

An Ecological Perspective of Marcus Island, with Special Reference to Land Animals

SHOICHI F. SAKAGAMI¹

MARCUS IS A SMALL, remote reef island in the vast western Pacific. It is located at N. 24° 20', E. 154° (Bryan, 1903), being 1,000 km. ENE. of Farallon de Pajaros (the northernmost of the Mariana Islands), 1,300 km. E. of Iwo Jima, and a little farther WNW. of Wake (Gressitt, 1954).² Prior to World War II the island was a Japanese dependency. Now it is a part of the Trust Territory of the United States, but there is no active establishment upon it except for a weather station belonging to the Central Meteorological Observatory of Tokyo. Through the courtesy of the Observatory, I had an opportunity to visit the island, together with Dr. N. Kuroda of the Yamashina Ornithological Institute (birds) and Mr. M. Yamada of our Institute (marine invertebrates), during April 30 to May 6, 1952, and to observe its land biota. Although our observations were not extensive because of lack of sufficient time, I believe that the results are worth publishing because of our scanty knowledge of the ecology of the smaller Pacific islands and the lack of comprehensive biological research on this island since Bryan's visit in 1903.

TOPOGRAPHY AND SOIL TEXTURE

Marcus Island is a raised atoll formed on an elevation of submarine mountains in northern Micronesia. As seen in Figure 1, it is triangular, with south and north shores of about 2 km., and the northwest shore a little longer. The

lagoon between the island and the fringing reef is about 200 m. on the NW. shore but is much narrower on the S. and E. shores (Fig. 2). All of the shores are lined by sandy beaches, except at the northernmost parts of the NW. coast, where the old, already mineralized reef occurs along the beach (Figs. 1, 3). The reef is connected with the outer ocean by means of two indentations in the E. and S. shores, respectively. Only the southern indentation is used, however, as the harbor for landing by boats (Fig. 1c), as large ships cannot approach the harbor because of the dangerous underwater reef. The island is very flat. Formerly, the highest altitude was reported as 22 m. by Bryan (1903), but now, because of the leveling undertaken during the war, it is only 7 m. near the northern cape. Also, the trace of an old lagoon discovered by Bryan was filled up with earth by the wartime activities (Matsubara, private communication to the writer). A runway of about 1,700 m. running across the island parallel with the NW. shore and a broad road near the southern shore now divide the island into three areas, the NW. zone, the S. zone, and the E. triangle (Fig. 1). As previously mentioned, the weather station and accompanying facilities are the only establishments now active on the island. But remains of ruined buildings constructed by both Japanese and American military forces during or after World War II are scattered everywhere. The earth consists exclusively of coral sand and pebbles. The latter vary in dimensions from mere large sand grains to pieces of gravel more than 5 cm. in length (Fig. 10). Accumulation of humus was observed only in the E. triangle, where the vegetation was relatively well developed.

In summary, Marcus is extremely poor in land area, soil texture, and topographical diversities. How such a poverty reflects on the land biota will be described subsequently. It must be men-

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² Location of the island differs slightly from one record to another: N. 24° 17' 30", E. 153° 58', according to the notification by the Tokyo Prefectural Office (1898); and N. 24° 17' 35", E. 154° 4' 30", and N. 24° 17' 02", E. 154° 1', respectively, according to observations by two Japanese cruisers, the *Kasagi* and the *Takachibo* (Yoshida, 1902).

tioned also that the fringing reef may serve to a certain degree as a physical barrier against the immigration of various terrestrial organisms.

CLIMATE

Thanks to the occurrence of a weather station, which initiated its postwar activities in

April, 1951, we possess a rather precise picture of this mere heap of sand and pebbles in the vast ocean. Means of maximum, mean, and minimum daily temperatures during my stay were 25.9°, 22.7°, and 21.0° C., respectively; the average annual trends of various climatic factors are shown in Table 1. From these data,

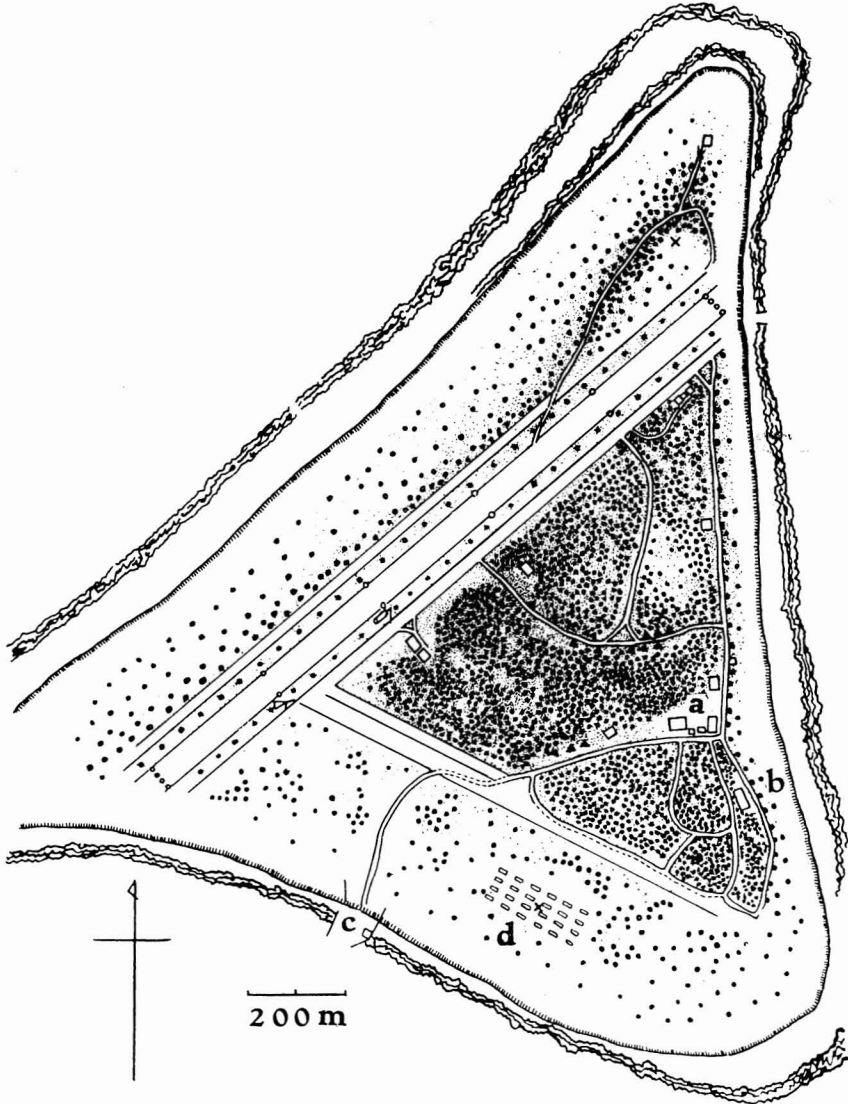


FIG. 1. Marcus Island. Drawing based upon a map used in the Observatory, showing *Messerschmidia* and *Pisonia* (dots), papaya (triangles), coconut palms (crosses), buildings (including ruined ones). Minute dots denote the density of *Ipomoea*. a, Office of weather station; b, lodging house; c, harbor; d, ruined barracks.

TABLE 1
CLIMATE OF MARCUS ISLAND
(The data are the averages obtained during 1952-4. Maximum and minimum values are the extreme ones noted during the four years.)

