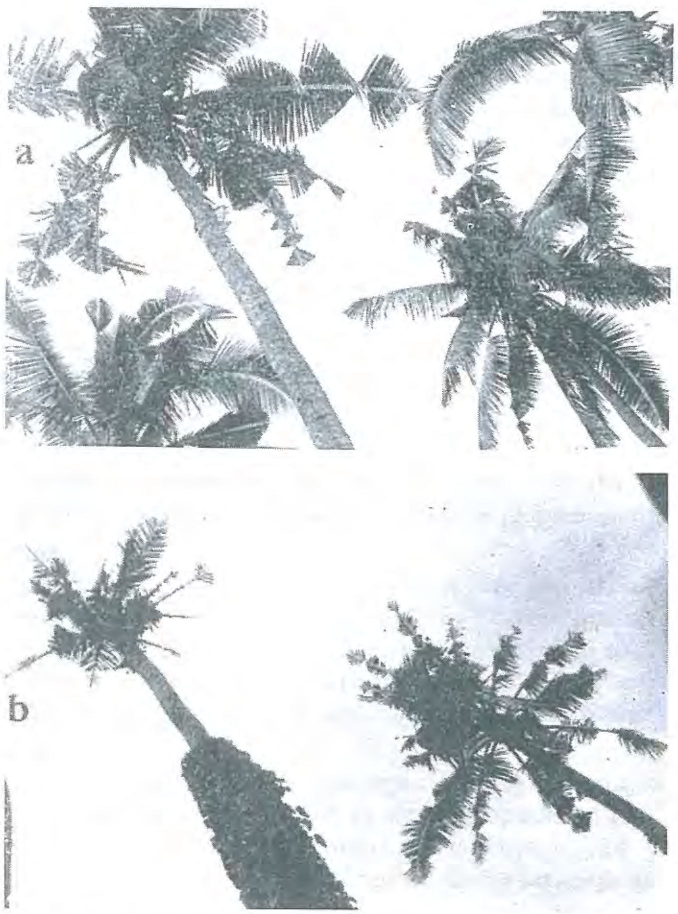

FIGURE 40.—**a**, Coconut palms damaged by adult feeding, Ngiwal village; seriously damaged, bearing very few nuts. **b**, palm at left dead, *Piper betle* on trunk; palm at right without nuts.

Ngaregur and Ngarekelau, two islets just off the northern tip of Babelthuap, are rather lightly affected by the beetle, which probably reached them about 1949. It is assumed that here, as on Kayangel main island, the beetle has been spreading and increasing slowy. This may be largely attributable to the lack of war damage, the small population (under 10 people), a lack of suitable compost, and the presence of monitor lizards. Only Ngaregur was briefly visited on September 16, but both islets were viewed from several directions. I estimate that of about 2,000 coconut palms on the two islets, 15 have been killed, 30 moderately to seriously affected, and 250 slightly affected.

KAYANGEL ATOLL

Among the major islands of the Palaus, Kayangel was the last to be reached by the beetle. It must have reached the atoll by small Palauan vessels from Babelthuap or Koror about 1947, or possibly by United States Navy craft as early as 1945. However, it has not spread with the severity it has in most parts of the Palaus, and the atoll, together with parts of the east coast of Babelthuap, has the best remaining coconut groves of the Palaus. There was little war damage here, and only Ngariungs Island, the second largest of the four, which was occupied by American forces toward the end of the war, suffered seriously from *Oryctes*. However, the beetle is slowly spreading, and control measures are necessary. There are about 13,000 coconut palms on the atoll, the great majority on the main island. The combined area of the islets is less than 1 square mile.

The beetle probably did not reach Ngajangel (main island) until 1949. It is spreading northward from the south end, and some 50 palms have been killed within 300 meters of the south end. From that area to the middle of the island damage is slight, with only about one of every three palms slightly affected. From the middle to the north end of the island the damage is very slight, with only about one palm in 10 affected. Some compost pits were examined and larvae found under a cut banana stalk in a ditch compost pit between banana plants in the village.

By December 1952 the beetle had spread farther northward on the main island, but probably with only a moderate increase in population. Around the cassava-papaya clearing in the southeastern part additional palms had been killed and six new standing dead trunks were seen without completely investigating the surroundings. A little more evidence of attack on palms was seen in the village area. The control crew moved to Kayangel in early 1953.

Ngariungs, the second island in size and second from the north, is most seriously affected. The beetle must have come first to this islet, then spread to the other three. Formerly the island had about 330 grown palms. Of these, north of the inlet there were 42 slightly damaged, 48 moderately damaged and eight seriously damaged by the beetle; in the central third of the island 26 moderately damaged, 21 more heavily damaged, 18 seriously damaged, three standing trunks and a number of stumps; in the southern third, 36 moderately damaged, 48 more heavily damaged, 43 seriously damaged, four dead trunks and many very young palms. In December 1952 there were more standing dead trunks.

Ngarapalas, the third islet had only about 60 bearing palms. Of 26 along the level west side of the islet, mostly just starting to bear, only seven were affected. The remainder of the mature palms—at the north end, in the north-central, forested part, and at the southeast cove (mostly just maturing)—are very slightly affected. A number of new palms have been recently planted on the west coast.

Gorak, the fourth islet is less than 100 meters in diameter. It has only 75 coconut palms, 55 of them 20 to 30 years old. Only one standing dead trunk was found. It contained two *Oryctes* pupae and two larvae possibly killed by mold (not *Metarrhizium*), besides a male and female in pupal cells, five pupae, and 22 mature larvae. No fronds of the other palms seemed to be affected, and no logs or stumps were present.

Central Palaus

Koror (Oreor, Koreor), a small island (area 9 square km.) and the political and business center of the Palaus, was populated by 10,000 Japanese before the war. Coconut palms lined the streets and grew on open slopes. Koror, or its port island of Malakal, was most likely the point of introduction of *Oryctes* to the Palaus. At present only about five mature, pre-war palms remain. There are some 300 one- to three-year-old palms which were planted mostly for ornamental purposes, but almost all are killed by the time they reach the age of three years. Though war damage in Koror was severe, the loss of the palms is principally attributable to the rhinoceros beetle, according to Fey. When he returned to Koror from Ngkeklau in September 1945, he observed that the palms were dying primarily from the feeding of the beetle. About March of 1946, by which time most of the coconut palms were already dead, he observed adult beetles tunneling in sugar-cane stalks. By 1947 practically no coconut palms remained on Koror. *Oryctes* are obviously breeding in media other than dead coconut wood on Koror, as that was largely eliminated in the initial clean-up campaign, though only to a slight extent in most other places. A significant population remains, as evidenced by frequent attraction of adult beetles to lights at night. Some breeding was found in the extreme base of an old stump and in the remaining part of its old log. Searching in sawdust brought no results. However, breeding is undoubtedly taking place in compost and *Pandanus*, and feeding in young coconut palms, ornamental palms (figs. 31, *b*, 32, *b*), *Pandanus*, sugar cane, and perhaps in pineapple and banana. About 50 introduced palms of five species remain, although some have been recently fed upon. Betel-nut palms used to be abundant on Koror, but according to a Palauan informant many were cut for poles by the Japanese during the war and the remainder were largely killed by *Oryctes*. The eastern two-fifths of Koror is a high ridge of raised coral limestone (fig. 2, *a*) and the above statements do not apply to this part, which is considered along with the limestone islands. Here, as elsewhere, *Oryctes* could reach the *Gulubiopsis* palms with ease.

Arakabesan Island (Ngerkebesang), which is 6 square km. in area, is connected with Koror by causeway. It had less war destruction than did Koror, but only a few mature coconut palms and a few old trunks or logs still remain, and there are some young palms. Betel-nut palms are also scarce, and presumably breeding is taking place in *Pandanus*. The small islet just south of Ngurur Island west of Arakabesan has a single palm, possibly coconut.

Malakal Island (Ngenelael), a small island (3 square km.) which is the port of Koror and is connected with it by causeway, is likewise denuded of coconut palms. It was recommended that *Pandanus* and other hosts be eliminated from Malakal, because of the danger of *Oryctes* flying onto ships and being carried to other island groups, particularly Yap and Guam. This plan was carried out in the summer of 1952 by the control crew, and about 12,000 *Pandanus* plants, 4,000 native palms, four betel-nut palms, and 400 very young coconut palms were destroyed.

Limestone Islands

The limestone islands between Koror and the low islets just north of Peleliu are high and rocky. Most of them are steep-sided and undercut at their edges (fig. 2, *a*). Some have no beaches and therefore no coconut palms. The islands are uninhabited, except for single houses used when people go to harvest fruit or during fishing trips or stormy weather. The cleanup programs have not been carried out here (Gressitt, 138).

Auluptagel Island, visited on October 28, has a few small beaches and inlets with beaches or mangrove on the southeast side. Several coconut palms grew on each of the several small beaches, but all the grown palms had apparently been killed and most of them had fallen into water. *Oryctes* had been breeding in a few stumps. Auluptagel meets each end of Koror Island, both islands being somewhat crescent-shaped and jointly enclosing a small inland sea with limestone islets. However, the beetle would have to be a powerful flyer to get from the volcanic part of Koror to the isolated beaches on the far coast of Auluptagel. This strongly suggests that *Oryctes* has been feeding upon and breeding in *Gulubiopsis* or *Pandanus*, or both, in the intervening areas.

Urukthapel Island, second largest of Palau (19 square km.), is extremely narrow and irregular in shape. It is almost entirely of high limestone covered with scrub of *Pandanus, Dracaena, Gulubiopsis, Bikkia,* and other plants, and has few beaches. Three were seen on the south side of the northeast corner of the island on November 17, 1951, and the middle and largest of the three (some 150 meters long) had 60 living coconut palms, all affected by *Oryctes,* but a few of them bearing nuts; 48 standing dead coconut trunks, some of them dead a long time and eaten down considerably; and 50 which had been eaten to the ground. In December 1952, 12 standing dead trunks of *Gulubiopsis* were seen on ridges on eastern Urukthapel but none were found where the ridge was ascended at the old lighthouse.

Eilmalk Island (Mechereher), second largest of the limestone islands (9 square km.), is largely steep-sided and undercut, but has a few beaches. On November 18 I visited the three large beaches of the southeast corner and encircled the whole island passing between the main island and the many off-shore islets on the west coast. The western beach (Kura-asemil) is not very wide, but some flat land extends behind it, and at the west end slopes gradually up to the limestone ridge. There were some taro fields on the flat land, a little cassava on the slope, and sugar cane near the single, rarely used house. Coconuts grew over most of this area, which is now largely covered with second-growth forest. The following were noted: 17 living grown coconut palms, moderately to severely affected (fig. 32, *d*) and few bearing; one newly killed palm; 40 dead trunks, mostly eaten down to about 2 m. in height; 15 additional trunks eaten to the ground; 20 young killed palms; one sugarcane stalk possibly tunneled by adult *Oryctes;* two affected *Pandanus* plants. The fact that one- or two-year-old coconut palms had been killed seems significant, suggesting that a high population of *Oryctes* had existed a few years earlier.

Two beaches on the southeast peninsula of Eilmalk (Kuroboroban) are on opposite sides of the narrow peninsula, and the land between them is level, forming an area of about 2 square km., largely covered with second growth. A house stands on the northeast beach. The following were seen: 12 tall, standing live coconut palms, seriously affected; eight dead or dying palms; 130 trunks, many eaten down to stumps or to the ground, mostly very old and some with old fallen logs; 150 young palms, one to three years old, many rather lightly affected; clear evidence of attack on *Pandanus.* Few *Oryctes* were still present, but some ?*Oxycetonia* and *Callirhipis* were found. There seemed to be evidence that several coconut trunks or logs had been torn open by monitor lizards feeding on *Oryctes* larvae. Some animals heard running off in the underbrush sounded heavier than the numerous land crabs or rats. Giant snails and toads appeared to be absent. The small beaches of northern Eilmalk had only an occasional very young coconut palm. This also suggests extermination of small former stands. No beaches were seen on the west or southwest, or the off-shore islets.

Ngaiangas (Gaianges), an islet between Urukthapel and Eilmalk, is narrow, extending east and west, and is partly raised limestone with north and south beaches having largely level land between them. The following were seen or estimated on November 18: 40 dead coconut palms, eaten to the ground; two trunks about 3 m. high; three old stumps with their fallen and eaten logs; 130 young (one- to three-year-old) palms, some severely affected; no mature palms. Some fairly clear evidence of *Oryctes* attack on *Pandanus* was seen, and some dead, half-grown papaya stalks seemed to have been hollowed, but not for certain by *Oryctes.* Megapodes and feral chickens were present. Bananas, and other crops grew on the islet, but second growth forest had overgrown the former coconut grove.

Abappaomogan (Omogan) Island, the largest of a group standing off to the west of Eilmalk and northeast of Ngemelis, had the following on the small beach at the north end, November 19: one stump or base of eaten trunk, quite old; 41 new palms, one- to two-and-a-half years old, unaffected by *Oryctes.* This suggests either that *Oryctes* was once present, killing the only palms, and later dying out or maintaining a very low population in *Pandanus* or *Gulubiopsis;* or that *Oryctes* was never here and the only palms had been cut down by Japanese forces for food.

Aulong is a high, narrow limestone island, the farthest west of the chain extending west of southwesternmost Urukthapel. The 0.5 km. beach visited on the south side near the west end is perhaps the only beach in this group. It is backed by a narrow flat area. Here, on November 19, the untouched evidence of a former high population of *Oryctes* was seen, as follows: 90 old dead coconut trunks, mostly eaten low; 40 additional trunks, eaten to the roots; 30 old logs, largely consumed; 30 three- to four-year-old living palms, affected by *Oryctes;* 40 two- to two-and-a-half year old living palms, mostly not affected by *Oryctes.* Some of the second-growth forest had been recently cut, baring some of the young palms. Megapodes, crabs, and lizards were common.

Two standing dead *Gulubiopsis* trunks were seen on the ridge of Apurashekoru Island on November 19, 1951. This suggests that *Oryctes* may have reached beaches where coconut trees grow by breeding in the native palms. A few young coconut palms were seen on a small beach at the west end of the island.

My general conclusions from the observations on the high limestone islands are that the beetle reached them several years ago and rapidly increased its population at each beach nearly to the point of exterminating the coconut palms, and that then the populations became much reduced, in some cases almost to extinction, as a result of reduced food supply and environmental resistance in the form of monitor lizards (toads are lacking), feral chickens, owls, rats, crabs and perhaps kingfishers, as well as predaceous insects. War damage probably aided the beetle in building large populations.

The Southern Islands

Ngereong (Ngeregong), a concave-triangular island about 3 km. long, lies at the northeast extremity of the Peleliu reef, near Eilmalk. The highest point is 5 or 6 m. above sea-level. It has a hamlet of five houses on the southwest side and taro, banana, and papaya fields near the south end, as well as roads, barbed-wire and other remains of American occupation toward the end of the war. There are mangrove swamps on the east side near the center of the island. The following coconut palms were counted during November 17 to 19: 16 bearing; 28 living, seriously affected; two dying; 11 dead standing trunks; 16 additional trunks eaten to the ground (fig. 41, *c*); 10 old stumps and fallen logs; eight young killed palms; 45 young (one-to-four-year-old) seriously affected; 42 affected five-year-old palms; eight young palms not affected; some probable attack on *Pandanus*. By December 1952 more palms had been killed. A resident of Ngereong told me that he had come to the island from Airai (Babelthuap) in 1945, and that the beetle had appeared in Airai in 1944 and on Ngereong in 1946. My general conclusion, from answers to my questions and from other evidence, is that Palauans as a rule noticed the beetle about a year after its arrival in each locality. This very man may have accidentally carried the beetle from Airai to Ngereong, and others, similarly, to other islands, from Babelthuap or Koror just after the war.

Ngerugelbtang, a narrow low islet on the reef between Ngereong and Peleliu, resembles Ngariungs Island of Kayangel Atoll, but it is smaller. The condition of the palms is also somewhat similar. The following were counted on November 17: 81 living mature palms, moderately to seriously affected; two recently killed; one log; 20 dead trunks or stumps; many young palms not seriously affected. It appeared that the beetle had reached this island much later than it did Ngereong, possibly as late as 1948 or 1949.

The Ngemelis Islands are a group of narrow islands lying northwest of Peleliu, resembling an atoll in some respects, though consisting in part of raised coral rock. Four islands are more than a kilometer long, and others are smaller, one being considerably raised and joined to Admasah Island by a sand spit. The islands are populated by 15 Sonsorol people, who came from Arakabesan after the end of the war. On October 24, 1951, I reached the village at the west end of Admasah Island and swam or waded to six other islands, including Lilbau and Heleu (Garyo). Most of the stand of 3,000 pre-war coconut palms was on Admasah and Lilbau, but some were seen on Heleu,

FIGURE 41.—Coconut palms killed by adults: a, stunted five-year old palm just dying, Ngaraard; b, 10-year old palm, remainder of dried crown persisting, Melekeiok; c, five-year old collapsed coconut palm killed by adults, hollowed by larval feeding, Ngereong Island.

Ngis, and Ngedos. On Admasah, damage by *Oryctes* was serious at the west end near the hamlet, with 14 palms killed and about two-fifths of the rest affected. On Lilbau the damage was greater, with 15 palms killed and at least one-half of the remainder recently fed upon by the adults. Evidence of *Oryctes* breeding or feeding in *Pandanus* was noted on Admasah and Heleu. The long-horned grasshopper (*Segestes*) has also done serious damage on Admasah Island (Owen, 218). Near the hamlet I observed several palms with only

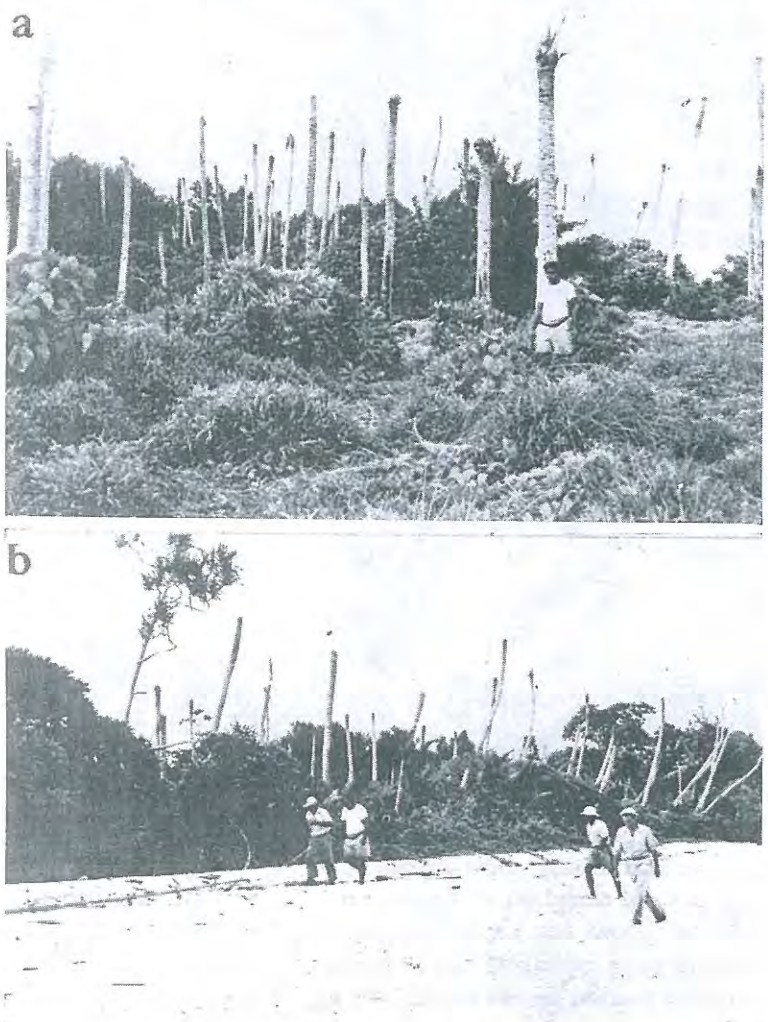

FIGURE 42.—Peleliu Island: a, standing dead coconut trunks on east coast, killed by adults and breeding young in large numbers. b, on beach near location of *a;* Chief Obok at left, Mr. Owen at right.

the midribs of the lower fronds remaining (fig. 44, *a*). However, the severe damage by this insect did not seem to be general in the group. From observation and questioning, I gathered that *Oryctes* must have reached the Ngemelis Islands some time after it reached Peleliu, perhaps in 1947 or early 1948. The situation seems to be somewhat similar to that at Kayangel Atoll. Thus the beetle may be still spreading, but not at a very rapid rate, because it did not have the start permitted by war-damaged palms. A beetle population of some 8,500 was estimated.

Ngergoi Island (Ngerekeu, Garakayo), north of Peleliu, is slightly higher than those nearest it, having some rocky forested hills. Behind the beaches on the north and northeast coasts there are some fairly extensive stands of coconut palms which appear to be rather lightly affected by *Oryctes*. Ngesebus and Holngoaol (Ongewaol) are two adjacent low islands just north of Peleliu. Ravaged during the war, a few coconut palms remain on the north side of one or both islands.

On Peleliu, the third largest island (12 square km.) of the Palaus, coconut palms are almost exterminated. In the area of the two villages, both near the north end, and from there to the south end, are no mature palms, and few remaining dead trunks or stumps and young palms. Early in 1951, 1,000 new palms were planted near the north end. Within six months, more than one-third of these had been killed by *Oryctes* and many were dying (fig. 43, *a, b*). A disease appeared to have followed the *Oryctes* damage. The only bearing palms were about 25 at the north end of off-shore Ngabad Islet off the east coast and possibly a few in second growth forest on the peninsula south of Ngabad. There were about 745 standing trunks and 280 dying or seriously affected palms along this peninsula and on Ngabad and the islet between them. At the southern end of this remaining growth, over 60 dead trunks stood in one group, with no living palms among them (fig. 42, *a, b*). These were not killed during the war, but by *Oryctes* during 1949-1951. These trunks were breeding a large population of *Oryctes,* which will have to shift to *Pandanus* when the few remaining living palms are killed. A few dead or young palms remained west of the peninsula. There were over 2,000 self-planted young coconut palms. A population of 60,000 *Oryctes* of all stages was estimated for Peleliu.

In December 1952 coconut wood had almost disappeared from the village areas; there were only 10 palms still bearing at the north end of Ngabad Island, and grubs were scarcer in the standing trunks on the peninsula to the south. This, and other evidence, indicated a considerable reduction in *Oryctes* population during the year. This is attributed partly to reduction of dead coconut wood by larval feeding, reduction of oviposition from scarcity of preferred adult food, and dessication of the unshaded, partly eaten dead trunks.

On Angaur Island (8.3 square km.) there are no bearing coconut palms and probably no living palms more than three years old. Most of those over one year old have been attacked by *Oryctes*. Only a few partial, standing dead trunks remain, and most of these are serving as telephone poles in the Palau village. According to Owen (217), 12 mature palms remained at the beginning of 1950, whereas there were about 6,000 bearing palms before the war. The initial clean-up campaign was relatively well carried out on Angaur. Most of

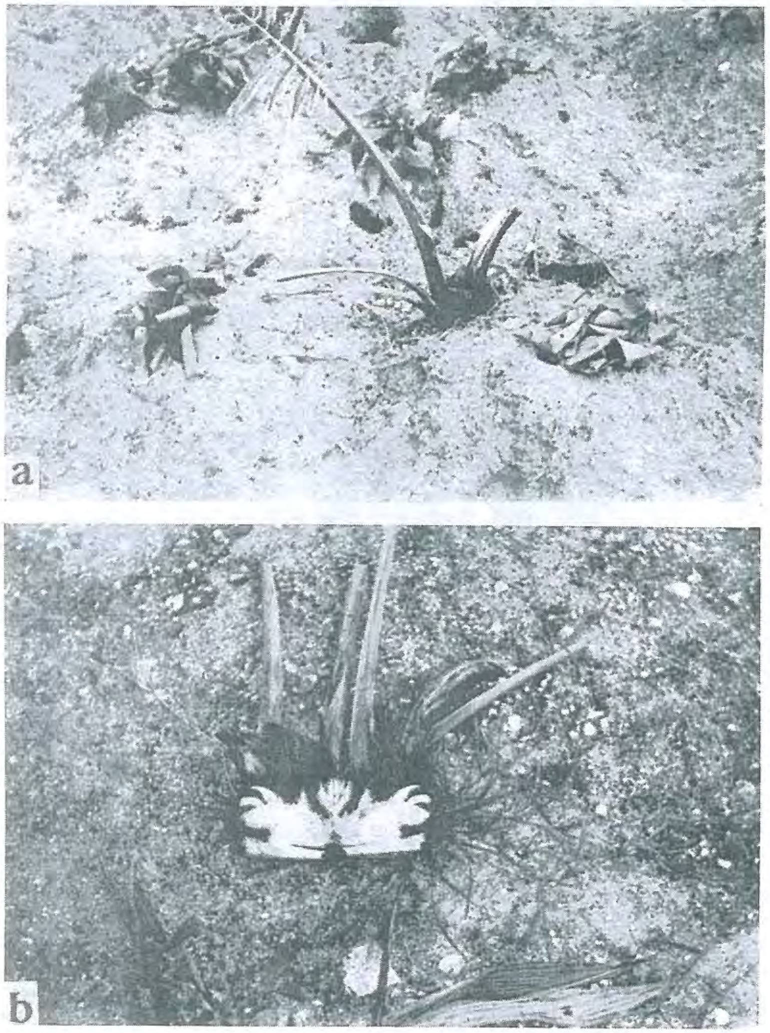

FIGURE 43.—a, Eight-month old coconut palm killed by adults at north end of Peleliu; b, eight-month old coconut palm showing malformed growth following adult feeding.

the palms remaining in late 1948 were cut down in an attempt to control the beetle, but the logs and stumps were not completely destroyed. Some logs still remain in the second growth vegetation, and perhaps 1,000 stumps remain in the village and elsewhere (fig. 35, *a*). Of about 400 young palms, mostly about two years old, approximately 80 percent had been affected by *Oryctes*. Some new palms planted early in 1951 near the south end were already being attacked. The beetle is both feeding upon and breeding in *Pandanus* (figs. 37, 38) to a considerable extent (Gressitt, 139) and has been reported by the villagers from a large banana plant and from sugar cane. I consider it significant that adults are feeding extensively on *Pandanus* when many young coconut palms remain. An estimate of 17,750 *Oryctes* of all stages was made. The bulk of this population is in the southern part of the island, in and around the main Palau village. The remainder is scattered in most other parts of the island, including the Japanese Phosphate Company camp section, isolated young palms or wood remains in the second growth jungle, and cultivated patches in the east and north, including the smaller Palau village.

Census Summary

Totaling the above estimates of the populations of *Oryctes* in the various islands or municipalities, including rough guesses for those areas for which estimates were not attempted, the sum of 450,000 is obtained. This represents the estimate of the total population of *Oryctes* of all stages for the Palaus in the late autumn of 1951. The more seriously affected areas may be listed roughly as follows in decreasing order of damage: Koror, Malakal, Arakabesan, Angaur, the limestone islands, Peleliu, Ngereong, Airai, Ngardmau, Aimeliik, Olei, Melekeiok, Ngiwal, and Ngariungs.

My visit in December 1952 showed that there was a marked decrease in population in most parts of the islands, perhaps in all but Kayangel, where there was probably a slight increase as well as spread. This indicates a tapering off of the former abnormally high population through depletion of favorable breeding media, as a result of both the work of the control crew and the feeding of the grubs. If control measures are vigorously continued, it may be possible to reduce the population to the point where copra production will again be profitable throughout Palau.

INVERTEBRATE CO-HABITANTS OF FEEDING AND BREEDING SITES

Other pests of the coconut palm in the Palau Islands are the red coconut scale, *Furcaspis oceanica* Lindinger, the long-horned grasshopper, *Segestes unicolor* Redtenbacher, and the hispid, *Brontispa palauensis* (Esaki and Chujo). Also, a slender lepidopterous larva and a small calandrine weevil were found in a new frond with *Brontispa*. The scale insect and the grasshopper are sometimes rather serious. The red coconut scale lives on the surface of mature leaflets and petioles of the fronds, sucking the juices, and occasionally kills coconut palms on islands where its parasites are lacking. The grasshopper chews off the borders of mature leaflets (fig. 44, *a*), but only reduces nut production to the extent that it reduces leaf area by its feeding. The hispid is presumably under natural biological control, but it may hasten the death of a

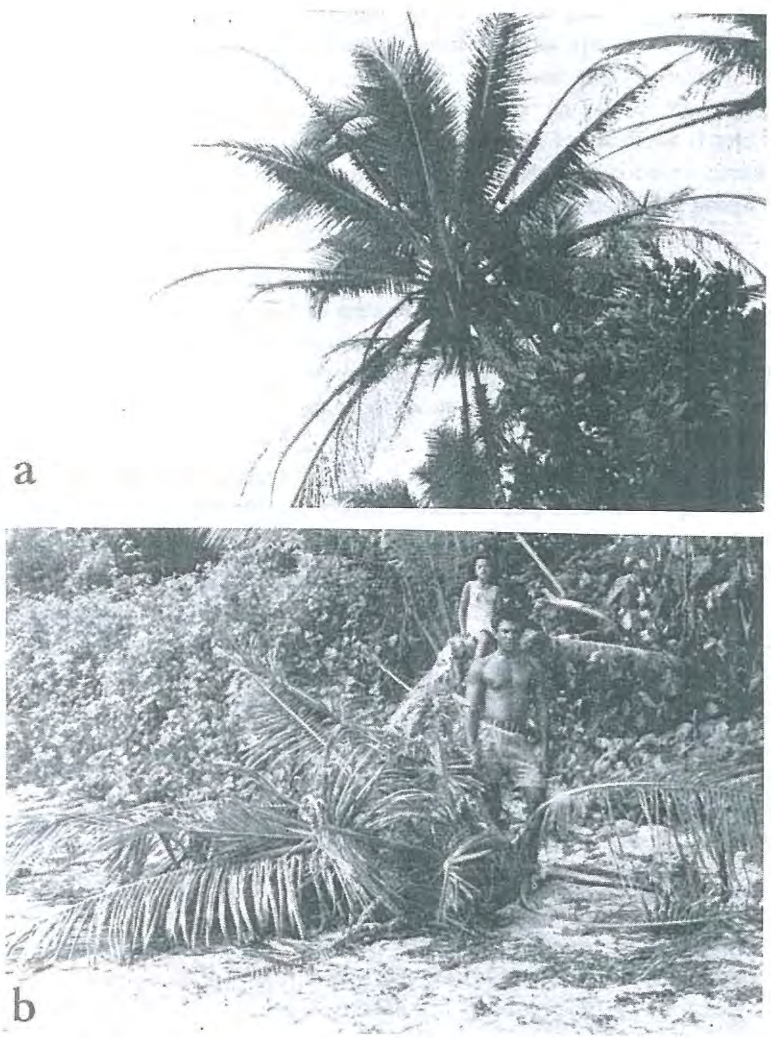

FIGURE 44.—Other coconut pests in Palau: a, work of long-horned grasshopper, *Segestes unicolor*, skeletonizing fronds, Melekeiok; b, palm killed by *Oryctes*, perhaps aided by *Brontispa* which mined in the fresh leaflets, causing them to shrivel, Ngiwal.

palm seriously affected by *Oryctes* (fig. 44, *b*). Both larvae and adults feed within the still folded leaflets of new fronds. The invertebrate inhabitants of the larval breeding sites of *Oryctes* in Palau include the following:

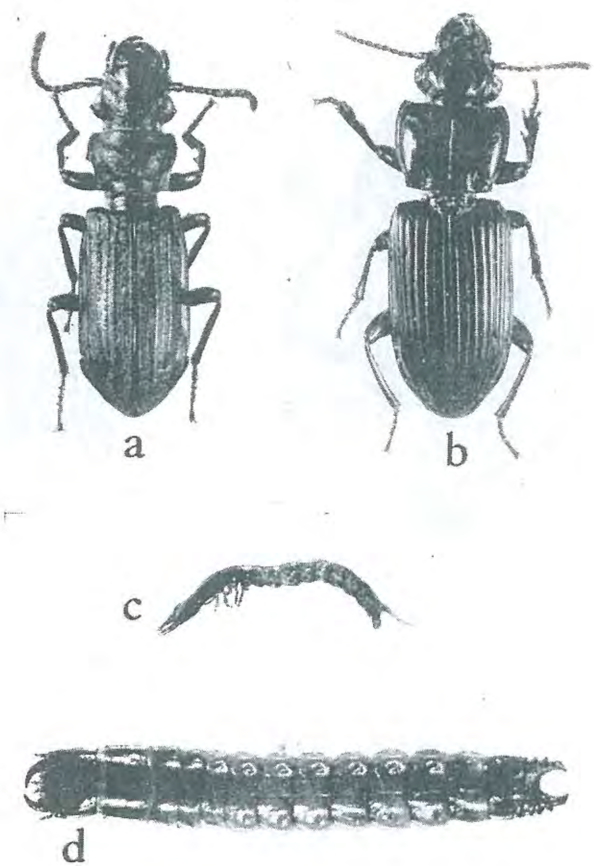

FIGURE 45.—Native Palau Coleoptera predaceous on early stages of *Oryctes:* a, *Pseudozaena tricostata opaca,* adult; b, *Morion ?orientalis,* adult; c, *M. ?orientalis,* larva, view of left side; d, *Alaus depressicollis,* larva.

COLEOPTERA

CARABIDAE: *Pseudozaena tricostata* (Montrouzier) subspecies *opaca* (Chaudoir) is a moderately common predaceous beetle in logs and trunks where *Oryctes* is found (fig. 45, *a*). One adult kept in the laboratory fed for five weeks on *Oryctes* eggs alone, and another lived for three weeks on eggs and young larvae only. *Morion ?orientalis* Dejean (fig. 45, *b, c*), a slightly smaller ground beetle, is a little less common than *Pseudozaena tricostata* but is found in similar situations. An adult in captivity ate two first instar larvae of *Oryctes,* and a larva also ate a few very small *Oryctes* grubs.

STAPHYLINIDAE: *Leptochirus* sp. is a black rove beetle which is often found in old logs near *Oryctes* galleries. Two submature larvae confined with two eggs and a 10-day old first instar larva of *Oryctes* died, while an adult in the same tube tried for some time to eat the *Oryctes* larva, finally killing it, but not showing interest in the eggs. This beetle is, at most, capable of feeding on newly emerged *Oryctes* larvae.

HISTERIDAE: *Pachylister chinensis* Quensel (fig. 46, *a*) was introduced from Samoa to Palau in 1952 because both larvae and adults feed on young grubs of *Oryctes,* as well as fly maggots.

ELATERIDAE: *Alaus depressicollis* Schwarz (fig. 45, *d,* larva) is predaceous in the larval stage and is often found near *Oryctes* in dead trunks and logs. Larvae in captivity readily ate *Oryctes* grubs, and one ate a *Morion* larva. *Simodactylus* sp., a pale click beetle, is found in rotting wood, but the larva is a scavenger.

RHIPICERIDAE: *Callirhipis onoi* Blair larvae live in dead coconut wood and other dead wood of more advanced stages of decomposition than do the above-mentioned beetles. Pupation takes place in a long cell consisting of an enlarged larval tunnel 0.5 inch in diameter, often far from the surface of the trunk. It is a scavenger. Members of this genus have been reported to be pests of the coconut palm in the Seychelles (Zacher, 309).

TENEBRIONIDAE: *Pediris sulcigera* (Boisduval) is a darkling beetle which in the larval stage bores under the bark of standing dead coconut palms (fig. 46, *b*). It is not abundant, but several may be present in the same trunk. Adult beetles may be found feeding in the same situations. Pupation takes place in a cavity bored by the larva close to the bark. *Toxicum quadricorne* Fabricius is a narrow, dull black beetle frequently found under the loose bark of dead coconut trunks or logs. The male has horns on the head. *Uloma orientalis* Castelnau, a shiny black, parallel-sided beetle, is found in dead logs of coconut, or stumps or trunks, generally under the bark. It is slightly broader than *Toxicum quadricorne. Amarygmus hydrophiloides* Fairmaire is only about 5.5 mm. long, is broadly ovate, and deeply striated on elytra. The bluish black adult jumps. It is common in coconut trunks, logs, and stumps. The larva is rather dark above and fairly active. The pupa has conspicuous processes on sides of abdominal segments.

PASSALIDAE: *Gonatas carolinensis* Gravely (fig. 47, *a*) is abundant locally, with larvae and adults under the bark of standing or fallen dead coconut palms. When present, a number of adults and larvae are generally found together.

Both feed under the bark, and pupation occurs in a cavity near the bark. This beetle is a scavenger, as far as is known.

SCARABAEIDAE: *Anoronotum rufum* Arrow, a smaller member of the same subfamily as the coconut rhinoceros beetle, is apparently endemic to the Palaus. It feeds in stems of sugar cane, but only two or three specimens have been taken by entomologists. *Parastasia guttulata* Fairmaire (fig. 47, *c, d*), a June beetle, is not very abundant. It feeds in old logs and stumps in the larval stage, and the adult is presumed to feed on leaves of plants other than the coconut palm. *Phyllophaga carolinensis* (Arrow) probably feeds on grass roots during its larval stages, but may occasionally be in association with *Oryctes. Adoretus* sp. is probably also a leaf-feeder in the adult stage and a root-feeder in the larval stage. Probably introduced during or after the war. A somewhat active hairy larva of *?Oxycetonia* sp. (fig. 47, *b*) was occasionally found in or near the galleries of *Oryctes.* No adults were collected.

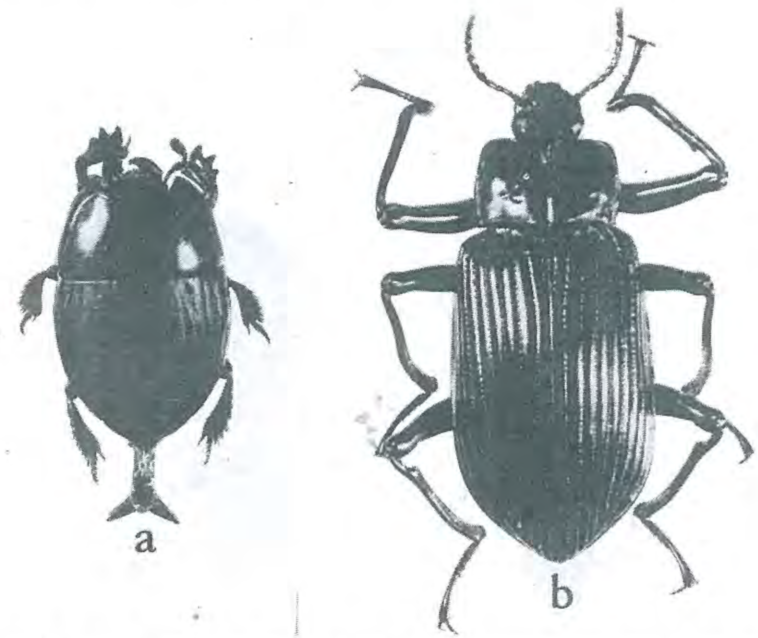

FIGURE 46.—a, *Pachylister chinensis,* adult with terminalia extruded (predaceous on early stages of *Oryctes;* introduced from Western Samoa to Palau, 1952); b, *Pediris sulcigera,* adult, found in trunks containing *Oryctes.*

LUCANIDAE: *Figulus integricollis* Thomson: Both larvae and adults feed in old, dead coconut logs or trunks, generally just under the bark. The galleries are shallow and generally contain black sawdust-like excreta.

CERAMBYCIDAE: *Olethrius* sp.: Many larvae, one pupa, and one adult of this large prionid were found once in company with *Oryctes* in an old kapok stump.

CHRYSOMELIDAE: The Palau *Brontispa* was discussed at the beginning of this section. It belongs to the same genus as the Mariana, or Saipan, coconut beetle.

BLATTARIA

Pycnoscelus surinamensis (Linnaeus) is a common cockroach in *Oryctes* larval habitats, particularly in compost and old rotten stumps. *Diploptera dytiscoides* (Serville) is less common than *Pycnoscelus*. *Periplaneta australasiae* (Fabricius) was found in debris. *Cutilia nitida* (Brunner) and *Homalopteryx pelewensis* (Saussure) are found in *Pandanus*.