	TEMPERATURE (°C.)			MEAN RELATIVE HUMIDITY (%)	WIND VELOCITY (m/sec)		RAINFALL (mm.)	
	Max.	Mean	Min.		Max.	Mean	Total	Max/hr
January.....	29.7	22.4	17.2	72	18.3	7.6	66.9	28.5
February.....	28.5	22.4	16.3	75	18.1	7.5	53.5	25.7
March.....	29.9	23.0	18.0	76	18.4	7.8	39.5	10.9
April.....	31.9	24.8	18.4	78	17.6	8.1	37.8	8.7
May.....	33.3	26.3	19.8	78	13.2	5.7	48.7	15.9
June.....	33.8	28.1	23.1	75	12.4	4.5	43.0	23.0
July.....	35.3	27.3	22.8	78	16.4	6.0	252.8	59.2
August.....	33.7	27.3	21.8	79	15.6	6.4	189.1	23.9
September.....	35.3	27.9	22.8	76	16.5	7.3	82.4	31.0
October.....	33.5	26.8	21.9	78	18.9	7.1	117.8	28.6
November.....	34.2	26.0	22.0	77	18.5	7.1	45.7	12.3
December.....	31.6	23.5	18.5	73	21.6	8.6	66.1	16.5

Warmth Index, $W = 245.8^{\circ} \text{C}$. Humidity Index, $K = 5.4$.

it is suggested that Marcus has a relatively dry climate in spite of its oceanic position. Actually, it occupies an intermediate position between Aw and Bs of Köppen's climate formula, although the differentiation of seasons is relatively less conspicuous. According to the climate classification by Kira (1953), who established an excellent climate system based upon two very simple indices, warmth and humidity,³ the island lies at the cool-arid corner of his type B₆ (tropical semiarid climate). From the climographs and hithergraphs shown in Figure 11,⁴ together with those of Chichijima (Bonin Is.), Yap, and Honolulu, the annual cycle can be roughly divided into two seasons, namely, October to April, which is dry, cool, and windy; and May to September, which shows the opposite

³ Warmth Index: $W = \sum_i (t-5)$, where t = mean temperature of each month; i = number of months when $t > 5$. Humidity Index: $K = 2P/(W+140)$, where P = annual rainfall, W = Warmth Index.

⁴ In the hithergraph, high rainfall in July is mainly caused by an abnormally rainy weather in 1953 (500.2 mm.). In other years, 76.8 (1951), 177.1 (1952), 144.7 (1953), and 189.3 (1954), respectively.

trends. Bryan also reported the danger of landing during October to April, because in that season the waves beat violently upon the reefs and shores. This was also confirmed in my trip by the staff of the weather station. As the island is located in the western part of the northeast trade-winds belt, the prevailing winds are from the east, but certain northern trends mingle during October to April. Furthermore, the influence of typhoons, which frequently visit in September and October, must not be overlooked. For instance, the island was completely washed by violent waves from the south to the northwest and eastern shores, when typhoon Sara passed over the island in October, 1951. Maximum wind speed was 40.5 m/s; maximal instantaneous speed, 50.9 m/s; rainfall, 154.9 mm. (For the effects of typhoons, see also the Appendix.)

The climatic features mentioned above may be well explained by the location and topography of the island. Gressitt (1954) mentioned that there was occasionally found a dry local climate within the generally wet, oceanic climate of Micronesia, especially in low islands

and atolls. Its minute size and the poor conservation of water by coral sand may be the main causes of the dry climate of Marcus, as in Wake Island with a similar topography and climate. Consequently, the climate of Marcus is, in spite of its subtropical position, inadequate to support a luxuriant flourishing of organic and ecological diversities. (Rain is the only source of fresh water in the island.)

FLORA AND VEGETATION

The flora of Marcus has been reported by Yabe (1902), Bryan (1903), and Tuyama (1938). The plants collected by me were kindly determined by Dr. Tuyama. They are listed in Table 2, together with those reported by the earlier publications. Comparison of the present flora with those of previous studies will be discussed later. Here the discussion is limited to the plants collected by myself. Judging from

the size and topography of the island, I believe that the collection of the plants which were growing there during my stay is almost complete. It is obvious from Table 2 that the flora is extremely poor both in number of species and in endemism. Most of the species are either cosmopolitan or tropicopolitan, or are those which behave as dominants in many communities because of their great vigor. In other words, we find here no more than a typical example of the poor flora of oceanic atolls.

The structure of the vegetation, too, is very simple. The arboreal stratum was composed of *Messerschmidia* and *Pisonia* mixed in an approximate ratio of 7:3, although the latter was relatively scarce outside the E. triangle (Figs. 1, 4). The density and resulting coverage was highest in the E. triangle and next highest along an abandoned road in the northern section of the NW. zone. In addition to these two dominants, about a dozen papayas were observed

TABLE 2
SYNOPTIC TABLE OF PLANTS RECORDED FROM MARCUS ISLAND

YABE (1902)	BRYAN (1903)	TUYAMA (1938)	SAKAGAMI (Identified by Dr. Tuyama)
Species recorded at least in two occasions			
<i>Tounefortia argentea</i>	<i>Tounefortia servicea</i>	<i>Messerschmidia argentea</i>	<i>Messerschmidia argentea</i>
<i>Cocos nucifera</i>	<i>Cocos nucifera</i>	<i>Cocos nucifera</i>	<i>Cocos nucifera</i>
<i>Morinda citrifolia</i>	Rubiaceae gen. sp.	<i>Morinda citrifolia</i>	
		<i>Carica Papaya</i>	<i>Carica Papaya</i>
		<i>Pisonia grandis</i>	<i>Pisonia grandis</i>
<i>Portulacae oleracea</i>	<i>Portulacae lutea</i>	<i>Portulacae oleracea</i>	<i>Portulacae oleracea</i>
Tobacco	tobacco		<i>Nicotiana Tabacum</i>
<i>Boerhaavia repens</i>		<i>Boerhaavia repens</i>	
		<i>Ipomoea pes-caprae</i>	<i>Ipomoea pes-caprae</i>
		<i>Eleusine indica</i>	<i>Eleusine indica</i>
Species recorded only once			
Graminae gen. sp.	<i>Euxolus</i> sp.	<i>Dactyloctenium aegypticum</i>	<i>Bryophyllum pinnatum</i>
	<i>Panicum pruriens</i>	<i>Setaria lutescens</i>	<i>Pennisetum setosum</i>
	<i>Rottboellia</i> sp.	<i>Syntherisma sangunalis</i>	<i>Cenchrus echinatus</i>
	a low trailing herb	<i>Scaevola frutescens</i>	<i>Erigeron sumatrensis</i>
		<i>Malvastrum tricupidatum</i>	<i>Euphorbia hirta</i>
	an unknown herb	<i>Lepturus repens</i>	<i>E. prostrata</i>
			<i>Sonchus oleraceus</i>
			<i>Boerhaavia diffusa</i>



FIG. 2

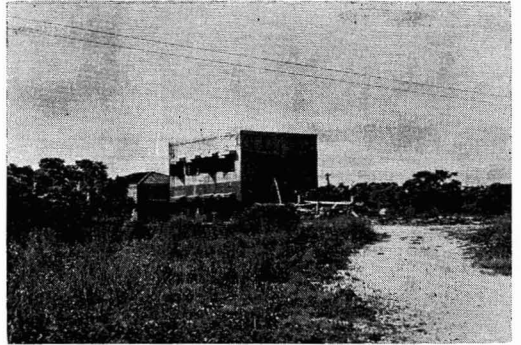


FIG. 5



FIG. 3



FIG. 6

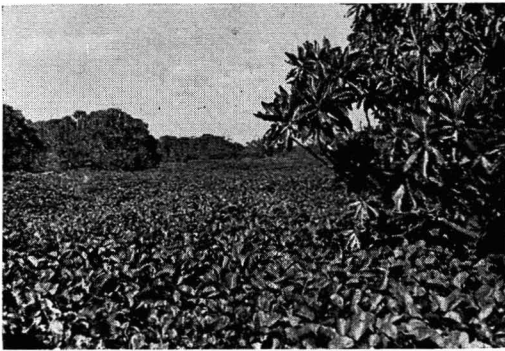


FIG. 4



FIG. 7

FIGS. 2-10. Some topographical and biological aspects of Marcus. Explanation in text.



FIG. 8



FIG. 9

along two paths penetrating the E. triangle (Figs. 1, 8). The coconut palm, which formerly had been the leading member of the arboreal stratum, was represented by only three undernourished saplings, as is indicated by the crosses in Figure 1.

The simplicity of the herbaceous layer was much more surprising. It was practically no more than an overwhelming dominance of *Ipomoea pes-caprae*. The density was also highest in the E. triangle, except its NW. section, but the stout runner extended its domain throughout the island except on the outermost margins of the sandy beaches. In the center of the E. triangle, this creeper constituted a pure community of about 1 sq. km., excluding all other herbs; there one could walk hundreds of meters on a thick bed of intermingled vines, both

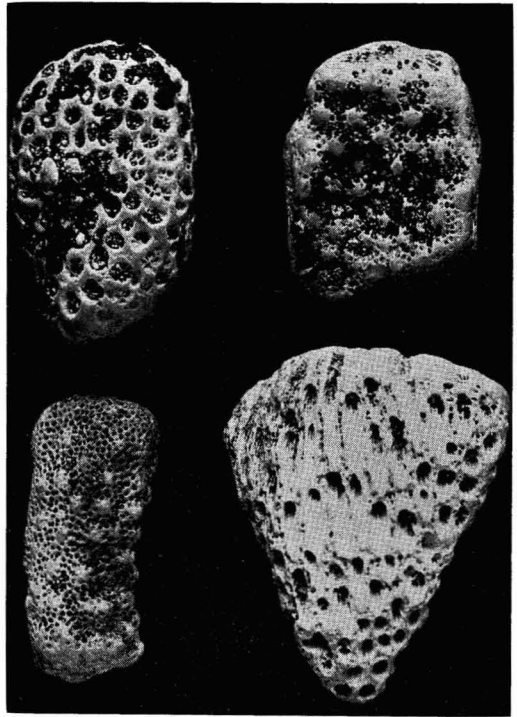


FIG. 10

living and withered, without touching the soil surface (Fig. 4).