ORTHOPTERA

TETTIGONIIDAE: *Segestes unicolor* Redtenbacher, a long-horned grasshopper, is at times a serious pest of the coconut palms in the Palaus. It was found seriously abundant only in Ngemelis Island, at Melekeiok (fig. 44, *a*), and in the Ulimang-Agol area.

GRYLLACRIDIDAE: *Salomona carolina* Willemse is a large species which is generally found in *Pandanus*.

GRYLLIDAE: *Acheta* sp. is a common cricket in compost.

GRYLLOTALPIDAE: *Gryllotalpa africana* is a common mole cricket in compost.

DERMAPTERA

Chelisoches morio (Fabricius) is a large earwig common in compost. *Euborellia* sp. and *Nesogaster* sp. are found in compost or old logs.

ISOPTERA

Neotermes kanehirae (Oshima), a large, broad termite, is common in damp stumps and logs. *Nasutitermes brevirostris* (Oshima) is a small nasute termite which occurs in small colonies in cavities or injuries in bark of standing dead palms and attacks the trunks earlier than *Neotermes*. Mature colonies are housed in large paper nests on trunks, and covered tunnels are also made. *Glyptotermes* sp., a slender species, is often found in small colonies in damp decaying stumps or logs. *Prorhinotermes* sp. is a small termite found in coconut logs. *Coptotermes remotus* Hill was found near *Oryctes* in a kapok stump.

HEMIPTERA

The red coconut scale was discussed at the beginning of this section. Flat black aradid bugs (*Mezira* and *Artabanus*) were common in old logs or trunks under bark, but probably have no direct relationship to *Oryctes*, as they feed on fungus. A reduviid nymph (?*Haematoloecha*) was once found near *Oryctes* in an old stump at Ngiwal. This predaceous bug might possibly feed on young grubs.

HYMENOPTERA

FORMICOIDEA: *Anoplolepis longipes* (Jerdon) is a slender, actively running red-brown ant found commonly in large colonies in dead stumps of coconut in various stages of decay. Its nests are often in close proximity to those of termites. It is predatory and attacks exposed larvae of the rhinoceros beetle, carrying them off to their nests. It apparently does not often remove them from the burrows of the grubs, however. *Solenopsis geminata* (Fabricius) is a short-legged, reddish fire ant, less abundant than *Anoplolepis longipes*. It has a painful bite and can easily kill small *Oryctes* larvae. *Odontomachus haematodes* (Linnaeus) is a large black ant with very large mandibles and frequently is seen nesting under the bark of old trunks or stumps of coconut palms. It is capable of giving a painful bite to human beings and can probably eat small *Oryctes* grubs. *Pheidole megacephala* (Fabricius) is a medium-sized, flattish, black species of ant with a large head, particularly in the soldier caste. It is somewhat infrequently observed under bark of coconut trunks and in other situations in Palau.

FIGURE 47.—**a**, *Gonatas carolinensis*, larva and adult (often found in trunks containing *Oryctes*); **b**, larva of ?*Oxycetonia* sp.; **c**, *Parastasia guttulata* larva; **d**, adult of *c*.

SCOLIIDAE: Introductions to Palau of *Scolia ruficornis* (fig. 48) from Zanzibar, and of *S. patricialis* and *S. procer* from Malaya were attempted (see section on biological control), but it is not yet certain that any is established.

Chilopoda

Scolopendra morsitans Linnaeus is a large broad centipede which is fairly common under the bark of old trunks and logs, including coconut. It feeds on insects, including *Oryctes*. Four fair-sized specimens were found under bark of one old trunk which contained only 13 *Oryctes* larvae. A medium-sized individual killed and ate a two-week old larva in the laboratory. One, 15 cm. long, confined for some days, ate several first and second instar larvae. *Mecistocephalus* is a predator not infrequently seen in logs in advanced stages of decay or in soil beneath the logs. It has not been observed to feed on *Oryctes* larvae. A second genus, a narrow centipede, is found in situations somewhat similar to the preceding. It probably does not feed on *Oryctes*. *Thereuonema* sp. is a long-legged centipede found in very rotten stumps or logs.

Diplopoda

Trigoniulus lumbricinus (Gerstaecker) is a medium-sized, slender, red millipede which is common in compost piles of advanced stages. It is generally found in the rotting debris just above the level where the *Oryctes* larvae are found. *Spirostrophus naresi* (Pocock) is a smaller, slender, gray, blackish, or annulated species which is common in old rotten coconut stumps, particularly those already attacked by *Oryctes* and *Callirhipis* larvae. *Polyconoceras callosus* Karsch is a large black millipede found in damp compost or roaming on damp ground. *Orthomorpha coarctata* (Saussure), a grayish, flattened millipede more than 25 mm. long, is often found in debris around or in old stumps or logs and in piles of chips. *Siphonophora* sp., a more slender, pale species, has been found inside old coconut logs.

Scorpionida

Hormurus sp., a small scorpion, was found occasionally near *Oryctes* but was never observed to feed upon it.

Acarina

A small, short-bodied, red-brown gamasid mite was found on the surface of the body of third-instar larvae. If abundant, it might hasten or cause the death of *Oryctes* larvae. Another small mite was found on adult *Oryctes*, particularly those kept in the large cages.

Crustacea

Decapoda: Hermit crabs (Coenobidae and Paguridae) of several species abound in Palau coconut groves, particularly those on low ground near beaches or mangrove swamps. When *Oryctes* larvae are exposed, the hermit crabs carry them off and feed on them. Some large coenobids carried off mature grubs just removed from the Ngiwal sawmill. Hermit crabs are often found in cavities in old stumps and logs containing *Oryctes* larvae and may search them out for food. Other crabs (Grapsidae: *Geograpsus*) are also found in such cavities, but have not been observed to feed upon *Oryctes*.

Isopoda: *Cubaris* sp. is a pill-bug abundant in old, rotting media, including both logs and compost. *Porcellio* sp. is a small isopod, common in damp places.

Mollusca

Vaginulus sp., a flat black slug, is found in damp situations and around compost. *Pupina difficilis* Semper is a minute, pale snail, common in old stumps and logs of coconut.

Invertebrate Parasites and Predators

Some of the above-mentioned species may feed on *Oryctes* grubs, at least occasionally, but the only one that feeds upon *Oryctes* alone is *Scolia*. Those that feed on *Oryctes* frequently probably include the *Alaus*, two carabids, *Scolopendra*, and the introduced histerid. Others that feed upon *Oryctes* only at times probably include hermit crabs, land crabs, smaller centipedes, predaceous bugs, and mites, which last are probably of little significance.

VERTEBRATE RELATIONSHIPS

Mammalia: *Macacus* sp., a monkey introduced on Angaur, Peleliu, and Babelthuap (?), might prey on the adult beetle, and also might open up advanced breeding sites where mature larvae occur. *Rattus ?exulans* enters rotten coconut logs and stumps and preys on larvae within them. Four stomachs examined at Kayangel contained copra only, and one examined at Ngiwal contained no *Oryctes*. However, rats frequently ate larvae kept in uncovered boxes at Ngiwal and Koror and even removed grubs or teneral adults from jars. Feral pigs are found in the forests of Babelthuap, but no evidence was obtained of their feeding on grubs.

Aves: *Aplonius opacus orii* is a black starling common in coconut groves and may feed on larvae in semi-exposed dead trunks or logs. Two stomachs examined contained only fruit remains. *Halcyon chloris teraokai* was reported by villagers of Ngiwal as feeding on adult beetles obtained in the daytime from the tops of coconut trunks or from dead logs. It is said to beat the beetles to death before eating, as it does lizards and snakes. One stomach examined contained only a long-horned grasshopper, but the kingfisher was shot in a grove in central Ngajangel where *Oryctes* is rare. Owen (217) reports that the rhinoceros beetle has been found by Palauans breeding in the communal nests of *Megapodius laperouse senex* (mound-nest builders). Two nests examined on Ngariungs Island contained no *Oryctes*. These nests were in jungle about 75 yards from a group of infested coconut palms. Other nests seen in former coconut groves on the limestone islands were not searched. *Otus podarginus* flies to coconut palms from the forests at night and perches near the bases of the fronds. It catches adult beetles, but the population of owls is said to have diminished as the result of swallowing live beetles, the spines of which cause stomach lesions. However, the owls still seem to be quite abundant in at least several localities, such as Ngiwal and Koror, where the beetle is common. A helper reported to me that he saw an owl catch an adult *Oryctes* which was attracted to a lighted house in Melekeiok in 1950. I observed and heard the owls in the palms nightly in Ngiwal village. Feral fowl (*Gallus*) are common, particularly at the edge of jungle, and probably frequently feed on grubs.

REPTILIA: *Varanus indicus indicus* Daudin, the monitor lizard, is said to prey upon the larvae of *Oryctes* by opening rotting logs; and logs were seen which seemed to substantiate this. The monitor has become rare in many parts of the Palaus since the introduction of the giant toad, as it dies from eating the latter. Monitors are more abundant in the northern parts of the Palaus where the better stands of coconut palms remain, but they have not prevented the elimination of palms on Angaur and the limestone islands, which are still populated by monitors. *Dasyo* sp., a common green skink, about 30 cm. long including the tail, ascends to the tops of the palms, including dead trunks, and may feed on young *Oryctes* larvae. Stomachs examined contained only the remains of small insects. *Emoia atrocostata*, a brown skink slightly larger than *Dasyo* sp., may likewise feed on *Oryctes* larvae. It is most commonly seen on or near fallen logs. Stomachs examined were negative. *Hemidactylus* (geckos) are often found in dead trunks containing *Oryctes*. One gecko in Western Samoa ate a first instar *Oryctes* larva in captivity.

AMPHIBIA: *Bufo marinus* is said to feed upon eggs or larvae in rotten stumps or logs, and it was found in stumps of coconut, *Pandanus*, and other plants. Of four stomachs examined at Airai, one contained termites and plant materials; two contained termites, miscellaneous insects, and plant materials; and one contained termites and a young giant African snail. One stomach examined at Koror contained a blind snake and miscellaneous small insects. In the laboratory, toads readily fed on large second instar larvae, consuming them instantly. Townes (282) found the scoliid wasp *Campsomeris annulata* Turner (284) in the stomach of this toad.

Of the few domestic animals in the Palaus, both chickens and ducks readily feed on accessible *Oryctes* larvae. Chickens catch those that are in sections of the top of trunks which fall and probably scratch some out of old collapsing logs and compost. Palau pigs do not eat the larvae when offered them, but there is the possibility that they might be taught to, as pigs root for them and eat them in Samoa and elsewhere. Cattle are so scarce in Palau that their dung probably is not important in the breeding of *Oryctes*.

As to relationships with man, the primary one is the destructive influence upon the Palauans' source of food and income. Although people of some countries, certain of those in Africa for instance, use large grubs like those of *Oryctes* for food, the abundance of food in the Palaus and the Palauans' extreme dislike of the insect rules out this relationship here. I roasted and ate a mature larva from which the gut was removed and found it not particularly distasteful.

ECOLOGICAL SUCCESSION IN ADULT HOST

As regards the primary pests of the living coconut palms—the rhinoceros beetle, the long-horned grasshopper (*Segestes*), the *Brontispa* beetle, and the red coconut scale (*Furcaspis*)—there is probably little or no ecological succession involved. Each is a primary pest of different parts of the living palm, and may occur quite independently of, or simultaneously with, any of the others. In the Palaus during the course of this study no heavy populations of the coconut scale were observed, and the *Brontispa* was observed rather rarely, though in large numbers on a few occasions in single palms (fig. 44, *b*). These palms were seriously attacked by *Oryctes*, and *Brontispa* undoubtedly hastened their death. Heavy infestation by the grasshopper where *Oryctes* damage is serious would no doubt make the death of the palm more certain.

Following severe attack by adult *Oryctes* on the living palm, various secondary effects set in. These include bacterial decomposition of the portions of the inner crown adjacent to the feeding tunnels of the adult and bud rot. Invasion by ants is common, together with various scavengers, such as earwigs and sowbugs. Rotting of the top of the trunk, just under the crown, may occur, and this may result in oviposition by female *Oryctes* or by filth-inhabiting flies (*Pseudeuxesta*, etc.) or both, as well as by earthworms. Adult oedemerid beetles of the genus *Sessinia* have been found resting in the daytime in the crown of a seriously affected palm. They are said to feed on new flowers of coconut (Lepesme, 190).

ECOLOGICAL SUCCESSION IN LARVAL HOSTS

Coconut palms killed by *Oryctes* adults are generally next attacked by the young stages of the beetle, after the adult female has entered the top of the standing dead palm to lay eggs some weeks after the crown has fallen to the ground. After a few to a number of weeks following an attack by *Oryctes* larvae, the various insect and other invertebrate co-habitants of the breeding sites join in the attack. Some of these generally appear in the following approximate order of ecological succession, several occasionally occur together, and any may occur at the same time in the same wood with *Oryctes* larvae. Almost never do they all appear together. Those preceded by an asterisk require greater moisture content and rottenness of the wood.

Rhinoceros beetle (*Oryctes rhinoceros*)	**Anoplolepis longipes*
Passalid beetle (*Gonatas carolinensis*)	**Solenopsis geminata*
Large tenebrionid beetle (*Pediris sulcigera*)	**Odontomachus haematoda*
Tenebrionid (*Toxicum quadricorne*)	**Pheidole megacephala* and other, smaller ants
Tenebrionid (*Uloma orientalis*)	
Lepidopterous larva (unidentified)	*June beetle (*Parastasia guttulata*)
Jumping tenebrionid (*Amarygmus hydrophiloides*)	*Callirhipis beetle (*Callirhipis onoi*)
Lucanid beetles (*Figulus*)	*Earwigs
**Nasutitermes brevirostris*	*Myriapods
**Neotermes kanehirae*	*Isopods
**Glyptotermes* sp. and others	*Small snails

Of the above, *Parastasia, Callirhipis,* and myriapods are rarely found in standing trunks, but generally in old stumps and logs. The lepidopterous larva is rare. Termites and ants may be found in small portions (often near injuries) of otherwise still rather sound trunks.

Under certain circumstances, a more rapid rotting—a sort of fermentation—takes place, attracting such other kinds of animals as earthworms and maggots of filth-inhabiting flies (*Hermetia,* otitids or muscoid flies). These may be present in the rotting top of a coconut palm before or after the crown falls to the ground. Sometimes a damp trunk becomes infected with an organism, perhaps bacteria, which in time turns the wood reddish and causes a strong offensive odor from large quantities of ammonia gas and other products. *Oryctes* larvae may be present in such trunks, but in reduced numbers, and rarely in the portions extensively affected by the fermentation.

After the various wood scavengers mentioned above come predators which feed upon them. These include the click beetle (*Alaus*), carabid beetles (*Pseudozaena* and *Morion*), centipedes (*Scolopendra*), hermit crabs (Coenobidae, Paguridae), a land crab (*Geograpsus*), and rats.

Some species of woody shelf fungus often attack logs or stumps. By the time the fungus mycelia have penetrated the wood and it becomes pithy, with the characteristic fungus odor, it is no longer attractive to *Oryctes* larvae. This generally occurs in damp shady places.

CONTROL

BIOLOGICAL CONTROL

Because *Oryctes rhinoceros* is such a large insect and is not susceptible to ordinary direct chemical control methods, and because collection of the adult beetles cannot easily be effected where they are feeding and doing their damage to the living palms, biological control is an important consideration. However, no parasite or predator has been found which satisfactorily controls *Oryctes rhinoceros*. One instance of satisfactory biological control of an *Oryctes* is that of *O. tarandus* on Mauritius by the wasp *Scolia oryctophaga,* introduced for the purpose from Madagascar (de Charmoy, *71, 72*; Jepson, *167*). It also appears from the observations of H. W. Simmonds (*253*) and others that *Scolia ruficornis* may be playing an important role in the keeping of *Oryctes boas* and *O. monoceras* under control in Zanzibar and neighboring parts of East Africa, in the native home of both the wasp and the *Oryctes*.

It is probable that the various species of *Oryctes* are held in natural check by a number of different forms of life as well as by competition for food in their native habitats. To date, the following animals have been found to feed on various stages of *Oryctes*: rats, pigs, tree shrews (or palm squirrels), flying lemurs, chickens, ducks, owls, kingfishers, crows, woodpeckers, monitor lizards and other lizards or geckos, toads, scoliid wasps, carabid beetles, histerid beetles, click beetles, hermit and other crabs, and scolopendrid centipedes. These and pathogens are discussed below in, roughly, the order of presumed importance or of knowledge concerning the relationships.

Insects

As has been shown, a number of species of the genus *Scolia* have been more or less associated with various rhinoceros beetles. The general habit for these wasps is for the adult scoliid to burrow into the ground to search out the scarab larva, which it stings, paralyzing the grub. It then carries the grub deeper down into the soil, sometimes as much as half a meter, and hollows a small cell in the soil, after which it lays a single egg on the ventral surface of the grub, on about the second or third abdominal sternite. The eggs hatch, sometimes parthogenetically (de Charmoy, *72*), in about five days and the wasp larva feeds as an external parasite on the *Oryctes* grub, chewing a small hole on its underside near where it hatches and imbibing the body fluids from the hole as the body of the host shrinks. The growth of the larval wasp is very rapid, occupying less than two weeks. The larva is soft-bodied, whitish, and somewhat tapering at each end. When the wasp larva is full grown it spins a tight, tapering cylindrical cocoon of fine pale brownish silk beside the shriveled *Oryctes* grub. Inside the cocoon the larva changes to the pupal stage and then, after some days, to the adult wasp. When ready to emerge, the wasp chews its way out of the anterior end through a hole, leaving a small, round, hinged cap.

The minimum life cycle of the wasp is much shorter than that of the *Oryctes,* often taking only a few weeks. However, for at least some scoliids, a cool period is required during the pupal stage or adult resting stage within the cocoon, and for others dryness retards emergence and the adults do not appear until the heavy rains which follow a dry season. These factors tend to limit the usefulness of the wasps as controlling agents when they are transported to a new environment with a climate different from that of their native home. *Scolia oryctophaga* in Madagascar may emerge from the cocoons six to eight weeks after pupation (de Charmoy, 69).

The habits of the adult *Scolia* wasps are not so well understood as are those of many insects. The adults are strong flyers and can cover great distances. The male wasps, which are smaller than the females (females are often two inches in body length), generally emerge first from the cocoons and crawl to the surface of the ground and commence flying. They may fly over the ground searching for female wasps and even burrow down into the ground, locating females in their cocoons and mating with them as soon as they emerge. A flying unmated female may be followed in flight by one or more males, and when the female alights on soft ground, such as a compost heap, the first male will follow her down into the soil where mating takes place. The adults usually fly in the morning, leaving their resting places in compost or sawdust before 10:00 a.m. and flying off some distance to feed on the nectar of certain types of flowers, particularly such large composites as the sunflower, *Urena, Cordia, Citrus, Eucalyptus* (Simmonds, 252), and *Stachytarpheta indica* (Jepson, 166), often returning shortly after mid-day to enter the ground again, rest, and later search for *Oryctes* grubs. One female *Scolia* may parasitize 30 submature *Oryctes* grubs over a two-month oviposition period. The adults are more active in warm sunshiny weather. On Upolu, female *Scolia ruficornis* were observed to burrow into the centers of the cacao-garbage compost pits where the temperature was up to 58° C., whereas the *Oryctes* larvae were only around the edge of the pit, where the temperature was 35° to 39° (air temperature 32°).