Consequently, other herbs and grasses, although most of them were very vigorous weeds, grew only in limited areas, apparently where the pressure of *Ipomoea* was not conspicuous, namely, in wooded edges, roadsides, and the NW. section of the E. triangle. In such zones, *Portulaca* and *Cenchrus* were dominant members of the lower stratum, and *Pennisetum*, *Nicotiana*, *Eleusine*, and *Sonchus* of the higher one. The area richest in species was the confluent point of the runway and the other broad road, where most species of herbs and grasses were collected. On the other hand, no plants other than *Ipomoea* were discovered on the beaches (Fig. 9). From this description, it may be recognized that the island is extremely simple in both floristic and vegetational aspects.

FAUNA

The birds and mammals collected or observed in our survey were described by Kuroda (1954).

All other land animals collected or observed by me, or those later sent me from the weather station, are listed in Table 3, accompanied by notes on distribution and abundance. The following remarks will explain the data presented in the table.

1. The number of species given in parentheses after the names of the major taxonomic groups does not always coincide with the number listed under each group, because the familial characters were not determined for some specimens which were not caught or were lost before or during the preparation of our data.

2. Under the column showing range, the distribution of identified species in other districts is mentioned. In the majority, however, only the pattern of geographic distribution is given, using the following abbreviations: E, endemic at present; C, cosmopolitan; T, tropicopolitan, including Indo-Pacificopolitan; P, Pacificopolitan; and Pa, Palaearctic. These patterns are naturally very conventional, for the distinction among C, T, and P is often subjective.

3. Under the column showing abundance, the relative abundance of each species is shown with marks: ++, very abundant; ±, abundant; +, common; —, rare. The last observation may express not an actual rareness, but only a cryptic life-mode.

4. The distribution and relative abundance of each species in the various habitats (see the definition of A, B, etc., in the next paragraph) are indicated by O (for occurrence) or A (for abundance). Where holometabolic insects are concerned, the distribution is considered only with respect to adults, but in the sphingid and noctuid moths, only with respect to their caterpillars, inasmuch as the adults were collected only at lights.

5. The species observed but not collected are marked with an asterisk, and those which were only indirectly confirmed are marked with a dagger.

DISTRIBUTION OF ANIMALS IN VARIOUS HABITATS

In order to obtain a closer perspective with regard to the ecological distribution of animals listed above, the island was divided into the

following habitat zones, based upon topography and vegetation (Fig. 12).

A: Areas with both arboreal and herbaceous strata (Fig. 4 and Fig. 5, back):

A₁: Floor stratum, including earth surface and sites beneath gravel and stones.

A₂: Herbaceous stratum, consisting of *Ipomoea* foliage alone.

A₃: Arboreal stratum, consisting of *Messerschmidia* and *Pisonia* as dominants.

B: Areas without arboreal stratum, with relatively tall grass and herbs, and with poor development of *Ipomoea* (Fig. 5, left):

B₁: Floor stratum corresponding to A₁.

B₂: Stratum of short grass and herbs.

B₃: Stratum of tall grass and herbs.

C: Areas with short grass and herbs alone; *Ipomoea* cover is more developed than in B (Fig. 5, middle):

C₁: Floor stratum corresponding to B₁.

C₂: Stratum of grass and herbs.

D: Areas largely exposed, with patchy development of grass and herbs; *Ipomoea* cover less developed than in C:

C' (C'₁ and C'₂): Littoral zones corresponding to C and D

in habitat structure.

However, C'₁ consisted of scattered

establishments of *Ipomoea*

frontiers alone, and D' is almost aphytic.

H: Areas disarranged by human activities.

The relative size of these habitats was approximately A greater than or equal to C' approximately equal to D' > D > B approximately equal to C. The richness of each habitat in number of species and in ecological endemicity may be roughly estimated by comparing the total species number with the number of species found exclusively in each habitat (see Table 4). Conclusions derived from these data are:

1. With respect to vertical distribution, the floor strata are far richer both in species number and in ecological endemicity than are the upper strata. Apparently, this is caused by the poor development of vegetation in the latter.

2. Horizontally, A is the richest section in

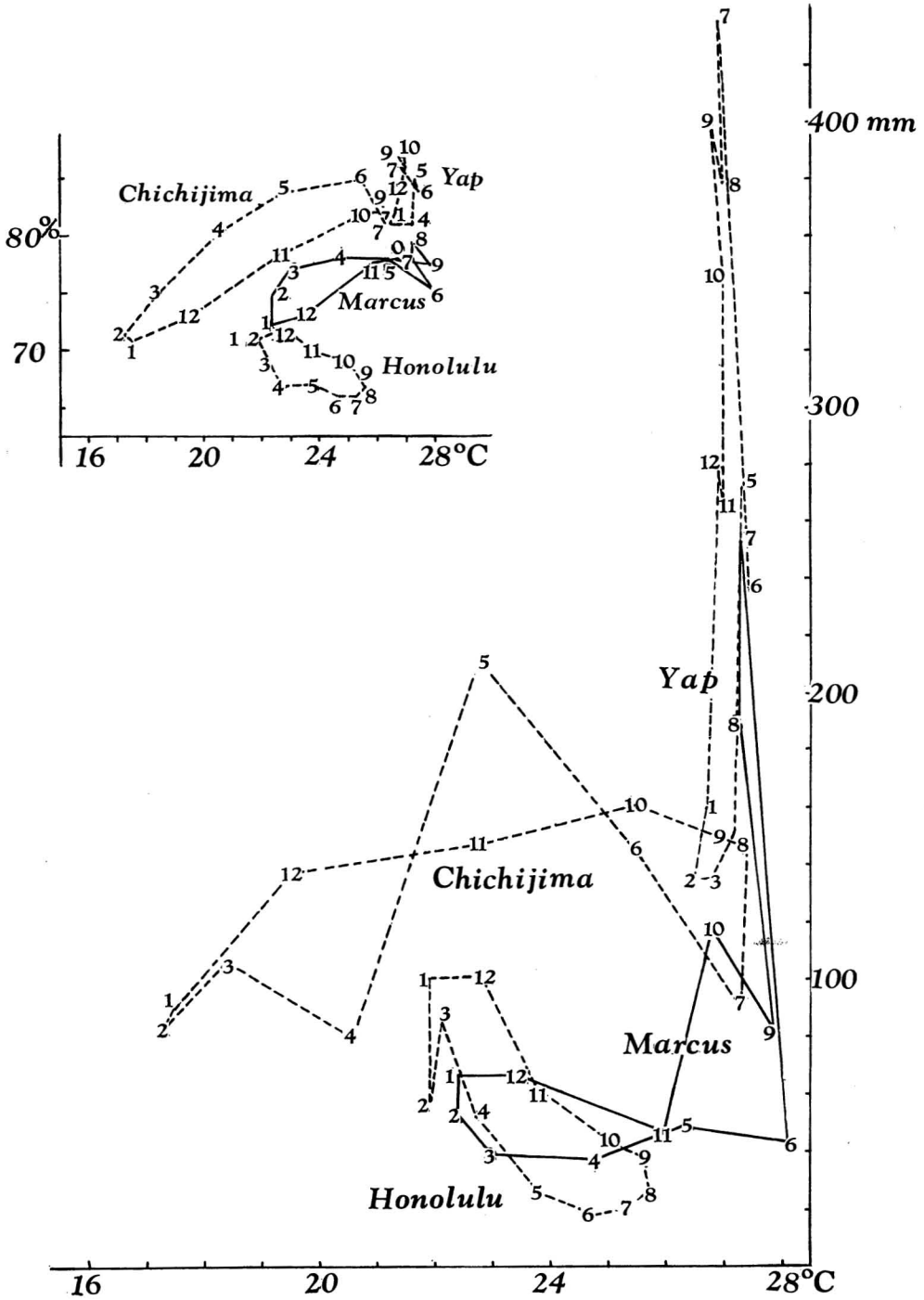


FIG. 11. Climograph (above) and hithergraph of Marcus, Chichijima (Bonins), Yap, and Honolulu.

both species number and ecological endemism. This is natural because this habitat occupies more than half of the island and is biologically the most productive and stable zone. It must be mentioned, however, that A has a relatively poor fauna, depending on its very simple vegetation, as in C'_2 .

3. D' is obviously the poorest habitat because of its aphytic conditions; this conclusion, of course, pertains only to our observations upon the macroscopic animals. Bio-economically, this habitat really is the front of the marine littoral ecosystem extending into the land. On the other hand, the relatively rich number of species found in B and C, in spite of their small size, is apparently due to their ecotonal character.

4. The poor differentiation of C_1 and B_1 (compare the two serial orders in Table 4) may be understood if these strata are considered as a mere extension of an ecological gradient, of which the peak lies in A_1 . The structure of the floor fauna varies, therefore, at first when the plant cover almost disappears in D. C'_1 has also a few characteristic species corresponding to its littoral nature.

DESCRIPTION OF EACH HABITAT

The several habitats distinguished above must not be considered to be like cages or walled areas which confine various inhabitants within them. They are merely devices of a coordinated system for the clear understanding of the ecological make-up of the island. Eventually, certain species pass freely from one habitat, or from one stratum, to another. Before describing each habitat and its inhabitants, brief notes will be given concerning these mobile species.

The rat, *Rattus rattus* ssp., is the only mammal inhabiting the island. Formerly, the staff of the weather station kept cats which controlled a considerable number of rats. In the absence of any intensive controls, the rats are now fairly abundant and their activities were traced everywhere in the island.

The skink, *Cryptoblepharus*, and the land crab, *Geograpsus*,⁵ were also seen everywhere, except

⁵ As most recorded genera are represented by a single species, only generic names will be given in the following descriptions.

B_3 and D' in the case of the former species, and except B_2 , B_3 , C_2 , C'_2 , and D' in the latter one. Both can climb up *Messerschmidia* and *Pisonia* to fairly high twigs. They even appear in the upper stories of buildings: crabs were often observed when they were crawling up vertical walls nearly to the ceiling. It is certain that these animals, one as a predator and the other as a scavenger, play important roles in the bio-economy of the island.

Two ants, *Lasius* and *Tapinoma*, may be added to the list of widely roaming species. They were observed utilizing the runners of *Ipomoea* to invade even into area C'_2 , where other animals were scarcely seen. Although it is a relatively sedentary creature, a cricket, *Landreva*, was collected in almost every floor stratum except C_1 and D' . Its songs could be heard in the daytime, but they were more impressive at night, dominating this tiny bit of land in the midst of the immense ocean.

Setting these mobile species aside, some characteristic features of each habitat will be outlined.

Zone A is the largest, richest, and most stable habitat in the island. This is also the only area where the formation of humus is relatively conspicuous. Consequently, because of the lodging it affords various cryptic animals (roaches, land-isopods, myriapods, etc., under stones, *Oxydema* in decayed wood), A_1 has the richest fauna in the island. A_2 consisted of *Ipomoea* foliage alone. *Sphinx*, *Prodenia*, and *Coccus* were the major pests of the vigorous creeper. *Prodenia*, especially, was locally very abundant, and considerable damage was observed, as is shown in Figures 6 and 7.

Locusta and *Utetheisa*, both feeding on *Messerschmidia*, surprised us by their spectacular abundance. The adults of *Utetheisa* are active irrespective of diurnal rhythm. In daytime, they were seen everywhere in the A zone, feebly fluttering from one tree to another. At night they swarmed abundantly around lamps. The first instar larvae live concealed within the young sprouts (Fig. 14); older ones feed on exposed leaf surfaces, and pupae are seen near the tips of leaves, in a thin hammock spun by themselves (Fig. 13).

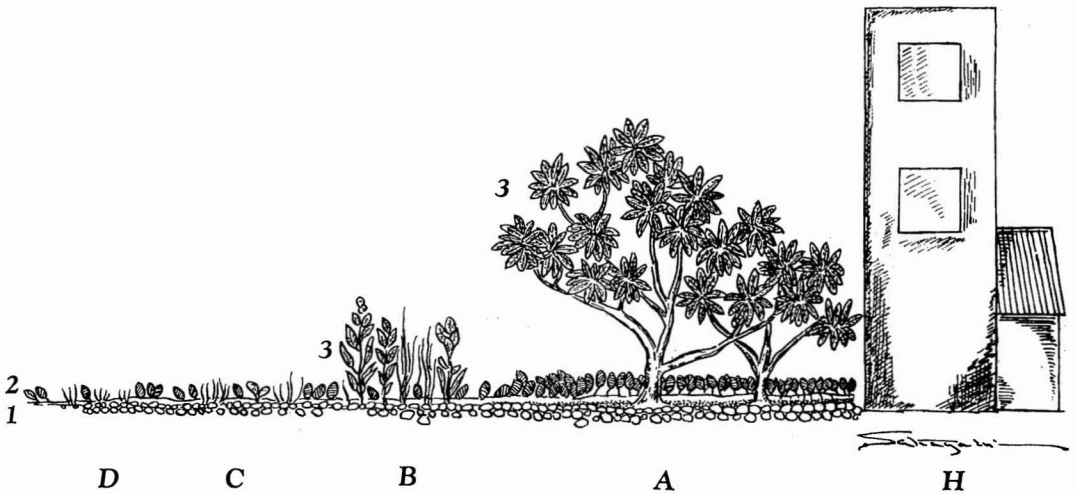


FIG. 12. Distinction of various habitats based upon vegetation and topography.

Adults and nymphs of all stages of *Locusta* were collected on *Messerschmidia*. From their extreme abundance, high activity, and great voracity, I have the impression that this population might change from *phasis solitaria* to *phasis transiens*. Inside still younger buds of *Messerschmidia*, a small cricket, *Ornebius*, was often discovered. They always directed the head and antennae upward (Fig. 15), and when disturbed rolled down very quickly into the earth.

Coccus were also found in *Pisonia* and, especially in papaya, were eagerly visited by two milkers, *Lasius* and *Tapinoma*. Moreover, various flies and their predators, *Heteropoda* and *Neoscona*, were abundant throughout the arboreal foliage. Considerable numbers of the latter species were found in nests of an introduced American wasp, *Sceliphron*.

Corresponding to their ecotonal nature, B and C were relatively rich in number of species but possessed only two characteristic bugs: *Cyrtopeltis* on tobacco and *Liorhyssus* on *Sonchus*. The activities of skinks and land crabs decrease in B due to a relatively thick growth of herbs and grass but increase again in C. The most characteristic species in these transient zones is *Aiolopus*, which, in contrast to its cousin, *Locusta*, does not invade zone A.

Aphis and its predator, *Ischiodon*, were found in this zone on *Portulaca*, the dominant plant

in C and D, although the former species was found in zone A as milk cows inside a nest of *Tetramorium*. *Solenopsis* was also found only in this zone.

With the further decrease of plant cover, animals adapted to bare surfaces appeared in D. The characteristic species was *Oligotoma*, which was extremely abundant in runways and adjacent exposed areas, dwelling in a characteristic nest spun by themselves (Fig. 16). If they were driven away from the nest, they were hunted by *Lasius* as soon as they were discovered by this ant. At night, winged adults were collected around the lamps situated near the runway.

Zones C' and D' are reproductions of C and D in the littoral zone. A characteristic animal assemblage was collected under the stones and large gravels in C'₁: it consisted of *Geogarypus*, an oribatid mite, two collembola, myriapods, etc. On exposed surfaces, however, there were very few animals, except for *Lasius* and *Tapinoma* walking on the runners of *Ipomoea*. D', especially, was macroscopically a complete abiotic zone. The only animals collected were *Anisolabis*, found under the decayed matter. Although it did not belong to the land biota, an endemic marine collembola, *Polyacanthella oceanica* Uchida, was discovered at the northern rocky reef of the NW. shore, together with some polychaetes, crabs, etc. According to a

staff member of the weather station, a marine strider seems to occur in the lagoon.