So far, only a few species of *Scolia* have been positively associated with species of *Oryctes;* others have been somewhat questionably associated. *Scolia hortorum* has been associated with *Oryctes nasicornis* in Europe (Fabre, 98) and *Scolia rufa*, with *O. tarandus* in Mauritius (de Charmoy, 67, 72). All those which have been considered parasites of *Oryctes rhinoceros* in the native environment are in the latter questioned category. Two, *Scolia oryctophaga* and *S. ruficornis* (fig. 48), are parasites of other species of *Oryctes*, but have been experimentally bred on *O. rhinoceros,* the former by Dutch entomologists in Java (Leefmans, 183) and both by H. W. Simmonds. Simmonds (252) introduced *S. oryctophaga* to Western Samoa from Madagascar in 1939, without establishment; but he successfully introduced *S. ruficornis* to Western Samoa from Zanzibar in 1945 (245). It was concluded that *S. oryctophaga* was not well-adapted to the climate of Samoa because it requires a cool season during its pupal stage. This was shown experimentally in Java, where it did not prove successful. In the laboratory there, the wasps sometimes remained in the cocoons for very long periods without emerging. In Western Samoa *Scolia ruficornis* has established itself and has spread at least 25 miles in one direction from the point of liberation. However, the population has been fluctuating considerably instead of growing steadily, and in early 1952, nearly seven years after its introduction, it was probably still playing a very small role in the control of *Oryctes,* perhaps hardly compensating for the *Oryctes* bred in special compost pits prepared for the encouragement and increase of the wasps (fig. 49, *a*). The wasps have been seen at several localities on Upolu, all to the east of Mulifanua, the liberation point near the west end, and mostly near Apia. They have been most abundant at Tuanaimata in the "Central Estates," south of Apia, around two especially prepared pits of cacao refuse mixed with leaves and garbage. In the spring of 1951 as many as 40 adults were seen at one time around these pits, but in January 1952, after an unusually long dry spell followed by only occasional rains, only two males and a female were seen at one time. Quite a number have also been seen at Curry's sawmill at Apia, but rarely did we see more than one at a time.

Scolia erratica (Burkill, 30) and *S. procer* (Corbett, 52; Richards, 235; Lepesme, 190) have been reported as parasitizing *Oryctes rhinoceros* in Malaya, but these relationships were later questioned or contradicted. *Scolia ruficeps* and *S. patricialis* have also been somewhat questionably implicated in Malaya (Corbett, 56; Gardner, 120; Simmonds, 252). No scoliids have been definitely associated with *Oryctes* under natural conditions in other parts of Asia. Several attempts have been made to introduce three species of *Scolia* (pp. 5, 99) to the Palau Islands, but more time must elapse before it is proved that even *S. ruficornis* is established.

Scolia larvae may be parasitized by rhipiphorid beetles which attack them when they are spinning their cocoons. Gamasid mites on *Oryctes* larvae may feed upon *Scolia* eggs (de Charmoy, 69).

No egg parasites of *Oryctes* have been reported. Muir (212) reared large numbers of eggs, larvae, and pupae in Java without obtaining any parasites whatever.

There have been some scattered records of parasitism of *Oryctes* grubs by flies, but most of them appear open to question or verification. Gater (121) mentions two cases of sarcophagid flies reared from *Oryctes* larvae, but indicated that parasitism was uncertain. Pillai (225) reports an *Oryctes* larva parasitized in coconut wood in Travancore by a dipteron, without complete information.

Among the Coleoptera there are several known predators of *Oryctes,* and probably many more not yet associated in the literature. Muir and Swezey (212) mention the larvae of two or three carnivorous beetles in Java as predators.

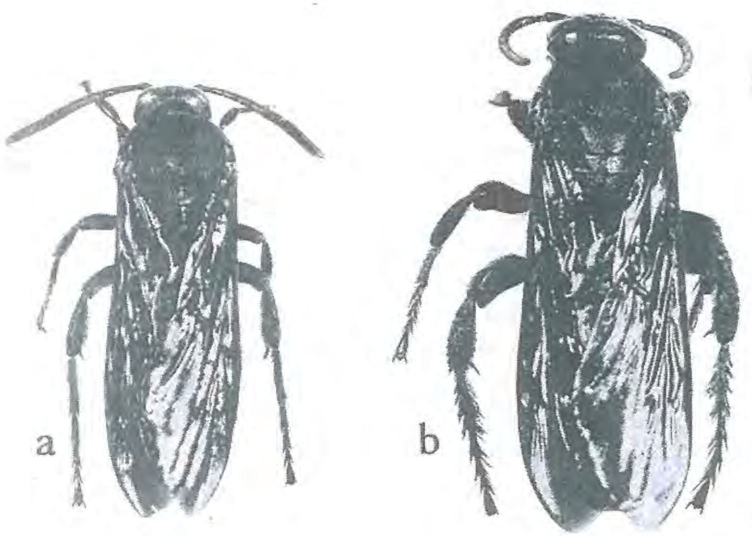

FIGURE 48.—*Scolia ruficornis:* a, adult male; b, adult female. Shipped from Zanzibar to Palau by Krauss.

The family Carabidae contains many useful predators of soft-bodied insects. Many members of this family are quite large in temperate climates, but large species are fewer in the tropics. Nevertheless, many members of this family found within the natural range of *O. rhinoceros* are capable of feeding upon first instar larvae, and at least some on second, perhaps third, instar larvae. However, the degree of effectiveness of control by members of this family depends greatly upon the type of situation in which the *Oryctes* are breeding in a locality. Larvae breeding in shallow, loose compost or in logs in late stages of decay should be quite vulnerable to attack by carabids, but those breeding in the tops of recently killed palms and in fairly solid logs may not be readily accessible to the predators. Most of the smaller members of this family can fly, and some are found in trees as a rule; but such species are generally small and feed on smaller insects. In the Palau Islands two moderately small members of the Carabidae were found apparently associated with young *Oryctes* larvae, upon which they fed in confinement (fig. 45).

About 16 species of Carabidae have been recorded in Samoa, but they are mostly quite small and seldom found close to *Oryctes* grubs. One species of *Chlaenius* ate first instar *Oryctes* grubs in captivity. H. W. Simmonds (251, 252) introduced the medium-sized green carabid *Catascopus facialis* (Wiedemann) to Upolu, Western Samoa in 1939. Though 113 individuals were released, the beetle has not been recovered in Samoa in 13 years. Friederichs (109) earlier released a few European *Carabus,* but these apparently failed to become established.

In Africa (Dahomey) the carabid *Neochryopus sauvagei* (Hope) was reported to prey upon adult *Oryctes* (*boas, monoceros,* or *agamemnon*) and other pests in crowns of coconut palms (Alibert, 3). Few, if any, carabids have been mentioned in the literature as being associated with *Oryctes* in other countries. N. L. H. Krauss, in 1951, searched for natural enemies of *Oryctes,* as well as predators of the giant African snail in East Africa and Madagascar. He found no carabids clearly associated with *Oryctes,* but did send some large carabids of the genus *Tefflus* which are predators of the giant snail. *Oryctes* grubs are probably not included in the normal food of *Tefflus.*

Of the Elateridae, the large Palau *Alaus* has been mentioned above, and Friederichs (109) considers this genus and the Madagascar *Ctenicera* the most important natural beetle predators. The Samoan *Alaus* has not been associated with *Oryctes.*

The members of the Histeridae are largely or entirely predaceous. They are usually found in such protected situations as under bark, beneath stones or logs on the ground, and in excrement, where they feed principally upon soft-bodied insect larvae. They may be recognized by their somewhat oblong shape, generally shiny black color, and the truncated and somewhat abbreviated elytra. The body is usually somewhat flattened, sometimes greatly flattened among species living under bark.

In 1939 H. W. Simmonds introduced the histerid *Pachylister chinensis* Quensel (fig. 46, *a*) from Java to Western Samoa, and the Solomon Islands, for the control of houseflies. The beetle exercises a control over the houseflies by feeding upon their maggots in cow manure, which is a favorite breeding place for flies. The introduction to Western Samoa was successful and control was at least partially obtained. The beetle is illustrated in Simmond's report (252, pl. 3, fig. 2), but the text was omitted as not pertaining to *Oryctes.* In January 1952 H. W. Simmonds, R. P. Owen, and I found larvae and adults of *Pachylister chinensis* abundant at certain points in central and western Upolu, Western Samoa, under split sections of coconut logs used as traps for *Oryctes*. In these situations there were no fly maggots, but young *Oryctes* larvae were present and apparently being fed upon by the histerids. Tests in confinement showed that both larvae and adults of the *Pachylister* would feed upon first instar *Oryctes* larvae. Whereas a larva of *Pachylister* would feed on at least two or three of the latter in 24 hours, an adult would not always eat as much as one each day. In view of these observations, over 100 *Pachylister chinensis* were shipped from Western Samoa to the Palau Islands, primarily for the control of *Oryctes*, and were liberated on Koror Island, Palau. Three species of histerids (*Hololepta scissoma* Marseul, *Hister geminus* Erickson, and *Placodes ebeninus* Lewis) were found associated with coconut beetles in decaying sisal bases (79). In December 1951 N. L. H. Krauss (175) found one of the above species, *Placodes ebeninus*, at Tanga, Tanganyika, which experimentally attacked *Oryctes* larvae. It normally feeds on larvae of the sisal weevil. Krauss shipped 25 adults of this histerid to Palau, via Honolulu. They were liberated at Airai, Babelthuap Island.

Other Invertebrates

Mites have been found upon both larval and adult *Oryctes* (p. 100), but it is questionable whether they perform any controlling influence of importance. However, they may weaken the hosts and make them more susceptible to fungus diseases or other pathogens.

Scorpions are mentioned as predators by Friederichs (109).

Large centipedes of the genus *Scolopendra* are very commonly found in places where *Oryctes* larvae are abundant, particularly under the loose bark of old coconut trunks and logs, under logs, and in compost. They frequently feed upon the younger grubs, but the larger centipedes are probably capable of killing mature grubs. The centipedes burrow their way into the tunnels or cells of the *Oryctes* grubs and attack the latter with a sudden bite of the poison fangs, sucking the body juices at their leisure after the grub has died. In laboratory tests the centipedes often left the grubs uneaten for some time after killing them. Sometimes a second grub was killed before the first was fed upon. It is probable that any species of the genus *Scolopendra* and members of several other genera of centipedes are at least occasionally predaceous upon *Oryctes* grubs. Species of *Mecistocephalus*, when mature, might feed on young grubs. Centipedes should not be killed or interfered with in areas where *Oryctes* occur.

Hermit crabs are quite capable of feeding upon *Oryctes* grubs. When a number of grubs were exposed in a coconut grove some meters from a beach, several large hermit crabs arrived promptly and started to carry away living

mature grubs, even though I was sitting only one meter from the grubs. Several hermit crabs were found in old rotten stumps or logs containing *Oryctes* grubs. Occasionally other kinds of crabs were found in logs or stumps close to *Oryctes* grubs. It was not observed whether they fed upon the grubs, but it appears likely.

Vertebrates

The giant toad (*Bufo marinus*) may feed upon grubs of *Oryctes* (p. 102), but it is unlikely that it plays an important role in control. It is also unlikely that amphibians other than *Bufo* attack *Oryctes*. Townes (282) states that *Bufo marinus* feeds upon *Campsomeris annulata*, the scoliid, so it may also feed upon *Scolia*.

Monitor lizards are probably important in the biological control of *Oryctes*, as they feed upon the grubs in rotten logs and stumps and in other situations (p. 102). T. R. Gardner informs me that in the Malay Peninsula he observed monitor lizards around the edges of compost pits where *Oryctes* were breeding. These lizards are found throughout much of the range of *Oryctes*, but not in Formosa or Samoa. Williams (307) reports the feeding of the large *Gekko gecko* on adult *Oryctes rhinoceros* in the Philippines. It is quite possible that other lizards occasionally feed upon young *Oryctes* grubs. In Tonga, the Pacific iguanid, *Brachylophus fasciatus* Brongniart, may learn to prey upon *Oryctes*.

It seems apparent that owls and kingfishers feed upon *Oryctes* in Palau. Doubtless on the mainland of Asia a number of species of birds prey upon the beetle. Crows feed on *Oryctes* grubs when compost pits are being turned. In Zanzibar, Simmonds (253) saw the local black and white crow and the Indian crow feeding on grubs of *Oryctes boas* or *O. monoceros*. The bulbul, *Molpastes* (*Pycnonotus*) *bengalensis*, has been recorded by Friederichs (109, after Mason) as feeding on the grubs. However, bulbuls appear to feed on *Scolia* adults in Samoa. The golden-backed woodpecker, *Brachypternus aurantius*, has been reported as probably feeding on *Oryctes* on toddy palms in Madras (Fletcher, 104); and Muir (203) reports woodpeckers as fond of the grubs in Java. Friederichs (109) records remains of rhinoceros beetles in the stomach of rollers (*Eurystomus*) in the Philippines. The Indian hoopoe (*Upupa epops indica*) is said to feed on scarabaeid grubs (Fletcher, 105). W. V. D. Pieris tells me that in Ceylon the hawk cuckoo, *Hierococcyx varius*, feeds on *Oryctes* grubs, as well as on giant African snails.

Rats feed considerably upon *Oryctes* grubs or adults (p. 101), and Simmonds (252) suspects tree shrews (*Tupaia* sp.) and palm squirrels (*Lariscus insignis jalorensis*) of attacking adult *Oryctes* in Malaya. He correlates the greater abundance of *Oryctes* in Celebes and farther east with the fact that these squirrels do not extend as far east as Celebes. Pigs feed extensively upon *Oryctes* grubs in Ceylon (Kunhi Kannan, 176), Java (Leefmans, 183), and in Samoa, rooting for them in compost and humus. Palau pigs have not yet learned to eat *Oryctes* grubs.

In the Philippines the flying lemur, *Galeopithecus,* has been semi-domesticated, at least on Bohol (Wester, 305), because of its useful hide and the fact that it preys upon *Oryctes* adults. In Madagascar the aye-aye, *Chiromys madagascariensis,* probably feed upon the grubs from rotting logs or other situations, and Friederichs (109) suspects the tanrek, *Centetes ecaudatus,* as a predator there. In Australia there is a marsupial with one very long finger with which it removes grubs from wood for its food. Such an animal might be used in biological control, if it could survive life on small Pacific islands or the competition in a foreign continental environment.

Diseases

Rather little is known of the diseases to which *Oryctes* is subject. The green muscardine fungus, *Metarrhizium anisopliae* (Metsch.) Sorokin, is the only such disease-causing organism widely studied. This fungus was tried out for the control of the beetle in Samoa (8; Friederichs, 108, 109; Moors, 208) and elsewhere (Bryce, 27; Rutgers, 243), without conclusive results. Moutia (211) considers it of little benefit. However, dead beetles infected with this fungus are found occasionally; a few in the Palaus by Steinhaus (267), Owen, and me. It is not always certain that the fungus is the cause of death. Apparently the fungus attacks the grubs principally under conditions abnormal for them (Bryce, 27, 28; Corbett, 59; Friederichs, 112). Bryce (27) states that the fungus infests young larvae but not those which are well grown and kept under conditions nearly approximating their normal environment. This statement is in question, though young larvae may be more susceptible than mature ones. Friederichs (109) states that bark-lice (psocids) are natural enemies of *Metarrhizium.*

As the temperature in a compost pit may range from at least 70° C. down to 35° C., the normal heat of decaying compost may be lethal or growth-inhibiting (above 48° C.) to *Metarrhizium* (Johnpulle, 169). In Samoa a number of infected grubs were found in a compost pit near the Casino Hotel at Apia by Simmonds, Owen, and me. Out of several dozen grubs, mostly of the third instar, more than one-fourth were infected with *Metarrhizium.* This was the first time so many had been seen together by any of us. It was apparently the result of unfavorable conditions for the grubs: (1) the long dry spell of a few months which was just ending and (2) the overcrowding of grubs and (3) physical disturbance resulting from removal of the compost. The pit contained quite a bit of debris, including tin cans and other metal objects.

Infected grubs were occasionally found in the rearing jars in Koror, but this environment was unnatural and could not be kept close to optimum conditions for the grubs in spite of the fairly wide range tolerated by the beetle.

In the spring of 1951 Steinhaus (269) went to the Palaus for two weeks to set up some experiments in infecting larvae of *Oryctes* with several disease-causing organisms, including *Bacillus popilliae* (Types A and B), *B. lentimorbus, B. thuringiensis,* Aspergilleae, *Beauveria bassiana,* and *Beauveria* strain 386. These experiments merely indicated that *Oryctes* was probably not highly susceptible to the disease organisms tested. There is also the question of whether effective pathogens, even if found, could be disseminated to the point where they would prove practical in control of the beetle because of the protected nature of many of the breeding situations. *Beauveria bassiana* is discussed in relation to *Oryctes nasicornis* by Rozsypal (242).

CULTURAL CONTROL, OR SANITATION

There is a rather close correlation between the abundance of available larval breeding environments and damage by adult rhinoceros beetles to palms. In order to properly control *Oryctes,* all such breeding places must be destroyed or the grubs collected regularly from them (Hutson, 151). Many examples are on record showing that energetic measures for eliminating breeding sources have materially reduced *Oryctes* damage (de Jong, 74; Ellis, 95; Richards, 294).

It has been stated that the presence of weeds or undergrowth in coconut groves is unfavorable to *Oryctes* (Fickendey, 100) and other dynastids (Van Zwaluwenburg, 294), and there seems to be evidence of this in Samoa. The reason given is that *Oryctes* adults are such poor flyers that a certain amount of obstruction hinders them from flying to the palm crowns readily. Another reason may be that more natural enemies can find hiding where underbrush exists. On the other hand, where underbrush is allowed to remain, *Oryctes* breeding places might remain hidden. It has been recommended that green manure crops be planted to take the place of humus lost by burning of refuse and wood (Hutson, 156).

Destruction of Dead Palms and Other Trees

The present beetle control program in the Palau Islands is based on the destruction of dead wood. This is a costly, slow process, but essential. It involves the destruction of palms killed by the beetle or by other means, and of dead trees of any sort. This is accomplished, where terrain permits, by dragging the logs to the ocean or to streams or swamps with the aid of water buffaloes. If the logs are soaked with water at intervals, or partly soaked most of the time, as by a small permanent stream, the wood becomes unsuitable for the breeding of *Oryctes*. Where logs are situated in rough country unsuitable for water buffaloes or tractors and not close to water, other methods must be used. One of these is the sawing of logs into sections and burying them in deep holes. In country with good drainage this may not prevent larvae in the logs from maturing and the resulting adults digging their way out, even when the logs are covered with a thick layer of soil. However, when larvae are abundant in logs, the fact is apt to be detected when they are sawed up, and most of the larvae destroyed before they can bury themselves in the soil. Another method is to burn the logs. Because of the high rainfall in the Palaus and the general proximity of water, burning is not considered practical or necessary.

Coconut stumps must also be destroyed after the trunks are felled and removed. This may be accomplished by sawing or chopping the stumps close to the ground, burning the chips, and removing the stump completely where possible. A stump which cannot be completely removed may be rendered unsuitable for the beetle if the stump is cut close to the ground and a cavity made in the center so that sufficient rain water can collect and soak the small amount of remaining wood (fig. 49, *b*). The addition of some oil will both prevent mosquito breeding and help to repel the beetle. Explosives have been used for the removal of stumps, but this did not appear to be practical for the Palaus. Burkill (29) recommends four cartridges of blasting gelatin for one trunk or stump.

Since the beetle oviposits in dead trees of various species, all dead trees, logs and stumps must be eliminated. The roots of many kinds of trees, however, are also a potential breeding medium, and special efforts may be necessary to eliminate them. The question of *Pandanus* is a difficult one and more serious than that of dead trees, because *Pandanus* also serves as an adult food host. Elimination of *Pandanus* is out of the question because of its abundance and its economic importance. However, where it is actually being fed upon or bred in by *Oryctes,* it should be destroyed.

After a coconut grove and the adjacent forest, fields, or village have been cleaned up, the area must be checked at intervals to determine whether recently killed palms or trees or other materials are not providing new breeding material. Since the larval period of *Oryctes* is under three months, each area should be checked at least every two months. Typhoons damage beetle-infested palms and the resultant dead trunks breed additional beetles (Copeland, 45; Mackie, 201).

Proper Care of Compost and Sawdust

Where composting is done in deep pits it may be possible to keep the openings of the pits covered with screening or hardware cloth on a frame well

fitted to the opening to prevent entrance of females for ovipositing. On the other hand, the beetles may dig their way through the soil or sand under the cover to lay eggs. If the pits can be covered, and unless pigs roam freely in the area, the use of deep compost pits is preferable to shallow pits or widespread dispersal of garbage, leaves, and other wastes on the surface of the

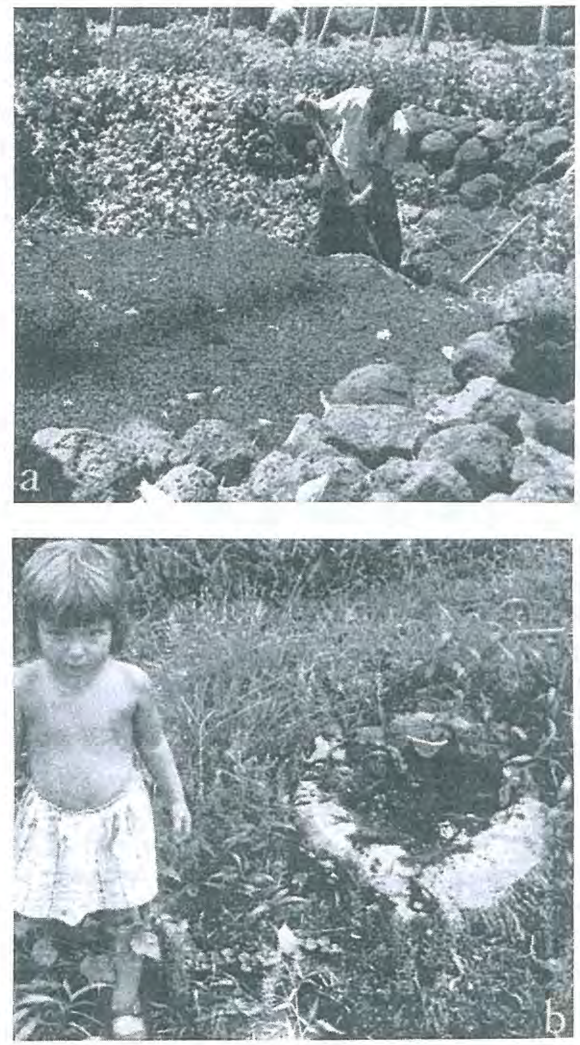

FIGURE 49.—**a,** Compost pit surrounded by lava rocks and mostly filled with cacao debris, for encouraging *Scolia ruficornis* near Vaitele, Upolu; **b,** base of coconut stump cut close to ground and partly chipped out three months earlier in Palau control program, Ngatpang.

ground. Deep pits with small surface area and vertical sides appear to be less attractive to the beetle and are easier to cover. Compost pits may be operated as traps (see next section). Another method of attacking the problem would be to burn the garbage and refuse as far as possible with dried palm fronds and use the ashes for fertilizer. If the above measures prove impractical, the construction of incinerators or of chemically treated liquid disposal pits may be necessary.

The practice of digging plant wastes into the soil is unsafe in organic soils, and must be handled cautiously in other soils to prevent soil breeding (Fickendey, 100; Paul, 221). Deep burial does not prevent breeding (Doane, 82). Larvae have been found in green manure (Jepson, 164).

Sawdust is best eliminated by burning. Trap control by accumulating sawdust in two piles and burning them alternately may prevent the escape of larvae into the ground. One pile should be burned at the end of each month, or more often. Sawdust may also be spread thinly over a large area or disposed of in water, but these methods are not practical where sawdust is produced in large quantities. Sawdust with moderate amounts of oil spilled on it from mill machinery may still be capable of breeding *Oryctes*. Sawdust should not be used for paving roads, as was done on Savaii with the result that palms along the road were severely damaged. Sawmills should not be located close to coconut groves, particularly where the latter are on peat soil (Corbett, 59).

Trapping

Where favorite breeding situations have been largely eliminated, trapping may prove an effective method of control, but it is of no avail if coconut groves, neighboring fields, forests, or villages have not been properly rid of decaying vegetation. Where compost is not a factor, effective traps may easily be constructed of split sections of coconut logs. The sections, split lengthwise in halves, are laid parallel and adjacent to each other, with the split surface on the ground. Several sections provide a trap of convenient size. After the wood has aged a bit, adult *Oryctes* will come to lay eggs in or under the sections. These traps should be examined at regular intervals, say once a week, and the adults, eggs, or grubs destroyed.

If compost pits exist in an area, they may be operated as *Oryctes* traps: but if the pits are numerous, or deep, a great deal of labor or special precautions may be involved in preventing the breeding of *Oryctes* in the pits. It would be more convenient to reduce the number of pits, make them shallower, and inspect them frequently, say every month, to remove the beetles and grubs (eggs are easily overlooked). The material may be sifted through wire netting to help remove the grubs. Compost should be used as soon as matured in order

to help reduce the bulk involved. Friederichs (108) suggests the treatment of traps with carbon bisulphide to kill the larvae. After an interval of time, the faint residual odor of the bisulphide in the treated traps is said to be attractive to the adult beetle. Trapping with rotting vegetable matter is recommended by Keuchenius (172). In Ceylon the beetle got out of hand from neglect of traps during an influenza epidemic (Hopkins, 149). Lester-Smith (191) suggests the following type of compost pit to be used as a trap for *Oryctes:* A pit three feet square and two feet deep into which are placed alternate layers of cattle manure and soil, then layers of coconut branches and leaf stalks and cut grass, each double layer sprinkled with a decoction of *Metarrhizium* fungus and the pit covered with leaves. After three months the pit should be opened and the contents removed. An earlier report (Bryce, 26) mentions failure of a test in Ceylon because no beetles were attracted to the traps. This may have been because of more favorable breeding materials in the neighborhood. Since *Metarrhizium* is not an effective control, three months is too long to leave a trap unchecked.

Reports have been made upon the successful use of coconut rubbish for trapping in pits in the ground in Ceylon (Harris, 143; Lyne, 197; Petch, 223) and elsewhere (Corbett, 53). Subramaniam (272) reports that cattle dung is the most attractive material for trapping adults.

Gokhale (134) carried out experiments on trapping with castor bean cake in India, not very successfully. The cake was allowed to rot in a semi-solid condition in earthen pots scattered on a coconut plantation on the theory that adult beetles drawn into the pots could not escape. However, such pots must be tended regularly or they will breed the beetle. Fermenting garbage water (Fletcher, 102), "ragi" water (Kunhi Kannan *et al.*, 176), and other materials used in the above manner have been reported as trapping adults.

Bait traps are also a conceivable method of catching adult beetles, but few tests have been made in this direction. Since the beetle is attracted to palms, *Pandanus,* sugar cane, pineapple, and other plants, some fruit essence or other chemical might appeal to adults. However, traps would have to be constructed with a deep tin or glass container to prevent the beetles from escaping. The use of "tuba trees" as traps, at the rate of one per 100 palms, has been recommended on the basis that the fermenting sap attracts adult beetles (Barrett, 17). But Friederichs (108) states that toddy is of no use for trapping.

Light traps might be effective to a slight extent, but would not be a sufficient control measure. The beetle is attracted to lights to only a moderate degree, as shown by the small numbers attracted at Ngiwal, which had a large population of *Oryctes*. A bright light is necessary, and where electricity is lacking pressure gasoline or kerosene lanterns would have to be used. In any case, each trap would have to be tended every morning and evening.

Other Control Methods

In the Philippine Islands boys are sent up to the tops of coconut palms with hooked wires which they insert in the feeding galleries of adult *Oryctes* in order to extract and kill them before feeding is completed (Barrett, 17; Mackie, 202). This method is similar to ones practiced in Burma (Friederichs, 109) and in southern India where adults are extracted from palm crowns with iron rods and the cavities filled with sand or clay (Cherian, 40). Neither method is practicable in Palau, where cheap labor is lacking and food is abundant. Barrett (17) also states that in the Philippines new adult boring is detected each morning by examining the ground at the bases of the palms for frass and that in India individuals are said to have developed the faculty of detecting adult feeding in the crown of a palm by holding an ear against the trunk.

Hutson (155) recommends that adult tunnels be filled with tar to prevent rotting after adult feeding or extraction. Capper (34) and Doane (82) dispute the repellent nature of the tar. Other repellents used in palm crowns are oil cake made from *Hydnocarpus* (Kunhi Kannan, 176), urine, or slaked lime (Ghosh, 127). Brown (24) says that in several countries the placing of sand between the petiole bases of palm crowns to discourage entry of adults has been successful. In Madagascar, according to Frappa (107), a solution of 2 to 3 percent $CuSO_4$ is injected into adult feeding galleries of *Oryctes* in the crowns, then the cavities filled with a clay paste in order to prevent crown rot or secondary invasion following feeding.

Caution in Planting of Coconuts

Where coconut palms have been exterminated by the rhinoceros beetle, dead trunks, logs, or stumps of killed palms remaining in the area must be promptly eliminated and some weeks or months allowed to elapse before replanting. Meanwhile, there must be periodic inspection of *Pandanus,* sugar cane, pineapple, agave, and similar plants and compost, garbage dumps and sawdust pits must be examined and destroyed or treated. When the beetle population has thus been greatly reduced, palms may be planted; but periodic inspections of surrounding habitats must be continued.

Where palms have been seriously affected but not exterminated, complete and repeated clean-up programs of breeding media and adult foods are necessary before planting of new palms is extensively undertaken. However, the planting of new palms need not be delayed so long where many grown palms remain, because adult *Oryctes* prefer mature palms to very young palms. Coconut palms should not be planted on newly cleared land; and even after stumps and other debris have been destroyed, a crop like cassava should be planted for a year or two, partly to aid elimination of minor breeding media and starve out adults. It has been recommended that palms not be planted within 250 meters of forest and that the latter be cleared of debris for 100 meters.

Chemical Control

Direct application of insecticides for control of *Oryctes* is seldom practical, for neither adults nor larvae are in sufficiently exposed situations, except for certain types of compost pits, to be readily reached by insecticides. Furthermore, the variety of habitats occupied make a single method of treatment ineffective for all. Any general application such as aerosol generation or airplane spray would have to be carried out with such high dosages that most other insects and perhaps domestic animals and human beings would be killed before all *Oryctes* succumbed. One adult which was repeatedly sprayed at very close range for considerable periods with an "aerosol bomb" took four days to die.

Treatment by creosote, other tar oils, or even crude oil, would prevent *Oryctes* oviposition and breeding in coconut stumps, if used in sufficient quantity. In Palau it has been deemed more practical to cut away the stump and impregnate the extreme base. Coconut logs or other soft wood to be used in construction should be chemically treated or soaked in water for a considerable period in order to harden the wood and make it unsuitable for breeding *Oryctes.*

If compost is to be utilized, application of oil or other chemicals harmful to plants is undesirable. Compost is little used in Palau, except in direct scattering of wastes near the bases of banana or papaya plants. In deep holes the material could be treated with a fumigant such as carbon tetrachloride and covered with sand or earth. For Palau the use of Paris green in the deep, covered pits would probably be safe. Jepson (159) fumigated compost pits with good results, but considered the treatment too expensive for Samoa. Experiments were made by Coleman (44) on treatment of larval breeding places without encouraging results. De Charmoy (73) treated breeding places with paradichlorobenzene without success. Earlier (68) he recommended a kerosene-soap emulsion with phenyl or creoline added to kill *Oryctes* larvae or subterranean caterpillars in soil. Tests with oils were made for grubs of *Oryctes nasicornis* in soil in Europe (Hilgendorff, 146; Trappman, 283). Friederichs (109) recommends barium sulfocarbonate and carbon bisulfide. Nirula, Antony, and Menon (213a, 213b) recommend benzene hexachloride (BHC) at 0.01 percent as successful for treating compost.

Furtado (117) suggests pouring oil of turpentine or tar into adult galleries after extracting adults with wire. Srinivasa Rao (262) recommends inserting a mixture of sand and salt into adult feeding galleries and plugging the hole with clay. He also recommends (260) the use of salt in palm crowns. Salt and lime as a repellent to adult beetles has been suggested. The spraying of young palms with Bordeaux has been practiced (Kunhi Kannan, 181). Stomach poisons have been discounted on the basis of tests with arsenates in compost (Kunhi Kannan, 178). Pieris tells me that Mason's mixture, containing creosote, seems to have a repellent effect against adults attacking young palms.

QUARANTINE AND LEGISLATION

In most parts of Micronesia, Polynesia, and Melanesia quarantine is of the greatest importance in preventing the spread of *Oryctes rhinoceros* to additional Pacific islands, for the beetle has already reached the Palau Islands and New Britain, and far to the east, Samoa, Wallis, Tonga and Fiji. Its rapid advance in recent years proves that quarantine measures must be strict and effectively enforced. Quarantines for *O. rhinoceros* or other species of *Oryctes* were summarized for the world in 1914 in the report of the coconut commission (78).

Fiji has long enforced strict quarantine measures in regard to incoming ships from Samoa (Taylor, 280). To prevent introduction of *Oryctes rhinoceros*, the importation of vegetable matter from several directions, including Samoa, was forbidden by proclamation in 1913 (Jepson, 159). Since that time, ships arriving from Samoa have been required to anchor some distance off shore until morning in order to prevent stowaway *Oryctes* adults from flying ashore during the evening. Some of the other regulations that have been in effect against *Oryctes* are mentioned below:

A proclamation was issued in 1931 by the High Commissioner for the Western Pacific (British), prohibiting importation of plant matter from Wallis and Futuna Islands into the Gilbert and Ellice Islands, because of recent discovery of *Oryctes* on Wallis.

The British Solomon Islands Protectorate also passed a plants and seeds control regulation in 1931 to prevent introduction of insects or diseases. This was especially necessary because ships load copra in Samoa and proceed to the Solomons for more copra.

The Territory of New Guinea passed a plantation diseases and pests ordinance (Dept. of Agric. Leaflet no. 54, Rabaul) in 1927 against *Xylotrupes* spp., *Trichogomphus* spp., *Oryctes* spp., *Scapanes* spp., and *Rhynchophorus ferrugineus*.

A Ceylon plant protection ordinance of 1924 prohibits the importation of living insects, invertebrates, *Hevea* or *Cocos* plants, and (except through Colombo) coconuts in husks, and others. Also (Ceylon Gov. Gaz., 1924) palms dead or attacked by both *Oryctes* and *Rhynchophorus* to be burned or completely submerged in water, or damaged area cut away and cavity filled with mortar, and rubbish heaps eliminated.

A Seychelles ordinance of 1919 provides for the destruction of plant pests, particularly *Oryctes rhinoceros*, and a plant pests ordinance of 1925 deals with importation and fumigation conditions, particularly against *Oryctes rhinoceros*.

The British Military Occupation of Samoa, in a proclamation of 1914 makes it mandatory that all dead wood be destroyed and permission be obtained before planting or cultivating new land. By another proclamation (1915) all plantation laborers are required to spend every Monday forenoon searching for and destroying *Oryctes*.

A Straits Settlements ordinance, 1890, orders the destruction of dead palms and stumps (Vermont and Kennedy, 298).

Zanzibar passed a plantation preservation decree in 1922.

THE RHINOCEROS BEETLE IN SAMOA

In comparing the situation in regard to the coconut beetle in the Palau Islands and Samoa, many factors must be taken into consideration, among them the climate, geography and soil conditions, methods of coconut palm culture, age of the palms, cutting of forests, use of sawmills, village sanitation, composting, presence of cattle, rate of destruction of coconut palms, food reservoirs, and local flora and fauna, particularly natural enemies or competitors.

The climate of Samoa is not greatly different from that of the Palaus. The Samoas are about seven degrees farther from the equator, and are south, instead of north, of the equator. Western Samoa, at the Apia Observatory on the north coast of Upolu, has a lower rainfall (113.37 inches, 61-year average, per year) than the central and northern Palaus, with more than 10 inches per month from November through March (summer) and less than six inches per month from June through September. At Pago Pago on Tutuila, American Samoa, the rainfall is greater than in the Palaus, with 196 inches per year (37-year average), and with more than 19 inches per month from November through March and less than 13.5 inches per month from June through September. The rainfall in the mountains of both Western and American Samoa is much higher. The temperature in Western Samoa has slightly greater variation at sea level than in the Palaus, with a minimum of 63.0°F. (August), a maximum of 93.0° (November), a highest monthly minimum of 69.6° (March), and a lowest maximum of 89.6° (June) (41-year averages). At Apia the average mean temperature is 78.95° (61-year average) and the average relative humidity is 83 percent (57-year average).

Geographically, the Samoan Islands are quite different from the Palaus. Samoa consists almost entirely of fairly high volcanic islands, with the land composed chiefly of lava or decomposed lava, instead of the coral rock, coral sand, or andesite or bauxite in which grow most of the coconut groves of the Palaus. The soils in Samoa are therefore probably a little more favorable for coconut cultivation.

The methods of coconut cultivation are somewhat different in Samoa than in Palau. In Western Samoa, a portion of the coconut land on Upolu and a little on Savaii is operated by the New Zealand Reparations Estates for the New Zealand government; and another portion of both islands consists of private European estates. The remainder, the majority of the area under coconuts, is owned and operated by the Samoans. The area under coconuts is much greater than was the area in Palau before the great damage by the beetle. The Samoas have an area about 15 times that of the Palaus, and almost all of the coastal borders are in coconuts, as well as some of the more gradual slopes. The coconut area in Western Samoa is 60,000 acres, which is more than in all the American Trust Territory (Micronesia exclusive of Guam and the Gilbert Islands). The Trust Territory coconut area was about 50,000 acres, of which 4,500 acres were in Palau. The acreage in American Samoa is much less, and the tonnage of copra exported has been low in proportion to acreage because the Samoans on Tutuila have derived much of their income from the Naval base there. The tonnage for American Samoa has been about 1,000 to 2,000 tons annually—varying inversely with the price of copra—in comparison with 17,000 for Western Samoa, 12,000 for the Trust Territory, and 1,000 tons (1951) for Palau.

Many of the palm groves in Western Samoa are nearly 100 years old, and the palms are commencing to die of old age, aided by *Oryctes* damage. This factor of old age is not present in Palau and American Samoa.

The fact that the mortality of palms has been 50 percent in Palau in 10 years and less than 15 percent in Western Samoa in over 40 years, emphasizes the extreme importance of abundant larval food supply. Damage by *Oryctes* in American Samoa is conspicuously less than in Western Samoa, perhaps because the palms are younger and because the clearing of forests and operation of sawmills are much less extensively practiced. Weekly collections are more or less irregularly operated by the villagers in American Samoa, but the material is generally taken from the compost pits without ever cleaning them out completely, so that they operate as partial traps. However, other breeding situations such as trunks and stumps have not been systematically eliminated. In Western Samoa the villagers collect the beetles when damage becomes serious, but in government estates damage is often worse in spite of regular trapping with split logs because removal of felled jungle or coconut stumps is deemed too expensive. New Samoan groves where jungle has been felled are apt to be severely damaged. The least damaged groves seen in Samoa belonged to a private European estate where all dead wood was eliminated and traps of split sections of coconut logs were checked twice a week by the supervisors. The abundance of undergrowth in the village groves would seem to work against *Oryctes* by interfering with adult flight and encouraging natural enemies. Also, the grazing of cattle in the government groves must provide limited additional breeding places where manure accumulates or enriches soil or small accumulations of vegetation. The worst government groves are being transformed into cacao plantations.

In Samoa, the relatives of *Oryctes* include the rose beetle, *Adoretus*, which feeds on cacao leaves in the adult stage and on roots as larvae; the flower-feeding *Oxycetonia*, which breeds in compost; the introduced coprid dung beetle and much smaller ones (*Aphodius*) of wide distribution; and several medium-sized stag beetles (*Aegus*, *Figulus*) which develop in rotting wood. (See Arrow, 10.)