The area receiving direct human influences possesses no more than a well-known assemblage of domestic species. The number of species is far less than that found in similar environments on continents, but, reflecting the diversity of environmental conditions, it is fairly large in comparison with other habitats, in spite of the small space. A rat, two roaches, some domestic flies as omnivorous scavengers, two granary beetles, and domestic silver fish, *Ctenolepisma*, were the chief members in or around the weather station and accompanying buildings. Skinks, land crabs, and the two ants invaded all buildings. Gecko and *Heteropoda* lived there as residential predators, although they were found in the A zone, too. Earthen nests of *Sceliphron* were abundant on ceilings, walls, and other parts of buildings. In a ruined cottage standing near the northern point of the island, a fairly large compound nest containing 62 cells was observed attached to a broken chimney (Fig. 17). In other nests, the number of cells counted was as follows: 1 cell alone (1 instance), 2 cells (3 instances), 3 (4), 6 (3), 7 (1), 8 (1), 12 (3), 14 (1), 30 (1), 57 (1).

Numerous dead insects were observed in window screens of the dining room, etc., due to treatment with DDT. Examination of these accumulations showed an overwhelming abundance of *Atherigona*, although the main species found within the dining room during our stay were *Musca*, *Lucilia*, and *Sarcophaga*.

SPECIES	INDIVIDUAL NUMBER (Sexes not separately counted)
<i>Atherigona excisa</i>	1,505
<i>Drosophila melanogaster</i>	43
<i>Lucilia sericata</i>	22
<i>Aneurira</i> sp.....	22
Dolichopodidae gen. sp.....	18
<i>Parasarcophaga misera</i>	16
Agromyzidae gen. sp.....	13
Sphaeroceridae gen. sp.....	10
<i>Musca domestica</i>	4
<i>Tribolium castaneum</i>	3
Ephydridae gen. sp.....	2
<i>Gardiastethus fulvescens</i>	1
<i>Lasius niger</i> ssp.....	1
A micro-moth.....	1

All of the moths listed in Table 3, as well as *Oligotoma* and *Eobia*, were attracted to lamps. Because of its oedemogenic secretion, *Eobia* is the only insect species injurious to human beings. No fleas, mosquitoes, or blackflies occur on the island.

After this brief sketch of the different habitats, a mystifying fact must be mentioned: a dragonfly, *Diplacodes bipunctata*, occurred on the island, even in the absence of fresh water. The adults of this species appeared a considerable time after our visit. I observed only a single specimen, at a passway penetrating the E. triangle, but a staff member of the weather station repeatedly confirmed the appearance of numerous dragonflies, and later he kindly sent me the specimen which was identified. If this species multiplies on the island, then not only must fresh water be available somewhere but also a number of aquatic organisms to be preyed upon by its nymphs. In the absence of any evidence of fresh water, the only other explanation must be the seasonal migration of this relatively delicate species across thousands of kilometers of ocean—although this is an explanation that I myself find hard to believe.

FURTHER ECOLOGICAL NOTES

Ecological interactions among various organisms in a given area, however few there may be, are always difficult to demonstrate clearly. But, the uncomplicated environment and simple biota of Marcus permit schematizing it as in Figure 18. Even if the schema is still far from complete in many points, the principal courses of biotic energy-flow in the island are obvious and may be classified into two major groups with respect to the energy sources: those starting from green plants, and those from the products of human activities. The two groups are relatively independent of each other, although, as discussed later, many elements constituting the former group were brought to the island by various human activities. As a glance at the figure will show, the extreme disharmony between the food chains and the occurrence of numerous unoccupied niches is impressive. The extraordinary abundance of a few dominant species depends, without doubt, on this too

simple bio-economic structure. Such disharmony, a common feature of remote oceanic islands, is also recognized by comparing the number of genera and species occurring upon the island. Except for birds, the total number of families, genera, and species of land animals is 54, 70, and 72, respectively. Only seven families contain more than two species: the Blattidae (5 spp.); Formicidae (4 spp.); Porcellidae, Entomophryidae, Lygaeidae, Noctuidae, and Muscidae (2). There are only two genera containing two species: *Periplaneta* and *Porcellio*.

In connection with this disharmony, it may be interesting to consider here the association of closely related species, for it has often attracted the attention of ecologists on account of competition or isolation. However, most species belonging to families represented by more than two species show obvious habitat-segregation. Species found in one and the same habitat were *Leucophaea* and *Blatta*, *Anisolabis* and *Euborella* in A₁ and D; two species of *Periplaneta*, *Lucilia*, and *Musca* in H; two *Porcellio* in A₁; *Sira* and *Lepidocyrtus* in C₁; *Lasius* and *Tapinoma* almost everywhere. But, most of them differ from each other either in habit, as in the two ants mentioned above, or in their relative abundance in various habitats. Those species possessing similar habits, eating similar food, and collected from the same habitat were only two pairs of cosmo- or tropico-

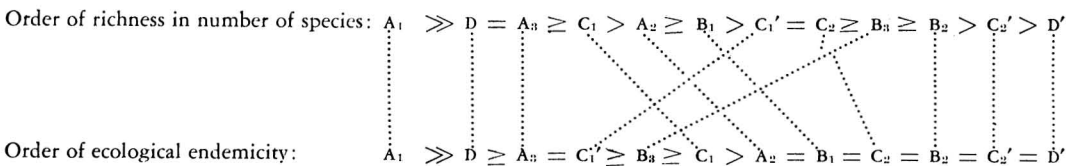
politan species, *Musca* and *Lucilia*, and two *Periplaneta*.

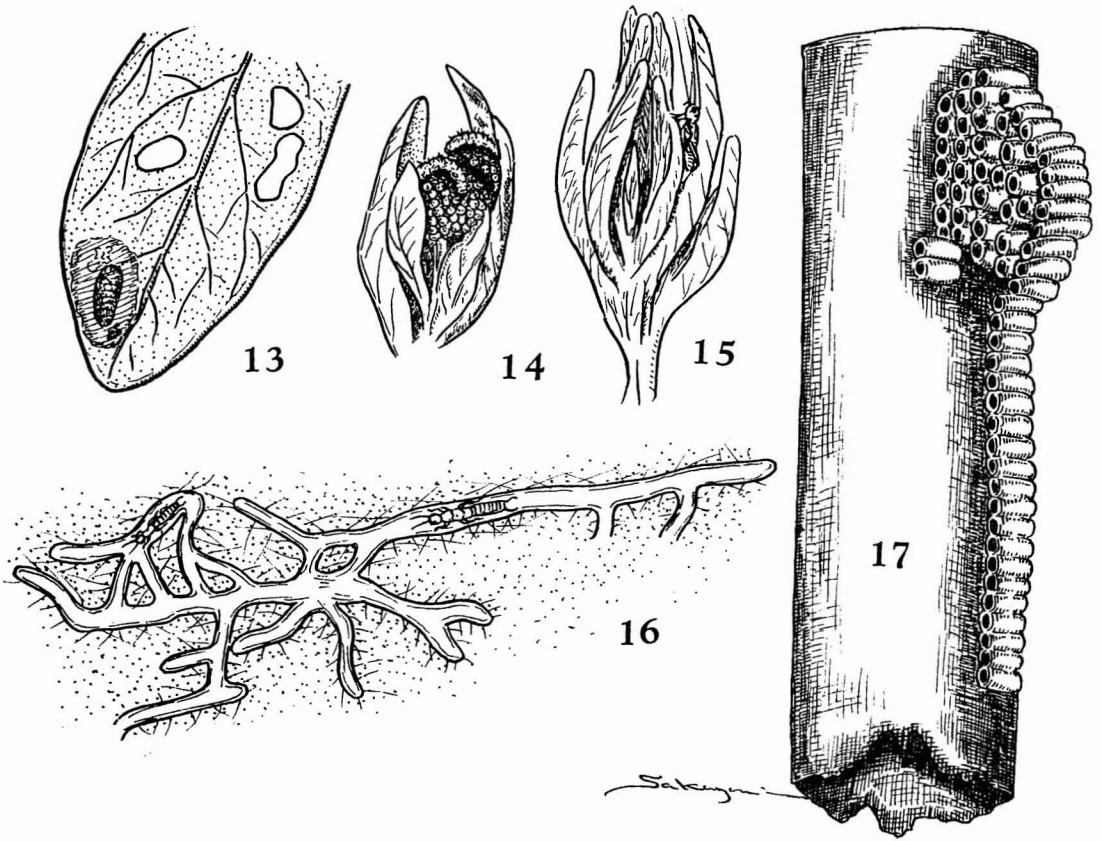
In former times, the island offered a favorable breeding site for various sea birds. Subsequent reckless catching resulted in a rapid decrease of both the species and numbers of individuals. During our visit, two species, noddy terns and sooty terns, still bred on the island. Moreover, about 20 golden plovers and five American wandering tattlers were seen. Of these birds, only the plovers may have an intimate relation to the land biota. They were seen usually on the surface of the runway or on other roads through the E. triangle. According to Kuroda (in litt.), some vegetable matter was found in their crops. On the other hand, he did not find any food other than cuttlefish in the crops of the terns. Therefore, terns and tattlers are connected intimately to the marine ecosystem but possess little relation to land biota.

Finally, some phenological trends are cited here, based upon the experience of the weather station staff (especially of Messrs. Y. Nakada and K. Fujisawa), as follows: Fructification of papaya, September to October; flowering of *Ipomoea*, April, and September to October; flowering of *Messerschmidia*, March to August; nymphs of *Locusta*, seen throughout the year, but abundant during July and August; *Diplacodes* adults, June to July, and September to October; larvae of *Herse*, throughout year, but

TABLE 4
NUMBER OF SPECIES FOUND IN EACH HABITAT
(Those in parentheses were found exclusively in that habitat.)

VERTICAL DISTRIBUTION	HORIZONTAL DISTRIBUTION							TOTAL
	A	B	C	D	C'	D'	H	
1	27 (15)	13 (0)	19 (1)	20 (4)	10 (3)	1 (0)		45 (35) } 29 (9)
2	14 (0)	7 (0)	10 (0)		3 (0)			
3	20 (3)	9 (2)						
Total	47 (19)	21 (2)	23 (1)	20 (4)	10 (3)	1 (0)		





FIGS. 13-17. Some aspects of insect life on Marcus. Explanation in text.

abundant in June; assemblage of *Eobia* in lamps, May to June, and August to October.

These data are still insufficient but indicate the monotonous and inconspicuous phenological trends on this island. This may be also recognized from the occurrence of all developmental stages of *Locusta*, *Landreva*, and *Utetheisa* during our short stay.

BIOGEOGRAPHICAL REMARKS

Marcus is of little interest from the point of view of regional biogeography. According to Tuyama, who not only identified all plants collected by me but also kindly informed me of their distribution and ecological characteristics, all the plants are species of wide distribution

and high vigor. After comparing the very simple flora of Marcus Island with that of the Bonin Islands—where 46 per cent of a total of 321 species are endemic, and where five endemic genera are found (Nakai, 1930)—it is probably futile to discuss the phytogeographical position of Marcus.

The same conclusion can be applied to land animals. According to Gressitt (1956), the island belongs by its location to the Oriental Zoogeographical Region, Polynesian Subregion, Division Polynesia Proper, and Subdivision Micronesia. But the order of frequency of the various distributional patterns is: Tropicopolitans (including Indo-Pacificopolitans) (18 spp.); Cosmopolitans (13); Pacificopolitans (6); Pan-Palaearctic (5); Endemic (4); Species with a

limited range (4). Distinction of these patterns is rather arbitrary but may be sufficient to conclude that most of the species belong to types which can hardly be said to be the regional, although in general the Oriental elements are predominant.

It is remarkable that four endemic terrestrial species, one centipede and three pseudo-scorpions, were discovered upon this tiny island. One of the latter group, *Lechytiia sakagami* Morikawa, is very interesting because it belongs to a genus which, up to the present time, has been recorded only from Nearctic, Neotropical, and Ethiopian regions (Morikawa, 1952).

FORMATION OF LAND BIOTA

The land biota described above has been compared to the earlier results published by Yabe (1902), Yoshida (1902), Bryan (1903), and Tuyama (1938). The plant species reported by those writers and by me are given synoptically in Table 2. From this table and from information kindly given me by Mr. Matsubara, the commander of Japanese Marcus Garrison during World War II, we can trace the floristic change of the island during the last 50 years.

With respect to trees and shrubs, only *Cocos* and *Messerschmidia* have continued to exist throughout half a century. This combination, one of the commonest edaphic climaxes on sandy beaches of the Pacific islands, in all probability had been already well established when the island was discovered. Later, but before 1938, the island received *Pisonia* as a new member of its flora, and it is now a chief member of the vegetation. On the other hand, *Morinda* disappeared between 1938 and 1940, because this was reported by Tuyama but not by Matsubara. Although still surviving at the present time, the coconut palms received remarkable damage from human interference (cf. Appendix). When Bryan visited the island in 1903, palms grew densely in the central area of about 3 acres. According to Matsubara, there were only 30 trees, about 4.5 m. high, when he arrived upon the island in 1941. Half of them were cut down at the end of that year. Moreover, as seen from the Appendix, all trees on the island were completely damaged by repeated bombing during

the war. The present arboreal stratum is, therefore, the outcome of postwar regeneration.

The origin of papaya now existing in the island is obscure. Bryan gave seeds of various plants, including papayas, to the Japanese inhabitants when he left the island. Later Tuyama reported this plant from the island. But no papaya trees were growing in 1941 according to Matsubara. He planted a few seeds in 1945, and some seedlings grew to the height of a child before being damaged by bombing. The plants now growing in the island seem to have been brought in by the U. S. Navy after the war.

Of the herbs and grasses, tobacco and *Portulaca* are the only species reported by all writers, including myself. Judging from the small size and simple topography of the island, which permit one to walk around it within 2 hours, it is hard to believe that any abundant plant species escaped the eyes of other collectors.⁶ Therefore, the lack of accord among four collections suggests the unstable character of the herbaceous strata, with new inhabitants appearing and being replaced in their turn by other ones, under the influence of human activities during the last 50 years. *Ipomoea* was first reported in 1938, but Matsubara wrote me that in 1943 it was found only in scattered patches on the island. The overwhelming dominance of this species throughout the island at the present time is, therefore, a postwar event.

Previous information concerning land animals is scanty. The most important change may be the extinction of numerous sea birds which bred on the island. A catastrophic decrease may well be recognized if the report of Bryan (1903) is compared with that of Kuroda (1953).

With respect to other land species, Yoshida (1902) briefly described a skink, gecko, "flies," "red moths," and "small flies." Bryan also reported a skink (*Ablepharus boutonii*) and a gecko (*Perochirus articulatus*). Therefore, both have been constant inhabitants during 50 years, although their scientific names have been changed since Yoshida's visit. Among three land crabs mentioned by him—*Grapsus grap-*

⁶ Actually, except for *Bryophyllum*, all of the plant species collected by me were discovered on the first day of our survey.