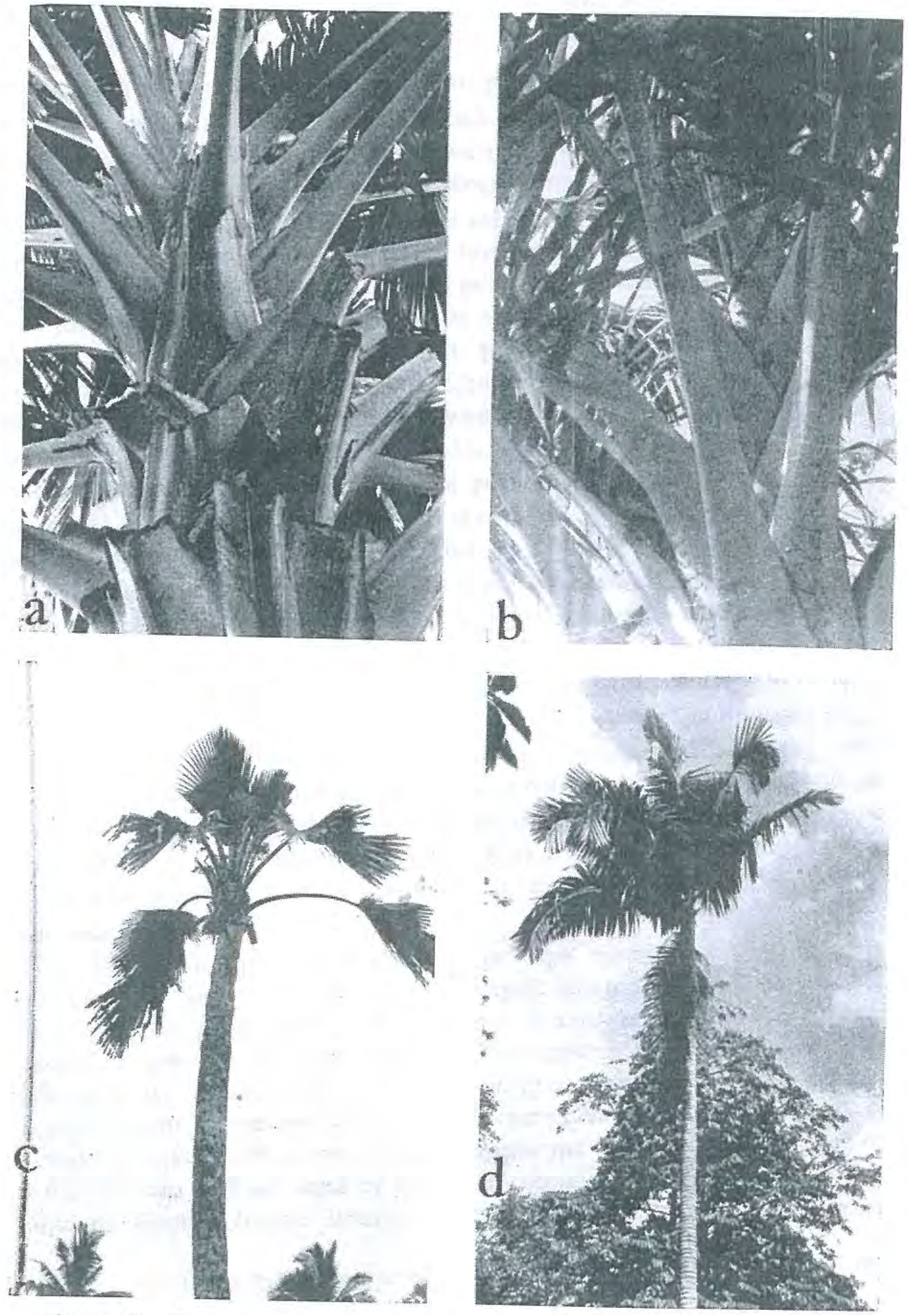

FIGURE 50.—Damage to palms on Upolu, Samoa: a, *Borassus flabellifer*; b, *Metroxylon sagu*; c, *Pritchardia* (*Eupritchardia*); d, *Archontophoenix alexandrae*.

Natural enemies of *Oryctes* in Samoa include the introduced histerid, *Pachylister chinensis,* a few small ground beetles (*Chlaenius* and others), centipedes, crabs, owls, chickens, pigs, and the *Metarrhizium* fungus. Pigs and centipedes are probably the most important. *Scolia ruficornis* has probably not increased its population beyond the point of counteracting the population of *Oryctes* grubs being bred in compost pits constructed to encourage the wasps (fig. 49, *a*). There is an apparently rare native predaceous click beetle (*Alaus samoensis* Van Zwaluwenburg) on Upolu and Tutuila.

I observed palms which had been attacked in Samoa, including the Palmyra palm, *Borassus flabellifer* (fig. 50, *a*); the oil palm, *Elaeis;* native fan palms, *Pritchardia* (fig. 50, *c*); the Alexandria palm, *Archontophoenix* (fig. 50, *d*), the sago palm, *Metroxylon* (fig. 50, *b*); the royal palm, *Roystonea;* and others not identified. The statement in the Review of Applied Entomology (Series A, vol. 26, p. 702) that Lever (193) recorded *Oryctes* from *Pritchardia* is incorrect, so this is the first record.

Some coconut palms observed at two spots near Vailoa, Tutuila, had rotting crowns but may have been killed by lightning.

The rhinoceros beetle has been studied in Samoa by Gehrmann (124, 125), Jepson (159, 160), Doane (82), Aulman (13), a committee (6), Friederichs (108, 109, 111-113), Swezey (276, 277), Simmonds (249-254), Bianchi (22), Dumbleton (88), Butchart (32), and Gressitt (139, 140).

THE RHINOCEROS BEETLE IN OTHER COUNTRIES

In the Pacific, *Oryctes rhinoceros* has been introduced into Samoa (1909); Wallis Island, 200 miles northwest of Samoa (1931); New Britain (1942?); Doom Island, between Salawati and New Guinea (1936?); Palau (1942); Vavau, Tonga Islands (1951); and near Suva, Fiji (1952).[2] In 1924 it was introduced into Niuatoputapu (Niuatobutabu or Keppel) Island, between Samoa and Tonga; but by diligent trapping with coconut logs examined twice a week, and by eliminating breeding situations which included long-abandoned latrines, the beetle was exterminated from the six-mile-square island after more than seven years of effort by Inspector Muller of Tonga (Simmonds, personal communication, 1952). The beetle is assumed to have reached Niuatoputapu, Wallis, and Vavau from Western Samoa, and New Britain and Sorong from Amboina, Ceram, or some other island of Indonesia. It was recorded from Wallis as *Oryctes centaurus* by Risbec (238).

After nine years on Wallis Island, *Oryctes,* though by far the most serious pest of coconut palms, has not materially reduced the amount of copra exported (Cohic, 43). This is explained on the basis of the rather haphazard methods of coconut cultivation existing there combined with the fact that now, in

[2] Years of introduction are probable dates.

order to obtain a similar quantity of copra for export, the islanders work harder in searching out more of the fallen coconuts from the underbrush. A Wallis Islander living on Savaii told me that the beetle was less serious on Wallis than in Samoa because of stricter sanitation methods, particularly as regards larval breeding sites. It is possible that somewhat differing circumstances or customs have enabled pigs to exercise more effective control of grubs breeding in compost, or possibly that a more rapidly growing human population in Samoa provides more breeding environment in the form of felled jungle. Recently (Thevenot, 281a) the situation on Wallis has worsened.

In New Britain, the beetle was assumed to have been brought in by Japanese forces in 1942, perhaps from Palau, as it became a very serious pest after the war, on the Gazelle Peninsula. It now occurs on both sides of the peninsula for as much as 30 miles from Rabaul, and it is reported to be attacking coconut, oil, betel, and sago palms, and banana plants and roots of cacao seedlings. The beetle was not identified as *Oryctes* until about 1950, as it was first thought the damage was caused by the great increase in populations of native rhinoceros beetles [*Scapanes australis* (Boisduval)] or *S. grossepunctatus* Sternberg from mainland New Guinea[3] as a result of abundant breeding media in the form of palms killed during the war. The elephant beetle, *Xylotrupes lorquini* Schauf. ["*gideon* (Linn.)"], had also been suspected by some, in New Britain, as elsewhere, though it is a much less serious pest as to damage and does not bore into the crowns of the palms. Another rhinoceros beetle, *Oryctoderus coronatus* Bates, also in New Britain, was found to be present in situations with *Oryctes,* and its adults fed upon *Oryctes* grubs and pupae in captivity (Dun, 89). Species of this genus are known to attack coconut palms, however. It has been suggested that *Oryctes* may have reached New Britain before the war, possibly about 1937. S. Dillon Ripley noticed in 1937 what appeared to be *Oryctes* damage at Rabaul and on Doom Island (Sorong), a trading center just west of New Guinea, though not on neighboring islands or the New Guinea mainland.

In New Ireland the beetle was reported in early 1952 to have been recently established on the midwest coast and also on the upper east coast in small numbers (Dun, 89); and it is now spreading.

The beetle presumably reached Vavau Island, Tonga, sometime in 1951,

[3] Other species of rhinoceros beetles known to feed on economic plants in New Guinea (Froggatt, 114, 115; Preuss, 231) include *Xylotrupes* ("*gideon*") *lorquini* Schauf., *Trichogomphus semmilinki* Ritsema, *Papuana laevipennis* Arrow (major pests) and *Oryctoderus nanus* Arrow (minor pest) on coconut palms; *Papuana semistriata* Arrow, *P. hübneri* (Fairmaire) and *P. splendens* Prell, *Camelonotus* [*Dipelicus*] *ritsemai* Heller, *Oryctoderus latitarsis* Boisduval, *O. godeffroyi* Fairmaire, on bole of young palms; *Oryctoderus nanus* on *Caladium* bulbs; *Papuana laevipennis* Arrow and *P. armicollis* (Fairmaire) [*woodlarkiana* (Montrouzier)] on *Colocasia.* In the Solomon Islands (Pagden, 219) *Trichogomphus semmilinki* Ritsema, *Scapanes grossepunctatus* Sternberg and *Xylotrupes* "*gideon*" were reported of moderate importance and *Papuana laevipennis* Arrow rather rare. In New Guinea species of *Pimelopus* and *Scapanes* are said to burrow into young palms from the ground (Burkill, 29).

as quite a population was noticed, though in a limited area, when the beetle's presence was discovered in mid-February 1952. As soon as it was noticed, great efforts were made by the Tonga Department of Agriculture to eradicate the beetle completely. Groups of men tried to destroy all breeding places and kill the beetles in all stages. The same inspector Muller who exterminated the beetle from Niuatoputapu was put in charge of operations, but by August 1952 the infestation covered an area of eight or 10 square km. (Dumbleton, personal communication and 88a).

Oryctes was discovered in Fiji in March 1953 (274a). It was found at Veisari, 10 km. west of Suva on Viti Levu, and had already infested an area from the Veisari River to both sides of the Tamavua River and more than 2 km. inland, so may have been introduced at least a year earlier (Dumbleton, personal communication, April 1953).

On the mainland of southern Asia and on the continental Asiatic islands—Ceylon, the Philippines, Hainan, Formosa, Sumatra, Java, Borneo, Celebes, and other islands of Indonesia—the situation in regard to *Oryctes* is quite different from that on such oceanic islands of the Pacific as Palau, Samoa, and Tonga. New Britain, again, presents an intermediate situation, since it is a continental island, but non-Asiatic and outside the natural distribution of the beetle. Thus it is assumed that in Asia various natural enemies, together with factors such as competition for food, tend to keep population of *Oryctes* at a lower level than in islands to which the beetle has been introduced. In New Britain many of the natural enemies are probably absent, but at least there are more which might potentially help to control the beetle than are naturally present in the oceanic islands.

A comparison of the relative damage by *Oryctes* in East Africa and Ceylon on the one hand and to Samoa on the other showed that, though the destruction was far greater in Samoa, there had been a cumulative destruction in East Africa of 2 percent during a few years (78). This may be compared with an estimated 15 percent destruction of palms in Samoa in 40 years and 50 percent in Palau in 10 years.

Serious damage by *Oryctes* in Asia is generally correlated with abundance of breeding materials and failure to take proper precautions (Dupont, 91; Gater, 121). The failure to destroy native palms when jungle was cleared is cited by Corbett (49).

Probably a large variety of insects and other invertebrates is found within the galleries of *Oryctes rhinoceros* in Asia. Such records are incomplete, but the presence of larvae of *Adoretus*, the rose beetle, and *Eubussaea*, a stag beetle, has been reported in *Oryctes* galleries in India (Friederichs, 113). Friederichs noticed more co-habitants of *Oryctes* in the Philippines than elsewhere (109).

Damage to palms by *Oryctes* in Asia and Africa is generally followed by feeding of the palm weevils, *Rhynchophorus ferrugineus*, and related species. The weevils lay their eggs in the feeding tunnels of adult *Oryctes* or other points of injury to the palms, and the weevil larvae often complete the killing of the palms (Beven, 21; de Mel, 76; Henry, 144; Leefmans, 184-186; Paul, 221) which paves the way for larval *Oryctes* feeding. Opinions vary as to which pest is more serious (Brand, 23; Burkill, 29; Copeland, 45; Corbett, 60; Crevost, 64; Ghosh, 127; Hutson, 150), but it may be *Oryctes*, since the weevil would undoubtedly be much rarer if *Oryctes* did not provide it with egg-laying sites. *Oryctes* control is often recommended as the best control for the weevil (Corbett, 50, 51; Henry, 144). It is fortunate that, to date, the palm weevil has not reached any of the islands of Polynesia or Micronesia. Presumably the wider larval food range and adult night flying of *Oryctes* make it more liable to be carried in commerce. Leefmans (183) states that *Oryctes* grubs in logs could survive temporary submersion in sea water; in fact, that the beetle repopulated Krakatoa by this method.

In Indo-China, *Oryctes rhinoceros* has been treated by Caresche (35), Carton (38, erroneously referring to *O. nasicornis*), Crevost (64), Duport (92, 93) and others (Friederichs, 109; Vincens, 300). Apparently it is ordinarily of only moderate importance there, as coconut is a minor crop.

In Siam, the beetle has apparently received little technical attention, as indicated by a scarcity of reports (Friederichs, 109).

In Formosa, *Oryctes rhinoceros* is recorded as a pest of sugar cane (Matsumura, 204; Clausen, 42; Esaki, 96; Takahashi, 278; Takano and Yanagihara, 279), and as a pest of coconut palms secondary to *Rhynchophorus ferrugineus* (Clausen, 42). I obtained adults at several places in the southern two-fifths of the island in 1934. It is also recorded from Korea (Arrow, 9; Clausen, 42), but this may be an error. Records for China are very incomplete (Arrow, 9; Clausen, 42). Donovan (84) recorded it as *nasicornis*. I collected a few specimens on Hainan Island in July 1935, at Hoihow on the northern coast and at Taipin, 325 meters in altitude, near the center of the island. In 1929 there was a serious outbreak near Hoihow in which many palms were killed (W. E. Hoffman, personal communication, 1952). In 1948 *Phoenix* palms were killed in Canton by *Rhynchophorus ferrugineus* after heavy pruning, apparently without the presence of *Oryctes*.

In the Ryukyu Islands, the beetle was recorded from the southern island of Ishigaki (Yaeyama) by Niijima and Kinoshita (213). In 1952 George E. Bohart found it in native forest, where there were native fan palms (*Livistona chinensis*), but he learned that there were only four coconut palms on the island at the time.

In the Philippines, *Oryctes rhinoceros* has been studied by Banks (15), Barrett (17), Mackie (201, 202), and others (Friederichs, 109; Hernandez, 145; Lopez, 196; Silayan, 248). It appears to be slightly more serious there than on the mainland of Asia.

For Indonesia, Dammerman (65) gave a general discussion and Leefmans (183) published a long report on the beetle with detailed information on habits. Leefmans reported extensive experiments in control methods, but Corbett (48) criticized Leefmans' tests relating to covering of compost or manure with thin layers of sand to prevent oviposition, because Leefmans used uncovered controls in his tests which thus provided attractive laying sites for females to which the tests were exposed. Corbett refuted the practicality of Leefmans' recommendations for burying stumps, on the basis of experience; for poisoning manure heaps, on the basis of danger to domestic animals. And he questioned the safety of trapping because forgotten or neglected traps can become breeding foci. Van der Goot (285) states that *Oryctes* does no damage to sugar cane and spends its whole life on decaying vegetable matter, but he was probably not aware of adult feeding habits and his observations were probably in an area where palms were abundant and no feeding was done by adults in cane. Van Hall (288-292) and others (Keuchenius, 172-173; Koningsberger, 174) report damage and control efforts. Serious damage has been done to oil palms in Sumatra (Milsum, 206).

In Malaya the beetle has been extensively studied by Corbett (48-60), Brown (24), Bryan (25), Burkill (31), Mornay (77), Flippance (106), Friederichs (109), Gater (121-123), Ponniah (229), Richards (234-235), Ridley (236), South (257-259), and Susainathan (274). The beetle occasionally becomes serious when larval food sources are provided. Corbett recommends scattering or disposal of wastes (54); and hand-picking (Burkill, 31) and various other control methods (Flippance, 106) have been suggested.

Oryctes has been of some importance in Burma, and the subject of some reports by Ghosh (127-133), MacKenna and Shroff (199), McKerral (200), and Shroff (247). MacKenna and Shroff (199) state that the beetle was introduced into Burma about 1896.

In India the beetle has been a moderate or serious pest in many parts of the south, where coconut palms are grown, often breeding in accumulations of manure and attacking various kinds of palms as well as sugar cane, pineapple, and sisal. It has been studied particularly by Cherian and Anantanarayanan (40, 41), and others (Arrow, 9; Ayyar, 14; Beeson, 19; Chatterjee, 39; Fletcher, 101-105; Furtado, 117; Kunhi Kannan, 176-181; Lefroy, 188-189; Patel, 220; Pillai, 224-226; Rahman, 232; Ramachandra Rao, 233; Sen, 246; Srinivasa Rao, 260-262; Stebbing, 264-266; Subramania, 271-272; Venkatsubba Iyer, 296-297).

In Ceylon the beetle was originally not considered a serious pest, but by 1930 had become a definite problem with the provision of abundant breeding situations (de Mel, 75, 76). Various studies of trapping (Bryce, 26; Lester-Smith, 191), *Metarrhizium* fungus (Bryce, 27, 28), or other aspects have been made (Capper, 34; Corlett, 61; Dias, 81; Friederichs, 109; Harbord, 141; Hutson, 150-156; Jebaratnam, 158; Jepson, 161-164; Joachim, 168; Lester-Smith, 192). Friederichs (109) suggests that in Ceylon the beetle might have less damaging feeding habits and that Ceylon coconut palms might possess natural resistance.

In Africa, a number of palm-attacking species of the genus *Oryctes* occur, but references to *O. rhinoceros* in Africa and Mauritius undoubtedly represent misidentifications. Since many of these species attack the coconut palm or other economic palms attacked by *O. rhinoceros*, it is helpful to refer to certain literature upon them, in order to further understand *Oryctes* under differing circumstances. Habits, predators, native palm hosts, and control of various species are treated by many workers (Aders, 1, 2; Alibert, 3; Anderson, 4, 5; Anonymous, 7; Beck, 18; Carter, 37; Cotterell, 62, 63; Dry, 86; Friederichs, 109; Ghesquière, 126; Hargreaves, 142; Kaden, 170, 171; Lommel, 195; Mayné, 205; Ritchie, 240; Vanderyst, 286; and Welsford, 304). A different larval food reported is rotting cinnamon leaf from distilleries (Vesey-Fitzgerald, 299).

In Mauritius, several scoliids have been introduced for *Oryctes* control (Carié, 36; de Charmoy, 66-73; Jepson, 165-167; Moutia, 210, 211; Tempany, 281; Vinson, 301). Breeding in the Seychelles was treated by Dupont (90) and Welsford (304).

In Madagascar, Scoliae (Coquerel, 47) and damage and control (Duclos, 87; Frappa, 107; Friederichs, 109) have been discussed by several workers for various species of *Oryctes*.

CONCLUSIONS

Since *Oryctes rhinoceros* is a vary large-bodied insect and feeds in a more or less hidden state in both larval and adult stages, it cannot be controlled readily by such chemical means as are now known. Furthermore, its principal host, the coconut palm, is grown as a commercial crop and a local food crop in many tropical countries where the standard of living does not permit extensive use of chemicals. Thus it is essential to understand the ecological relationships of the beetle in order to cope with it in all of its breeding environments and to make the best use of biological control.

In addition to the coconut palm, the adult beetle feeds in most other kinds of palms and in sugar cane, pineapple, *Pandanus, Agave*, banana, and probably in taro and some large succulent plants. The larva breeds in dead wood or semi-woody plants in many forms and in sawdust, compost, garbage, manure, bagasse, various decaying vegetable materials, and soil containing humus.

It may even feed on living roots or in unhealthy living plant stems. Since it is difficult to detect or destroy the adults while they are feeding inside the crowns of living plants and doing the damage, it is important to eliminate or constantly inspect all possible larval breeding situations, at least until biological control can be more successfully exploited. To effect control over the beetle by reduction and inspection of larval breeding environments often requires great expenditure of labor, but after this has been accomplished to a fair degree, certain materials such as compost or, in its absence, coconut wood may be used as traps to reduce the remainder of the population. However, the checking and eliminating of grubs and adults must be done effectively and consistently. In palm groves adjacent to jungle the situation is complicated and special local studies may be necessary to determine extent of breeding in natural habitats. In these and other situations all native natural enemies should be recognized and encouraged. Enemies include *Scolia* wasps, predaceous beetles, such as ground beetles and certain click beetles and histerid beetles, centipedes, owls, woodpeckers, chickens, ducks and certain other birds, pigs, and certain insectivores, rodents, primates and other mammals, including *Galeopithecus*.