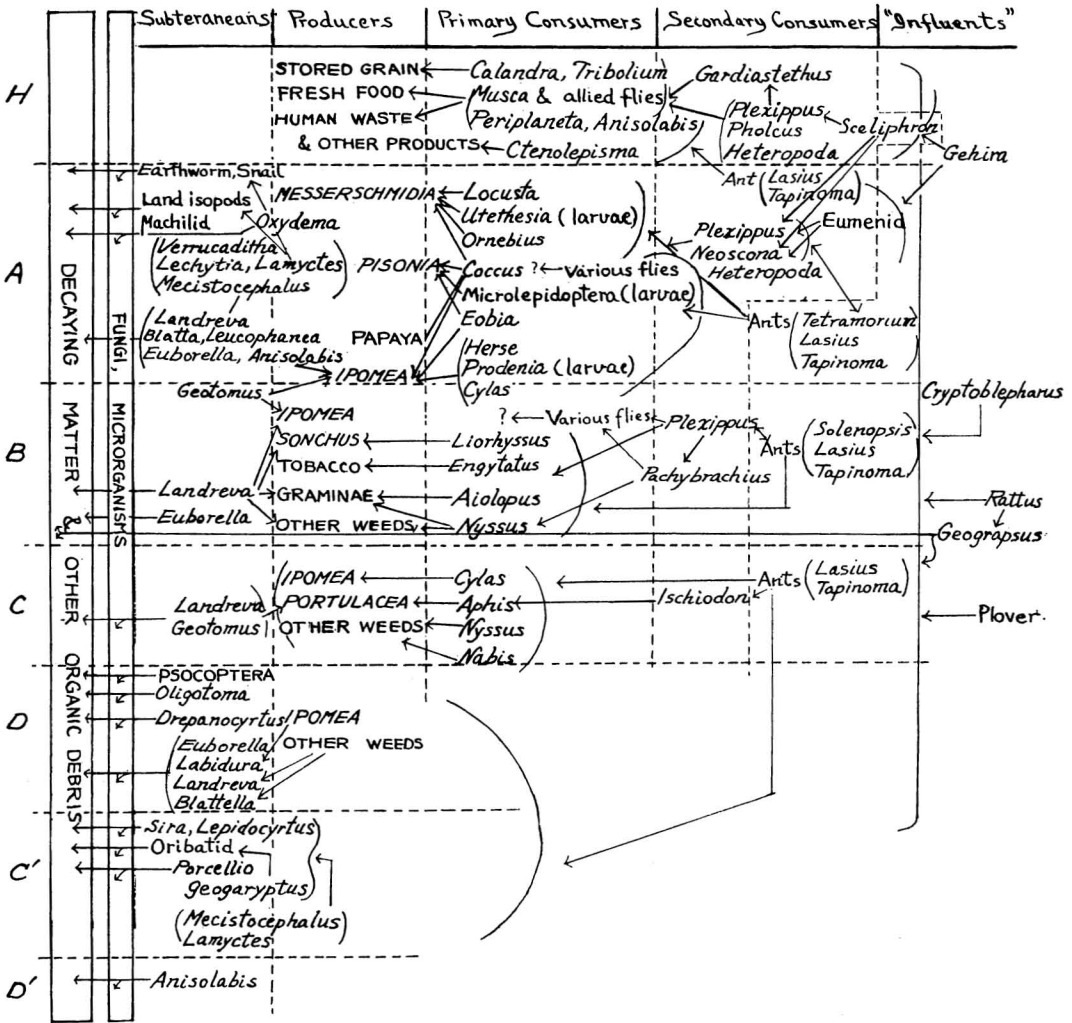


FIG. 18. Food-nexuses in Marcus Island.

sus (abundant), *Geograpsus crispipes* (less abundant), and *G. grayi* (abundant)—only the last species still remains on the island. According to a personal communication from a staff member of the weather station, he is sure that at least one species of land hermit crab still exists on the island. But it is uncertain whether this species is either *Coenobita olivieri* or *C. compressa* reported by Bryan, for no specimens were collected by myself.

It is very regrettable that Bryan's collection of insects, which he made by various methods (including lantern collecting, barking, attract-

ing with decaying flesh, etc.) was damaged by ants and other pests during his return voyage. His miscellaneous notes based upon memory are so interesting, however, that I will cite them here:

A small red ant was quite common as well as troublesome, especially about the settlements. I fancy it had been imported since the colony was established. Two species of flies were very abundant, one a blowfly (*Calliphora*?) which persisted in laying its eggs on the birds both before and after they were skinned; the other species, a small vinegar fly of a genus unfamiliar to me,

...were to be seen in moist, shady places all over the island. A small miller was common during the night, and I am of the opinion that the skinks and geckos feed on it as well as on the small flies just mentioned....

The only spider that had established itself was the widely distributed web-spinning species, *Epeira nautica*.... Trees and grass showed little or no signs of insect pests. In fact, I found only one species of plant that had been molested by biting insects. Since these depredations were to be seen only in a very limited area, and as I was unable to secure the miscreant either by day or night, I concluded the species must have been a recent Japanese introduction that had not had time to thoroughly establish itself. No species of Coleoptera were secured [pp. 117-8].

No land shells were noted, and I believe there were none [p. 120].

Believing that a collection of any earthworms that might occur on the island would be of interest I requested Mr. Sedgwick and his assistants to keep a close lookout for them. Although they made a large number of excavations in various places while prosecuting their investigations, they were unable to discover a single specimen.... I am persuaded that worms of this class have not as yet found their way thither [p. 122].

Compare these citations with results obtained by me, and remember that both surveys were made approximately in the same season and during the same interval (cf. Appendix, 1902). It may be assumed that, in all probability, many species now inhabiting the island were established there after 1902.

Only *Neoscona theisi* (Walckenaer) (= *Epeira nautica* Bryan nec Koch) and, seemingly, some domestic dipterans are the inhabitants collected in both surveys. It is not certain whether Bryan's "red, small ant" corresponds to any of four ant species collected by me or not. But it surely differs from *Lasius niger*, the commonest ant in 1952.

Consequently, judging from their conspicuousness and present abundance, the following species may safely be regarded as immigrants since 1902:

Plexippus paykulli *Prodenia litura*
Heteropoda venatoria *Herse convolvuli*
Periplaneta americana *Sceliphron caementarium*

P. australasiae *Lasius niger*
Landreva clara *Calandra oryzae*
Locusta migratoria *Cylas formicarium*
? *Allolobophora* sp. *Tribolium castaneum*
A land snail *Eobia chinensis*

Although with less certainty, the following species are also assumed to be relatively recent immigrants:

Armadillo sp. *Anisolabis martima*
Ctenolepisma villosa *Aiolopus tamulus*
Euborella annulipes *Oligotoma saundersi*

It is uncertain whether or not a "red moth" mentioned by Yoshida corresponds to *Utetheisa*. But, from Bryan's notes, it is highly probable that the number of individuals was very small, even if this species was present in 1902.

Matsubara wrote me only about the skink, gecko, land crab, flies, and cricket as being the impressive animals during his wartime service. From these accounts, we can assume that *Landreva* was established before 1943. On the other hand, *Locusta*, *Eiobia*, and *Periplaneta* must have arrived after World War II, for these animals, if they occurred, certainly would have attracted the attention even of persons not biologically observant, either by their conspicuousness (as in *Locusta*) or by their sanitary importance. Needless to repeat, the species now most abundant are, in general, the relatively recent immigrants.

Thus, most members of the land biota of Marcus are immigrants since 1902. Considering the extremely isolated location of the island, it must be obvious that most of these species gained their chances to arrive on the island and to establish themselves there only through direct and indirect human interference at the island. My conclusion, therefore, is that the present land biota is, in its origin, largely an outcome of human activities directed upon the island.

CONCLUDING REMARKS AND GENERAL CONSIDERATIONS

In connection with the zoogeography of Pacific islands, Gressitt (1956) gave an appropriate summary on the nature of land fauna in

low coral islands: "Atolls and other low coral islands have a small fauna—similar in widely separated groups of islands—which is limited by the lack of ecological diversity, the limited haplophytic strand flora, the presence of brackish ground-water, the scarcity of soil, and exposure to salt-spray."

The land biota of Marcus, with its extreme poverty in both taxonomic and ecological components, offers nothing other than a very typical example of Gressitt's generalization. He also wrote: "The extent of speciation is directly related to the island's age, size, isolation and diversity of environment." This proposition can be applied to biocoenology if the word "speciation" is replaced by the phrase "differentiation of ecological components." On Marcus Island the isolation is fairly great, but its size and its diversity of environment are incomparably small to be able to promote any ecological differentiation. Moreover, this isolation may modify a given biota only when human interference is absent or at least negligible, because this factor acts, however locally, with an incomparably more rapid tempo and more violent means than do other natural agents. It would be rather surprising if Marcus Island had maintained any ecological peculiarities—even if such had existed in this most simple environment—despite the accumulation of various human interference during 50 years, including intensive skinning, coconut collecting, public works which modified the appearance of the island, a high human population during wartime (when 4,000 persons were living on this mere heap of coral sand and pebbles), and, finally, violent bombing.

However, although Marcus Island may be little more than a disappointment to biologists who approach the island to study its flora or its biogeography, investigation of such an undifferentiated biota does reveal some important problems, as follows:

1. Our knowledge of the ecology of Pacific islands, as mentioned by Gressitt (1954), is still very far from complete. In this account, the study of a relatively simple biota as that of Marcus may serve as a useful guide either to study more complex biotas or to find general principles underlying their diversities.

2. Considering the fact that any given ecological assemblages, either simple or complex, consist of interactions among numerous parts and processes, it is obvious that the analysis of such entities is far easier to do in simpler biota than in more complicated ones. It should be remembered that, while we may be interested in discovering any specificities and comparing them with each other, we must always seek general rules governing such specificities.

3. Because of their extreme isolation, ecological simplicity, and lack of industrial importance, the remote low islands such as Marcus may serve as the best laboratories in field ecology for the study of the intra- and inter-specific ecology of given species, both native and purposely introduced, as living isotopes. The clarification of land biota should be a prerequisite for such experimental studies.

ACKNOWLEDGMENTS

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The survey was made with the permission of Dr. S. Wadachi, Head of Central Meteorological Observatory in Tokyo, aided by numerous staff members of the Observatory, especially Mr. N. Yamada, Chief Secretary, Mr. Y. Nakada, Head of the Remote Islands Section, Mr. T. Doi, Head of the Supply Section, Mr. H. Hasegawa of the Entomological Laboratory, the National Institute of Agricultural Sciences, Tokyo, and Mr. H. Okuyama, Botanical Laboratory of the National Science Museum, Tokyo.