In such environments as oceanic islands of the Pacific, where many of the natural enemies are absent, greater efforts are necessary to restrict the larval food supply; and introductions of safe natural enemies such as *Scolia* and certain carabid, elaterid, and histerid beetles are necessary until other controlling agents are better understood. In the Palau Islands, the abundant provision of war-killed palms enabled the beetle to build up such a great population that it was able to kill one half of the palms on the entire group of islands within 10 years of its introduction. This is an example of a "biological explosion" of a species in a new area with little environmental resistance in the form of enemies, competition, or limitation of food. During such a period "giant" individuals develop which are about 10 percent larger than normal. However, with the gradual depletion and elimination of the surplus larval food in Palau the population is diminishing and the remaining palms are not necessarily doomed. It is even possible that lost copra export may be regained within a reasonable period.

In Samoa, where natural enemies are similarly scarce, the beetle has done great damage in the 43 years since its introduction, but it has probably not killed more than one-eighth of the palms. When breeding situations are more effectively cleaned up in Samoa the damage should be reduced to a low level, with the help of the already introduced *Scolia ruficornis* and *Pachylister chinensis*, as well as the protection of centipedes and the possible introduction of additional *Alaus* or other predatory beetles. Special care and control must be exercised when new forest clearings are made, as well as of sawdust, compost, manure and wood piles. Trapping must be rigidly supervised.

The possibility of exterminating the beetle on a small island was proved in the case of Niuatoputapu, but this would be very difficult on a larger island because of jungle breeding. It might be impossible after the coconut palms were already exterminated because the beetle feeds in *Pandanus*, but attack on *Pandanus* is rare unless the palms have been eliminated by the beetle. Thus its extermination on Vavau Island, Tonga, may be within the realm of possibility.

Rigid quarantine is necessary to prevent further spread of the beetle. It would be helpful to eliminate palms and breeding materials in the neighborhood of docks or anchorages at infested ports and to search all ships, planes, and baggage leaving such places. Also, searching at non-infested ports and requiring entry of ships from infested ports in the morning is advisable, to prevent possible stowaway adults from flying ashore.

Large clean stands of coconut palms are less affected by the beetle than mixed stands or scattered palms, particularly those around villages where compost and manure accumulate. Centralization of *Oryctes* control over large areas, with proper enforcement of regulations concerning breeding environments, is essential.

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[5] Review of Applied Entomology Series A is abbreviated to R. A. E. throughout.

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INDEX

Important references in boldface type, native names in italic.

A

Abappaomogan Island 87
abo 10
Acanthophoenix rubra 2
Acarina 100
Achatina fulica 13
Acheta 68, 98
adaptability 2
Admasah Island 88, 90
Adoretus 97, 122, 126
adult, anatomy of 29-32
adult foods **2-3**, 5-6, **51-58**, 71-73, 78, 103, 129-130
adult habits 4, **39-51**, 51-57, 59, 78, 129-130: feeding 40-57, 78; flight 51; mating 39-40, 59
Aegus 122
aerosol bomb 119
Africa 1, 5, 14, 103, 105, 109, 126, 127, **129**
African snail 13, 57, 102, 109, 111
africana, Gryllotalpa 98
agamemnon, Oryctes 109
agave 118
Agave 57, 129: americana 3; sisalana 3
Agol 54, 55, 70, 82, 98
Aimeliik 10, 53, 54, 56, 66, 67, 77, 78, 80, 93
Aimeong 81
Aiphanes caryotifolia 2
Airai 5, 36, 52, 54, 56, 66, 67, 69, 75, 76-77, 79, 80, 81, 88, 93, 102, 110
akaboek 10
Alap 81
Alaus 61, 63, 101, 104, 109, 130: depressicollis 95, 96; samoensis 124
album, Dictyosperma 2
alexandrae, Archontophoenix 123
Alexandria palm 124
Alocasia 57: macrorrhiza 71
Amarygmus 61, 65, 66, 67: hydrophiloides 96, 104
Amboina 1, 124
American forces 83
American Samoa 3, 73, **121-124**
American Trust Territory 122
American Trusteeship 10
americana: Agave 3; Persea 73
Amphibia 9, 13, 64, 86, **102-103**, 105, 111
amphipods 61, 63
Ananas 3, 57: comosus 57, 72
anatomy 24-32
Angaur Island 4, 6, 9, 34, 53, 57, 64, 66, 67, 68, 72, 78, 79, 92, 101, 102
anisopliae, Metarrhizium 112
angustifolia, Dracaena 72
Annona: muricata 13; squamosa 13
annulata, Campsomeris 102, 111
Anoplolepis 61: longipes 38, 99, 104
Anoronotum rufum 97
ants 38, 52, 60, 61, 64, 65, 66, 67, 69, 98, 99, 103, 104
Aphodius 122
Apia 50, 107, 112, 121
Aplonius opacus orii 101
Apurashekoru 87
aradids 99
Arakabesan 6, 34, 53, 57, 85, 88, 93
Archontophoenix 124: alexandrae 123
Areca 54, 57: cathecu 2, 10, 54, 71
Arecastrum plumosa 2
Arenga 57, 66, 77: pinnata 2, 54, 56
arm-ar-alius 15
armicollis, Papuana 125
arsenates 120
Artabanua 99
Artocarpus 35
asbo 10
Asia 1, 2, 14, 107, 111, 126, 127
Asia Minor 14
Asiatic islands 126
Aspergilleae 113
atrocostata, Emoia 102
attraction to light 50-51
Auluptagel 6, 12, 85
Aulong 87
aurantius, Brachypternus 111
australasiae, Periplaneta 98
Australia 112
australis, Scapanes 125
avocado 73
Aves 101-102
avi'i-vi'i 15
aye-aye 112

B

Babelthuap Island 3, 4, 5, 6, 10, 11-13, 34, 36, 47, 54, 57, 67, 70, 74-83, 88, 101, 110: damage evaluation 74-83; east coast of 3, 11, 82; north 81-83; south 5, 6, 10, 34
Bacillus: lentimorbus 113; popilliae 113; thuringiensis 113
bagasse 1, 70, 129
bait traps 117
Baioudh disease 14
bamboo palm 10
banana 3, 5, 13, 57, 68, 69, 70, 72, 83, 85, 87, 88, 93, 125, 129
bark-lice 112
barium sulfocarbonate 119
Barringtonia 9, 10, 67
bassiana, Beauveria 113
bats 9
Beauveria: bassiana 113; strain 386, 113
beetles other than Oryctes 15, 52, 60-63, 64, 69, 70, 76, 95-96, 103, 104, **105-110**, 122, 124, 126, 130
bengalensis: Molpastes (Pycnonotus) 111
benzene hexachloride 119
betel-nut palm 2, 5, 10, 13, 54, 77, 81, 85, 125

betle, Piper 82
Bikkia 10, 86
biological control **105-113**, 124-125, 126, 129-130: in Asia 126; in Samoa 124-125
biological explosion 130
biology 32-51
birds 6, 9, 87, 88, **101-102**, 105, 111, 124, 130
Blattaria 98
boas, Oryctes 14, 105, 109, 111
Bohol 112
bottle palm 2
Borassus flabellifer 2, 123, 124
Bordeaux spray 120
Borneo 126
Bourbon 14
Brachyloplus fasciatus 111
Brachypternus aurantius 111
breadfruit 13, 35, 51, 68
breeding media 1, 4, **58-75**, 76, 78, 79, 81, 84, 91, 93, 113-119, 129-130; depletion of 93
breeding sites 4-5, 35-38, **58-71**, 93-101, 126, 128, 129-130
brevirostris, Nasutitermes 98, 104
Brontispa 1, 93, 94, 98, 103: palauensis 93-95
bud rot 2, 103
Bufo marinus 13, 102, 111
bulbul 111
Burma 1, 2, 14, 70, 118, **128**

C

cacao 70-71, 77, 107, 122, 125; refuse of 70-71, 107, 115
Caladium 125
calandrine weevils 52, 93
Calophyllum 9, 10, 67: inophyllum 13, 35
Callirhipis 61, 63, 64, 65, 69, 89, 100, 104: onoi 96, 104
callosus, Polyconoceras 100
Camelonotus [Dipelicus] ritsemai 125
Campsomeris annulata 102, 111
Canary Islands 14
Canton (China) 127
Carabidae 63, **95-96**, 104, 105, **108-109**, 130
Carabus 109
carbon bisulfide 117, 119
carbon tetrachloride 119
Carica papaya 72
carolina, Salomona 98
Caroline Islands 1-120, 129-131
Caroline ivory-nut palm 3, 10, 77
carolinensis: Coelococcus 3; Gonatas 96-97, 99, 104; Phyllophaga 97
Caryota 57: urens 2
caryotifolia, Aiphanes 2
cassava 13, 64, 83, 86, 118
Cassia 9
castor bean cake 117
Casuarina 9
Catascopus facialis 109
caterpillars 119
cathecu, Areca 2, 10, 54, 71
cattle 70, 103
caution in replanting 118-119
Celebes 1, 111, 112, 126
centaurus, Oryctes 14, 34, 124
Centetes ecaudatus 112
centipedes 52, 61, 63, 66, 99, 101, 104, 105, 110, 124, 130
central Palaus 84-85
Ceram 1, 124
Cerambycidae 98
Ceylon 1, 111, 112, 117, 120, 126, **128-129**
chamissonis, Cyrtosperma 71
Chelisoches 61: morio 98
chemical control 116, 117, **119-120**, 129
chevrolati, Oryctes 14
chickens 87, 88, 102, 103, 105, 124, 130
Chilopoda 100
China 1, 127
chinensis: Livistona 2, 54, 55, 127; Pachylister 96, 97, 109-110, 124, 130
Chiromys madagascariensis 112
Chlaenius 109, 124
chloris teraokai, Halcyon 101-102
Chrysalidocarpus 10, 57
Chrysomelidae 98
Citrus 13, 106
cinnamon 129
classification of O. rhinoceros 13-14
click beetle 96, 104, 105, 124, 130
climate 8-9, 121: Samoa 121
cockroaches 52, 59, 61, 63, 67, 68, 98
coarctata, Orthomorpha 100
coconut cultivation method 121
coconut husks and shells 68, 70
coconut logs 62-63, 66, 68: used in construction 66
coconut palm 1 ff.: ecology of 10-11; home of 10; habitat of 10
coconut stumps **63-66**, 68
coconut trunks **58-62**, 68
Cocos 57, 120: nucifera 2, 10, 56, 71
Codiaeum 10
Coelococcus 57: carolinensis 3
Coenobidae **100-101**, 104
coffee refuse 71
co-habitants 36, 52, 60-62, 63-69, **93-101**, 124, 126-127; of feeding sites 93-101
Coleoptera 95-98, 108-109
Collembola 67
Colocasia 3, 57, 125: esculenta 71
Colombo 120
common names of beetle 15
Comoro Island 14
comosus, Ananas 57, 72
compost 1, 35, 36, 68-69, 76, 83, 106-107, 111, 114-116, 118, 122, 129, 130; traps 5
coniferous wood 69
control 4-6, 53, 70, **105-120**, 122, 128: biological 105-113, 122, 124; chemical 116-117, **119-120**, 129; cultural 113-119; other methods 118
copra 120, 122, 124-125
coprid dung beetle 122
Coptotermes 67; remotus 98
Cordia 9, 106
Cordyline 13: terminalis 72
coronatus, Oryctoderus 125
Corypha: elata 2; umbraculifera 2
crabs 13, 61, 63, 64, 67, 86, 87, 88, 100-101, 104, 105, 110-111, 124, 130
creosote 119, 120
cricket 61, 65, 98
Crotalaria 9
crow 105, 111
crucifers 14
crude oil 119
Crustacea 100-101
Cubaris 61, 101
cultural control 113-119
Curry's sawmill 107
Cutilia nitida 98
Cyathea 3
Cyphokentia samoensis 3
Cyrtosperma 57: chamissonis 71

D

dactylifera, Phoenix 2
damage evaluation 74-93: Babelthuap 74-83; central Palaus 84-85; Kayangel Atoll 83-84; limestone islands 85-88; southern islands 88-93
Dascillidae 61, 67, **69**
Dasyo 102
date palm 2, 14
dead heart disease 2
Decapoda 100-101
depressicollis, Alaus 95, 96
Dermaptera 98
destruction of dead trees 113-114
detailed analyses of hosts: coconut palm 51-52, 61-62; dead coconut logs 63, 66; dead coconut trunks 61-62; dead Pandanus trunks 67; misc. wood 66-67; other palms 66
Dictyosperma album 2
difficilis, Pupina 101
Diplopoda 100
Diploptera dytiscoides 98
dipteron 108
diseases of beetle 76, 110, 112-113
diseases of palm 2, 14, 91, 103
diseases of sugar cane 2
discolor, Rhoeo 72
distribution in Pacific 1, 124-129
Doom Island 125
Dracaena 10, 86: angustifolia 72
dubius, Pandanus 53
ducks 103, 105, 130
dynastids 113
Dypsis gracilis 2
dytiscoides, Diploptera 98

E

earthworms 52, 61, 65, 67, 68, 103, 104
earwigs 52, 65, 66, 68, 98, 103, 104
ebeninus, Placodes 110
ecaudatus, Centetes 112
ecological relationships 2, **51-105**, 112, 129
ecological succession: in adult hosts 103; in larval hosts 103-105
ecology of the coconut palm 10-11
economic importance 1
economic survey 5
Eilmalk Island 6, 55, 56, 86, 87
Elaeis 14, 57, 124: guineensis 2, 55, 56
elata: Corypha 2; Roystonea 2, 55
Elateridae 60, 63, **96**, **109**, 130
elephant beetle 125
Ellice Islands 120
Emoia atrocostata 102
enteric biota 33
entomological survey 5
environmental resistance 2
epops indica, Upupa 111
erratica, Scolia 107
Euborellia 98
Eubussaea 126
Eucalyptus 106
Eugenia 9
Euphorbia 9
Eupritchardia 123: pacifica 3
Europe 14, 106, 119
Eurystomus 111
experiments 3-4, 47-50, 71-74, 128: control 128; feeding 3-4, 47-50, **71-74**; laboratory 47-50, 71-74
exulans, Rattus 101

F

facialis: Catascopus 109; Brachyloplus 111
fan palm 2, 10, 54, 124, 127: Fiji 3
fauna of Palau 9-10
feeding experiments 3-4, 47-50, **71-74**
feeding habits of adults 40-57, 78
feeding sites, co-habitants of 93-101
fermenting garbage water 117
fermenting sap 117
ferrugineus, Rhynchophorus 120, 127
Ficus 9
field and laboratory work: control 118-120; feeding 3-4, **47-51**, 51-57; **71-74**; habitat studies 11-13; methods of 3; rearing 3
field headquarters 3-4, **11-13**, 47-51, 71-74, 113, 117
Figulus 61, 62, 104, 122: integricollis 97
Fiji 1, 120, 124, 126
Fiji fan palm 3
fishtail palm 2, 10
flabellifer, Borassus 2, 123, 124
Flagellaria 77
flies 68, 103, 104, 107, 108, 109, 110
flight 51, 59, 75, 113
flora of Palau 9-11
flying lemur 105
food of scolia 9
foods: adult **2-3**, 5-6, **51-58**, 71-73, 78; larval 1, 23, 33, 35-38, **58-71**, 73-74, 93-101, 129
Formicoidea 99
Formosa 1, 4, 9, 70, 111, 126, **127**
fowl 87, 88, 102, 103, 105, 124, 130
fruticans, Nypa 2, 10, 54
fulica, Achatina 13
fungus 52, 60, 61, 63, 67, 93, 94, 99, 103, 104, 110, 112, 117, 124, 129
fungus diseases of beetle 110

Furcaspis 103: oceanica 93
Futuna 120

G

Gaianges (Ngaiangas) 87
Galeopithecus 112, 130
Gallus 102
gamasid mites 107
Garakayo 91
garbage 1, 68, 115-116, 118, 129: disposal of 115-116; dumps 118
Gareru Islet 77
Garyo (Heleu) 88, 89, 90
Gasupan 79
Gazelle Peninsula 125
geckos 52, 59, 102, 105, 111
gecko, Gekko 111
Gekko gecko 111
geminata, Solenopsis 99, 104
geminus, Hister 110
geography 6-7: of Samoa 121
Geograpsus 101, 104
geology 6
German regime 10
("gideon") lorquini, Xylotrupes 125
Gilbert Islands 120, 122
gigas, Oryctes 14
Glyptotermes 61, 98, 104
godeffroyi, Oryctoderus 125
Gonatas 61, 63: carolinensis 96-97, 99, 104
Gorak 84
gracilis, Dypsis 2
grape vines 14
Grapsidae 100-101
grasshopper, long-horned 90, 93-94, 98, 101, 103
green manure 116
grossepunctatus, Scapanes 125
ground beetles 124, 130
Gryllacrididae 98
Gryllidae 98
Gryllotalpa 68: africana 98
Gryllotalpidae 98
grypus, Odynerus nasicornis 14
Guam 85, 122
guava 13
guineensis, Elaeis 2, 55, 56
Gulubiopsis 54, 57, 85, 86, 87: palauensis 3, 10
guttulata, Parastasia 97, 99, 104

H

habitats: normal **1-3**, 70-75; studies of 11-13
habitat of coconut palm 10
habits: adult 4, **39-51**, 40-57, 59, 78, 129-130; larval 35-38
haematodes, Odontomachus 99, 104
Haematoloecha 99
Hainan Island 1, 126, 127
Halcyon chloris teraokai 101-102
Hanguana malayana 73
hawk cuckoo 111
Heleu (Garyo) 88, 90
Hemidactylus 102
Hemiptera 99
hermit crabs 13, 61, 63, 64, 67, 100-101, 104, 105, **110-111**
Hermetia 68, 104
Hernandia 10
Heterospathe 57, 70, 77, 82: elata var. palauensis 3, 10, 13, 54, 55, 56, 66, 71
Hevea 120
Hibiscus 9
Hierococcyx varius 111
Hister geminus 110
Histeridae 52, 96, **109-110**, 124, 130
Hoihow 127
Holngoaol (Ongewaol) 91
Hololepta scissoma 110
Homalopteryx pelewensis 98
Hong Kong 1
hoopoe 111
Hormurus 61, 100
hosts **2-3**, 5-6, **51-74**, 93-101, 103-105, 129-130: adult **2-3**, 5-6, **51-58**, 71-73, 103, 129-130; larval **58-71**, 73-74, 93-101, 103-105
hortorum, Scolia 106
houseflies 109
hubneri, Papuana 125
Hydnocarpus 118
hydrophiloides, Amarygmus 96, 104
Hymenocallis littoralis 73
Hymenoptera 99

I

iguanid 111
India 1, 36, 70, 118, 126, **128**
indica, Stachytarpheta 106
indicus, Varanus 13
indicus indicus, Varanus 102
Indischer Nashornkäfer 15
Indo-China 1, 4, 34, **127**
Indonesia 1, 14, 126, 127 **128**
inophyllum, Calophyllum 13, 35
insecticides 119
insignis, Pseudopinanga 3, 10, 13, 54
insignis jalorensis, Lariscus 111
integricollis, Figulus 97
internal anatomy: of adult 29-32; of third instar larva 24-29
introduction of beetle into Pacific 1, 4-6, 34, 84, 124-125, 129: Fiji 1, 124; New Britain 1, 124-125; New Guinea 124-125; New Ireland 1, 124; Palau 4-6, 84, 124; Tonga 1, 124; Samoa 1, 34, 124; Wallis 1, 124-125
invertebrate co-habitants of breeding sites 93-101
Ishigaki (Yaeyama) 127
Isopoda **101**, 104
Isoptera 98
Italy 14
ivory-nut palm 3, 10, 77
Iwang 77