The specimens collected by me were identified by the following gentlemen, who also gave me valuable information on the distribution and habits of the species collected: Mr. T. Aoto (Reptilia), Dr. S. Asahina (Odonata), Mr. S. Ehara (Acari), the late Dr. T. Esaki (Embiop-tera), Mr. H. Hasegawa (Heteroptera), Mr. K. Hori (Muscidae and Sarcophagidae), Dr. A. Kawada (moths), Mr. S. Kato (Anthomyidae), Mr. M. Konishi (Cossoninae), Mr. K. Kosugi (Coleoptera), Mr. Y. Miyoshi (Myriapoda),

Mr. K. Morikawa (Cheriferidea), Mr. M. Moritsu (Aphidae), Dr. T. Nakane (Coleoptera), Mr. N. Nozawa (Orthopteroidea), Mr. H. Nishijima (Diptera), Dr. S. Saito (Araneae), Dr. T. Sakai (land crabs), Dr. T. Shiraki (Orthopteroidea), Dr. R. Takahashi (Coccidae), Dr. K. Tsuneki (ants), Dr. H. Uchida (Apterygota), Mr. T. Yaginuma (Araneae), Dr. E. Yamaguchi (Oligochaeta), and Dr. T. Tuyama (plants).

Some names have been added or changed on the basis of studies done upon the insects of Micronesia by J. C. M. Carvalho, H. G. Barber, and H. de Souza Lopes not cited in my references.

Valuable information on the animals and plants during wartime was obtained from Mr. M. Matsubara, the commander of the Japanese garrison on Marcus Island during World War II. Messrs. Y. Nakada and K. Fujisawa of the Remote Islands Section of the Observatory gave me suggestions on the land biota. Dr. T. Kira of Osaka City University kindly answered my inquiries on the climatic and vegetational features of the island.

Suggestions for improving the manuscript were given by Dr. J. L. Gressitt of the Bernice P. Bishop Museum, Honolulu, based upon his wide biological knowledge on the Pacific islands.

I should like to express my sincere thanks to all of these gentlemen, whose help was indispensable in preparing the present paper.

SUMMARY

Based upon information obtained directly during the period from April 30 to May 6, 1952, and from previous works and personal communications, a general perspective of the land biota of Marcus Island in the western Pacific is outlined. As might be expected from the small size and lack of environmental diversity, the land biota shows the typical poor structure common to low reef islands of the Pacific. Most constituents of the biota seem to have been introduced during relatively recent years, probably aided by direct and indirect human activities upon the island.

APPENDIX

AN ANNOTATED HISTORY OF MARCUS ISLAND

As mentioned by Bryan, the discovery, naming, and early history of the island cannot be thoroughly traced in the obscurity of the chronicles from the last century. The following table was prepared from the accounts of Yoshida (1902), Bryan (1903), and Shiga (1903), and from personal communications from Mr. Matsubara and staff members of the weather station.

Before 1860: Some reports of Pacific whalers give some information on the island, but with much confusion about its name and location (Bryan).

1868: Captain Kilton, aboard the "David Hoadley," visited in May and described the place as a low sandy island covered with trees and bushes (Bryan). Discovered in this year by an American, and thereafter visited occasionally by French and British ships (Shiga).

1874: U. S. survey ship "Tuscarora" (Commander Belknap) visited. The Hawaiian Mission ship "Morning Star" (Captain Gelett) visited and reported a dense cover of trees and shrubbery, with a white sandy beach (Bryan). Tsunetarô Shinzaki visited as a passenger in a British ship (Yoshida). This was the first visit by a Japanese (Shiga).

1889: Captain Rosehill landed in June while engaged in trading in the Pacific. He recognized the island's value as a source of coconuts. Believing himself to be the discoverer, he claimed it for the United States (Bryan, Yoshida).

1896: A stone lantern (Ishi-dôrô), with an inscription of February 12, 1896, written in Japanese, existed on the island until its destruction by U. S. bombers during World War II (Matsubara). Shinroku Mizutani, Chief of the South Sea Section, Tokyo Animal Company (Tokyo Kinjû Gaisha), while he was a sailor aboard the "Tenyû-maru," was cast ashore in a storm (Yoshida, Matsubara).

- 1898: In July, the Tokyo Prefectural Office claimed the island as a Japanese dependency, named it Minami-Torishima (South Bird Island), and incorporated it into the Ogasawara Section (the Bonins) of Tokyo Prefecture (Yoshida). In September, tenating the island from the Tokyo Prefectural Office, Shinroku Mizutani began the skinning of sea birds, aided by the investment of Shichigorô Kamitaki, a trader in Yokohama (Yoshida). Haruzo Ogawa, a lieutenant in the second reserve of the Japanese Navy, called the inhabitants of Hachijôzima and of the Bonins to Marcus Island for help in skinning the sea birds (Matsubara).
- 1899–1902: According to grave posts (now missing), three Japanese died in the island during these years (Matsubara).
- 1901: In October a violent typhoon attacked the island for 10 days, sending the sea as far as 22 ft. above the normal level (Bryan).
- 1902: Hearing of Captain Rosehill's expedition (see below), the Japanese Government sent the cruiser "Kasagi" to the island. Akiyuki Toyoguchi, a sub-lieutenant, landed with 15 men (July 27). Captain Rosehill arrived at the island on July 30, accompanied by Dr. Bryan and Mr. Sedgwick, in order to claim it as a U. S. territory, but left on August 5 because of its occupation by the Japanese Navy. Bryan and Sedgwick made a scientific survey of the island during the 5 days. August 28, the Japanese Government sent another cruiser, the "Takachiho." S. Kamitaki (a trader mentioned above), S. Shiga, M. P., and O. Yoshida, a geologist, landed. Two Japanese shrines, *Kotobira* and *Ohtori*, were built there ("Tengaisei"). September 2, a typhoon passed over the island. All inhabitants sought safety at the highest point. Until December 25, no food other than birds and fish was available. Sixteen died during this period (Nakada). In September, the Japanese Department of Foreign Affairs again claimed the island for Japan. The following publications appeared: Plants of Marcus (Yabe), Miscellaneous notes on the geology and topography (Yoshida), Chronicle of a journey to the island ("Tengaisei").
- 1903: Shiga published an essay describing the discovery of this island. He asserted its importance from the national standpoint. Bryan's comprehensive monograph was published. Han-emon Tamaoki, a Japanese, went to the island to collect coconuts but left without success (Matsubara).
- 1906–16: Many Japanese were landed for phosphate mining. Nineteen died during these years (Matsubara).
- 1930: In November, all 32 inhabitants, who had been engaged in coconut collecting and fishing, left the island (Matsubara).
- 1931: The island was purchased by the Japanese Navy (Matsubara).
- 1935: The Hydrographical Department of the Japanese Navy began meteorological observations (Matsubara).
- 1937: Establishment of the Japanese Navy airport commenced (Matsubara).
- 1938: Tuyama published his *Flora of Marcus Island*.
- 1939: February 22, a large flock of terns visited the island. March 15–16, a large flock of "swallows" passed through. Terns and swallows appeared also in autumn (Matsubara).
- 1941: The island was armed with six 15 cm. cannons and six 8 cm. aeroguns (Matsubara). Japan declared war upon the United States.
- 1942: March 4, the island was bombed by 40 U. S. carrier-based planes (Matsubara).
- 1943: A garrison consisting of 1,100 navy, 2,250 army, and 650 civilian personnel was installed with M. Matsubara as commander.
- 1944: May 20–21, bombed by 132 U. S. carrier-based planes. October 9, bombarded by a U. S. naval squadron consisting of one battleship (Pennsylvania type), two heavy cruisers (Pensacola type), and five large destroyers (Matsubara).
- 1945: Received 171 attacks by a total of 759 bombers from September, 1944, to the armistice on August 15, 1945. October 7, the Japanese garrison left the island (Ma-

- tsubara). November, occupied by U. S. Navy (Weather Station).
- 1946: U. S. Navy left the island because of the great damage to the establishment by typhoon Martha (Weather Station).
- 1950: The Central Meteorological Observatory in Tokyo made a survey in order to re-establish the runway and weather station on the island (Weather Station).
- 1951: Meteorological observations began again on the island (Weather Station).

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