J

jalorensis, Lariscus insignis 111
Japanese beetle milky disease 76
Japanese forces 85, 87, 125
Japanese regime 10, 76, 81, 84, 85, 87, 125
Java 4, 70, 107, 108, 109, 112, 126

jumping tenebrionid 104
June beetle 104
jungle 69-70, 102

K

Kaisha 76
kanehirae, Neotermes 98, 104
kapok 13, 66, 67, 98
Karamado Bay 79, 81
Karasumau 81
Kayangel Atoll 4, 6, 11, 57, 69, 70, 83-84, 91, 93, 101: damage evaluation 83-84
Keppel (Niuatoputapu) 124, 126, 131
kerosene-soap emulsion 119
kingfishers 88, 101-102, 105
Klappertor 15
Korak 77
Korea 1, 127
Koror (Koreor, Oreor) 3, 4, 5, 6, 8-9, 10, 12, 34, 47, 50, 51, 54, 55, 57, 64, 66, 69, 71-74, 77, 83, 84-85, 88, 93, 101, 102, 110, 113
Krakatoa 127
kumbang badak 15
kumbang kelapa 15
Kura-asemil 86
Kuroboroban 86

L

laboratory methods **3-4**, 47-50, 71-74
Lachnosterna 2
laevipennis, Papuana 125
lagenicaulis, Mascarena 2
land crabs 86, 101, 104
laperouse senex, Megapodius 102
Lariscus insignis jalorensis 111
larva, anatomy of 24-29
larval foods 23, 33, 35-38, **58-71**, 73-74, 93-101, 129: abnormal 73-74
larval habits 35-38
larval hosts 4-5, 35-38, **58-71**, 93-101, 103-105, 129
Latania 2
latecavatus, Oryctes 14
latitarsis, Oryctoderus 125
lemurs 105, 112: flying 105
lentimorbus, Bacillus 113
leontopetaloides, Tacca 73
Leptochirus 63, 66, 95
lepidopterous larvae 93, 104
life cycle 33-34
Lilbau 88, 90
lime 120
lime tree 51
limestone islands 9, 10, 12, 57, 70, **85-88**, 93, 102: damage evaluation 85-88
Lithobius 52, 67
littoralis, Hymenocallis 73
Livistona 57: chinensis 2, 54, 55, 127
lizards, 6, 9, 13, 81, 83, 86, 87, 88, 101, 102, 105, 111
long-horned grasshopper 90, 93-94, 98, 101, 103
longipes, Anoplolepis 38, 99, 104
lorquini, Xylotrupes 125
Lucanidae 60, 62, **97**, 104
lumbricinus, Trigoniulus 100

M

Macacus 101
macrorrhiza, Alocasia 71
Madagascar 14, 34, 105, 106, 107, 109, 112, 118, **129**
madagascariensis, Chiromys 112
Madras 111
maggots 62, 66, 68, 104, 109, 110
Malakal 6, 34, 57, 84, 85, 93
Malay Peninsula 1, 111
Malaya 2, 5, 99, 107, 111, **128**
malayana, Hanguana 73
Mammalia **101**, 130
Mangifera 35
mango 35, 67
mangrove 10, 11, 75, 76, 79, 88
manu-i-niu 15
manure 1, 70, 103, 116, 117, 129: green 116
Mariana Islands 5, 98
Mariana (Saipan) coconut beetle 1, 98
marinus, Bufo 13, 102, 111
Marshall Islands 5
marsupials 112
Mascarena lagenicaulis 2
mating 39-40, 59
Mauritius 2, 9, 14, 34, **129**
Mechereher 86
Mecistocephalus 100, 110
Mediterranean 14
megacephala, Pheidole 99, 104
megapodes 6, 87, 102
Megapodius laperouse senex 102
Mehebehuel 80
Melaleuca 71
Melekeiok 10, 57, 66, 68, 75, 76, 89, 93, 94, 98, 102
Messerschmidia 10
Metarrhizium 112, 117, 124, 129: anisopliae 112
methods of coconut cultivation in Samoa 121
Metroxylon 10, 57, 124: sagu 2, 54, 123
Mezira 99
micronesica, Pinanga 3, 10
milky disease of Japanese beetle 76
millipedes 52, 60, 61, 63, 64, 67, 68, 70, 100
Mimosa 9
Minhla 14
Miscanthus 74
mites 49, 100, 101, 107, 110
mold 62, 84
Mollusca 101
Molpastes (Pycnonotus) bengalensis 111
monitor lizards 6, 13, 81, 83, 86, 88, 102, 105, 111
monkey 9, 101
monoceros, Oryctes 14, 36, 105, 109, 111
Morinda 10
morio, Chelisoches 98
Morion 104: orientalis 95, 96
morphology 23-32
morsitans, Scolopendra 100
mosquito control 114
molting process 38
moth 61, 63, 66, 67
Mulifanua 107
muricata, Annona 13
Musa 3, 57, 72
muscardine fungus 67, 112, 117, 124
myriapods 104

N

Namai Bay 12, 75
nanus, Oryctoderus 125
Nardueis 77
naresi, Spirostrophus 100
nasicornis, Oryctes 14, 34, 36, 106, 113, 119, 127
nasicornis grypus, Oryctes 14
Nasutitermes 61, 65, 67: brevirostris 98, 104
native home of beetle 1
native home of coconut palm 10
native palm 5-6
Neochryopus sauvagei 109
Neotermes 61: kanehirae 98, 104
Nesogaster 98
New Britain 1, 120, 124, 125, 126
New Guinea 10, 14, 34, 120, 124, 125
New Hebrides 14
New Ireland 1, 125
New Zealand Reparations Estates 121
Ngabad Island 62, 91
Ngabaral 76
Ngaiangas 87
Ngajangel 67, 83, 102
Ngaraard 81, 89
Ngarakis 12, 75, 76
Ngaramlengui 81
Ngardmau 54, 55, 67, 81, 93
Ngarapalas 84
Ngaregur 83
Ngarekeai 77
Ngarekelau 83
Ngargol 6
Ngarhelong 54, 55, 70, 81-82
Ngariungs Island 83-84, 93, 102
Ngatpang 5, 54, 55, 77, 79, 80, 81, 115
Ngchemiangel 77
Ngchesar (Nghesar) 10, 76
Ngedebus 6
Ngedos 90
Ngemelis Islands 6, 57, 87, 88, 91, 98
Ngenelael 85
Ngerekeu 91
Ngereong (Ngeregong) 88, 89, 93
Ngergoi 6, 91
Ngerkebesang 85
Ngermetengel 81
Ngerugelbtang 88
Ngesbus 91
Ngis 90
Ngiwal 3-4, 8-9, 10, 11-13, 48, 51, 52, 54, 56, 58, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71-74, 75-76, 80, 81, 82, 93, 94, 99, 101, 102, 117; field headquarters 11-13
Ngiwal pier 11-12, 69
Ngiwal sawmill 12, 69, 74, 75, 101
Ngkeklau 4, 13, 81
Ngothugothu 77
ngu, Oryctes 14
nipa palm 2, 10, 11, 12, 48, 54, 70, 81
nitida, Cutilia 98
Niuatoputapu 124, 126, 131
normal habitat 1-3
Normanbya 3
nucifera, Cocos 2, 10, 56, 71
nudicauda, Oryctes 14
Nypa 57: fruiticans 2, 10, 54

O

oceanica, Furcaspis 93
Odontomachus 61: haematodes 99, 104
odor 23
odoratissimus (tectorius), Pandanus 3
oedemerid beetles 103
officinarum, Saccharum 55, 72
oil palm 2, 5, 10, 13, 51, 55, 124, 128
Old World tropics 1
Olei 63, 82, 93
Olethrius 67, 98
Omogan 87
Oncosperma 3
Ongewaol (Holngoaol) 91
onoi, Callirhipis 96, 104
opaca, Pseudozaena tricostata subsp. 95-96
opacus orii, Aplonius 101
Ophyra 68
Oreodoxa regia 2
orientalis: Morion 95, 96; Uloma 96, 104
orii, Aplonius opacus 101
Orthomorpha coarctata 100
Orthoptera 98
Oryctes 120: agamemnon 109; boas 14, 105, 109, 111; centaurus 14, 34, 124; chevrolati 14; gigas 14; latecavatus 14; monoceros 14, 36, 105, 109, 111; nasicornis 14, 34, 36, 106, 113, 119, 127; nasicornis grypus 14; ngu 14; nudicauda 14; owariensis 14, 51; pyrrhus 14; ranavalo 14; rhinoceros 1 ff.; simiar 14; tarandus 2, 14, 105, 106; trituberculatus 14
Oryctes du cocotier 15
Oryctoderus: coronatus 125; godeffroyi 125; latitarsis 125; nanus 125
Orycetonia 61
oryctophaga, Scolia 5, 105, 106-107
Orthomorpha coarctata 100
otitids 104
Otus podarginus 102
owariensis, Oryctes 14, 51
owls 88, 102, 105, 124, 130
Oxycetonia 86, 97, 99, 122

P

Pachylister chinensis 96, 97, 109-110, 124, 130
Pacific iguanid 111
pacifica, Pritchardia (Eupritchardia) 3
Pago Pago 121
Paguridae 100-101, 104
Palau 1-120, 129-131: map of 7
palauensis: Brontispa 93-95; Gulubiopsis 3, 10, 54; Heterospathe elata var. 3, 10, 13, 54, 55, 56, 66, 71; Ponapea 10
palm census 74-93: summary of 93
palm squirrels 111
palm weevils 127
palms other than coconut 2, 3, 5, 10, 11, 12, 13, 14, 48, 51, 54, 55, 66, 70, 77, 81, 85, 124, 125, 127, 128, 129

Palmyra palm 2, 124
Pandanus 1, 2, 6, 10, 13, 35, 44, 67, 68, 69, 70, 76, 77, 78, 79, 82, 84, 85, 86, 87, 88, 90, 91, 93, 98, 102, 114, 117, 118, 129, 131: dubius 53; odoratissimus 3; tectorius 3, 13, 52-53, 57, 71
papaya 9, 13, 72, 83, 87, 88
papaya, Carica 72
Papuana: armicollis 125; hübneri 125; laevipennis 125; semistriata 125; splendens 125; woodlarkiana 125
paradichlorobenzene 119
parasites 5-6, 52, 95-103, 107-108, 112-113
Parastasia 104: guttulata 97, 99, 104
Paris green 119
Passalidae 60, 62, 96-97, 104
pathogens 110, 113
patricialis, Scolia 99, 107; var. plebeja 5
Pediris 61: sulcigera 96, 97, 104
Peleliu 4, 6, 9, 34, 44, 48, 51, 52, 53, 57, 62, 66, 70, 75, 85, 90, 91, 92, 93, 101
pelewensis, Homalopteryx 98
Periplaneta australasiae 98
Persea americana 73
pests of coconut palm other than beetle 93-95
Pheidole megacephala 99, 104
phenyl 119
Philippine Islands 1, 4, 111, 112, 118, 126, 127-128
Phoenix palms 14, 127
Phoenix: dactylifera 2; sylvestris 2
Phyllophaga carolinensis 97
physiology 33
pigs 9, 101, 103, 105, 112, 124, 125, 130
pill-bug 101
Pimelopus 125
Pinanga micronesica 3, 10
pineapple 2, 3, 13, 57, 70, 72, 76, 85, 117, 118, 128, 129; fields 13; waste 70
pinnata, Arenga 2, 54, 56
Piper betle 82
Pkulata Prival 11
Placodes ebeninus 110
plebeja, Scolia patricialis var. 5
plumosa, Arecastrum 2
podarginus, Otus 102
Polyconoceras callosus 100
Polyscias 10
Ponapea palauensis 10
popilliae, Bacillus 113
population studies of beetles 74-93
Porcellio 52, 61, 101
potash 70
predators 5-6, 63, 88, 95-103, 105-113, 124, 130
prima, Pseudeuxesta 62
primates 130
Pritchardia (Eupritchardia) 123, 124: pacifica 3
procer, Scolia 99, 107
Prorhinotermes 69, 98
Pseudeuxesta 103: prima 62
Pseudopinanga 57, 70, 77: insignis 3, 10, 13, 54
Pseudozaena 68, 104: tricostata 96; tricostata subsp. opaca 95-96
psocids 112
Puerto Rico 15
pupation 38-39
Pupina 65: difficilis 101
Pycnoscelus 63: surinamensis 98
Pycnonotus bengalensis 111
pyrrhus, Oryctes 14

Q

quadricorne, Toxicum 96, 104
quadrifoveatus, Strategus 15
quarantine measures 120, 131

R

Rabaul 125
"ragi" water 117
ranavalo, Oryctes 14
Raphia vinifera 2
rats 9, 64, 67, 86, 88, 101, 104, 105, 111, 130
Rattus exulans 101
rearing methods 3-4
red coconut scale 52, 93, 94, 99, 103
red palm 2
reduviid nymph 99
regia, Oreodoxa 2
relatives of O. rhinoceros 1, 13-14, 122; in Samoa 122
remotus, Coptotermes 98
repellents 118, 120
Reptilia 102
Reunion 14
rhinoceros, Scarabaeus 14
rhipiphorid beetles 107
Rhipiceridae 60, 96
Rhoeo 57; discolor 72
Rhynchophorus ferrugineus 120, 127
rice hulls and straw 1, 70
ritsemai, Camelonotus [Dipelicus] 125
Rodriques Island 14
rollers 111
rose beetle 122, 126
royal palm 2, 10, 55, 124
Roystonea 57, 124: elata 2, 55
rubra, Acanthophoenix 2
rufa, Scolia 106
ruficeps, Scolia 107
ruficornis, Scolia 5, 99, 106, 107, 108, 115, 124, 130
rufum, Anoronotum 97
Ryukyu Islands 1, 127

S

Saccharum 3, 57: officinarum 55, 72
sagittifolium, Xanthosoma 71
sago palm 2, 10, 13, 54, 77, 124, 125
sagu, Metroxylon 2, 54, 123
Saigon 3
Saipan (Mariana) beetle 1, 98
Salawati Island 124
Salomona carolina 98
salt 119-120
Samoa 1, 2, 3, 34, 72, 73, 102, 103, 107, 109, 111, 112, 113, 119, 120, 121-124, 130; American 3, 73, 121-124; Western 3, 72, 97, 102, 107, 109, 110, 121-124

Samoan Alaus 109, 124
samoensis: Alaus 109, 124; Cyphokentia 3
sanitation of coconut groves 53, 70, 113-119
São Thomé Island 14
sarcophagid flies 108
sauvagei, Neochryopus 109
Savaii 116, 121, 125
sawdust 1, 69, 114-116, 118, 129
sawmills 116
Scaevola 10
scale, red coconut 52, 93, 94, 99, 103
Scapanes 120: australis 125; grossepunctatus 125
scarab wasps 105
scarabaeid grubs 111
Scarabaeidae 97
Scarabaeus rhinoceros 14
scissoma, Hololepta 110
Scolia 9, 77, 101, 102, 105-107, 111, 124, 130: erratica 107; hortorum 106; oryctophaga 5, 105, 106-107; patricialis 99, 107; patricialis var. plebeja 5; procer 99, 107; rufa 106; ruficeps 107; ruficornis 5, 99, 106, 107, 108, 115, 124, 130
Scolia liberations 77
Scoliae 129
Scoliidae 99, 105, 111, 129
Scolopendra 61, 101, 104, 110: morsitans 100
scorpions 65, 100, 110
Scorpionida 100
Segestes 90, 103: unicolor 93-94, 98
semistriata, Papuana 125
semmilinki, Trichogompus 125
senex, Megapodius laperouse 102
Solomon Islands 125
splendens, Papuana 125
Serdang palm 2
Sessinia 103
Setenis 62
sex ratio 34-35
Seychelles 120, 129
Siam 1, 127
Sida 9
simiar, Oryctes 14
Simodactylus 96
Singapore 4
Siphonophora 100
sisal 36, 71, 110, 128
sisalana, Agave 3
skink 102
slugs 61, 63, 101
snails 13, 57, 61, 66, 86, 101, 102, 104, 109, 111; African 13, 57, 102, 109, 111
snakes 9, 101, 102
Socotra Island 14
Solenopsis geminata 99, 104
Solomon Islands 109, 120
Sorong 124, 125
South America 10
sowbugs 52, 63, 67, 68, 103
southern Palaus 88-93
Spanish regime 10
spider lily 73
Spirostrophus 61, 65: naresi 100
splendida, Verschaffeltia 2
spraying, chemical 119, 120
spread of O. rhinoceros: in the Palau Islands 4-6, 74-93; in Samoa 124
squamosa, Annona 13
squirrels, palm 105, 111, 112
Stachytarpheta indica 106
stag beetles 122, 126
Staphylinidae 96
starling 101
Stevensonia 2
stomach poisons 120
Straits Settlements 120
Strategus 49: quadrifoveatus 15
stridulation 35
stridulatory structures 21
succulents 128, 129
sugar cane 2, 3, 5, 6, 13, 14, 35, 45, 55, 70, 72, 84, 85, 86, 93, 117, 118, 127, 128, 129
sugar palm 2, 10, 54, 77
sugar water 73
sulcigera, Pediris 96, 97, 104
Sumatra 126, 128
surinamensis, Pycnoscelus 98
surveys: U. S. Commercial Co. 5
Suva 124, 126
sylvestris, Phoenix 2

T

Tacca leontopetaloides 73
Taipin 127
taiwan-kabutomushi 15
talipot palm 2
Tamavua River 126
Tanga 110
Tanganyika 110
tanrek 112
tapioca 13, 72
tar 119
tarandus, Oryctes 2, 14, 105, 106
taro 3, 13, 57, 62, 72, 75, 86, 88, 129; fields 13, 57, 62, 72, 75, 86
taxonomy 13-23
technical descriptions 15-32: adult 20-23, 24, 27, 28, 29-32; egg 15; larva 15-20, 24-29; pupa 20
tectorius, Pandanus 3, 13, 52-53, 57, 71
Tenebrionidae 36, 60, 62, 63, 96, 104
Tefflus 109
teraokai, Halcyon chloris 101-102
Terminalia 9
terminalis, Cordyline 72
termites 38, 60, 64, 66, 69, 98, 102, 104
Tettigonidae 98
thatch 1, 70
Thereuonema 61, 67, 100
Thespesia 10
Thrinax 3
thuringiensis, Bacillus 113
toad 13, 64, 86, 102, 105, 111
toddy palm 2
Tonga 1, 111, 120, 124, 125, 126, 131
Tonga Dept. Agriculture 126
Toxicum 61, 63: quadricorne 96, 104
trapping 5, 116-117, 122, 124, 128, 129, 130; Samoa 122
Travancore 108
tree fern 3
tree shrews 105, 111
Trichogomphus 120: semmilinki 125
tricostata, Pseudozaena 96; subsp. opaca 95-96

Trigoniulus 61, 63, 65: lumbricinus 100
trituberculatus, Oryctes 14
"tuba" trees 117
Tupaia 111
turpentine, oil of 119
Tutuila 47, 121, 122, 124

U

U. S. Commercial Co. 5
uang 15
Ulimang 66, 81, 98
Uloma 65: orientalis 96, 104
umbraculifera, Corypha 2
unicolor, Segestes 93-94, 98
Upolu 107, 109, 115, 121, 124
Upupa epops indica 111
Urena 106
urens, Caryota 2
Urukthapel Island 6, 86, 87

V

Vaginulus 101
Vailoa 124
Vaitele 115
Varanus: indicus 13; indicus indicus 102
varius, Hierococcyx 111
Vavau Island 125, 131
vertebrate predators 111-112
vertebrate relationships 101-103
Veisari 126
Veisari River 126
Verschaffeltia splendida 2
vinifera, Raphia 2
Viti Levu 126

W

Wallis Island 1, 120, 124, 125
war damage to palms 4, 70, 74, 76, 79, 81, 84, 91
wasps 5, 9, 77, 99, 101, 102, 105-107, 108, 111, 115, 124, 129, 130
water buffaloes 113-114
weevils 36, 52, 66, 93, 127
West Indies 15
Western Samoa 3, 72, 97, 102, 107, 109, 110, 121-124
white tannas disease 2
wild date palm 2
Woodlark Island 14
woodlarkiana, Papuana 125
woodpecker 105, 111, 130
woody shelf fungus 104

X

Xanthosoma 57: sagittifolium 71
Xylotrupes 120: lorquini 125

Y

Yap 85
yashi-no-kabutomushi 15

Z

Zanzibar 5, 36, 99, 105, 107, 108, 111, 120