INSECTS OF HAWAII

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A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on Their Origin, Distribution, Hosts, Parasites, etc.

VOLUME 1

INTRODUCTION

WITH A NEW PREFACE AND DEDICATION

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PREFACE TO THE REISSUE OF *INSECTS OF HAWAII*, VOLUME 1

James K. Liebherr

In a world far different from the one we inhabit today, Elwood Zimmerman founded a taxonomic series he called *Insects of Hawaii.* His goal was to produce a series of handbooks that would permit identification of all Hawaiian insects. More importantly, these identifications would be linked to biological information inherent in these taxa, opening the Hawaiian insect fauna to intense biological study. Through this reissue of Volume 1 of the series, long out of print and unavailable to interested workers, we reintroduce the observations of Dr. Zimmerman—known as Zimmie to the many colleagues who hold him dear—to a new audience. Through this reintroduction to the series, we are reminded of the immense opportunities for fruitful biological endeavor available in the Hawaiian arthropod fauna. Why reissue a book after a 50-year interval that has witnessed revolutions in geology with the acceptance of plate tectonics and biology with the discovery of the underlying nature of genetic mechanisms and, more specifically, the development of sophisticated cladistic methods for determining phylogenetic relationships? The answer is simple. Elwood Zimmerman observed and interpreted the Hawaiian insect fauna in the broader context of the Oceanic biota, including the surrounding continental regions, and the conclusions he drew about Hawaiian biological phenomena have been largely corroborated by the immense wealth of information accumulated since this volume was published.

Zimmerman's initial nine volumes of *Insects of Hawaii* provided taxonomic treatments for the ametabolous and hemimetabolous orders, plus the Lepidoptera. These volumes amount to 4,500 pages, a prodigious body of work for nearly anyone, made all the more staggering by Dr. Zimmerman's subsequent monographic treatment of Australian weevils conducted under the auspices of the Australian National Insect Collection. Nevertheless, the Hawaiian insect fauna will humble any entomologist, and the dipterous radiations proved to be beyond his reach as he focused on other pursuits. Elmo Hardy provided us with the key to understanding the Hawaiian flies, taxonomically revising not only the well-known Hawaiian *Drosophila,* but also the impressive radiations of lineages in the long-legged fly family, Dolichopodidae, and the other less speciose taxa of the order. Hardy and his colleagues provided the taxonomic underpinnings for the Hawaiian *Drosophila* Project (Spieth 1980). The study of Hawaiian *Drosophila* has contributed incalculably to our understanding of speciation mechanisms (Carson & Templeton 1984), the diversification of mating systems (Kaneshiro & Boake 1987), and the evolution of host use and life histories (Kambysellis & Craddock 1997) in an explosive radiation of species.

In this preface I will adopt a practical approach, as often espoused by Zimmie, and discuss two aspects necessary for understanding this book at this time. First, I put the *Insects of Hawaii* series in the historical context of developing Hawaiian entomology. Second, I briefly discuss current thinking regarding some of the major topics presented in Volume 1, including geological origin and age of the islands, patterns of diversity, and evolution of the islands' endemic fauna.

HISTORICAL CONTEXT

When Elwood Zimmerman started the *Insects of Hawaii* series, taxonomic understanding of many groups of Hawaiian insects rested almost entirely on the contributions in the *Fauna Hawaiiensis* series. Whereas that multi-authored collaboration provided terse descriptions of the local species, diagnostic keys were often absent or, when included, led only to groups of genera. To identify an insect specimen, one had to go to the boxes and drawers of the Bishop Museum collection to compare that specimen with those included in the *Fauna* series. Entomologists at the Experiment Station of the Hawaiian Sugar Planters' Association (H.S.P.A.), such as Frank Muir, Otto Swezey, and F. X. Williams, described numerous species in many groups using the classificatory framework established in *Fauna Hawaiiensis.* As applied entomologists working with the H.S.P.A., their work focused on groups of agricultural importance such as Delphacidae, microlepidoptera, and insects of aquatic habitats. Despite their contributions, however, many rare species described from the islands were not available to Hawaiian entomologists because of the previous division of specimens used in *Fauna Hawaiiensis* between The Natural History Museum, London, and Bishop Museum (Manning 1986).

A locally produced publication on Hawaiian insects required a combination of entrepreneurial acumen, organizational skill, and sheer determination. As laid out in the original preface, support from Bishop Museum, H.S.P.A., and University of Hawaii was essential to the series' success. The division of the *Fauna Hawaiiensis* specimens between Honolulu and London required transport of representatives of more recent Hawaii collections to London for careful comparison with the types. Moreover, taxonomic practices in the early 1900's, when *Fauna Hawaiiensis* was completed, did not always include designation of a holotype—the single specimen to which a scientific name can ultimately be tied—and so the reviser was left to determine whether all specimens in a type series actually represented the same species. Zimmerman undertook the task of reuniting specimens divided among institutions, as well as those collected by post-*Fauna* entomologists, permitting accurate delineation of species and the development of workable identification keys.

The logistical obstacles faced by Elwood Zimmerman in his undertaking *Insects of Hawaii* have been reduced considerably by the relative ease of world travel today. Visits to museums for type study are still required to ensure sound taxonomy, but the trips can often be made in hours and are supported both by natural history institutions and governmental agencies. Locally, Hawaiian field surveys during the past 20 years have sampled many previously unexplored areas with the help of helicopters, lightweight and waterproof gear, and other technological innovations. Access to these areas today is facilitated by the cooperation of governmental, non-governmental, and commercial organizations and through the coordinated construction of boardwalks and trails. Prior to air transport, access to natural areas had not changed much since Perkins' time. One walked uphill as far as possible along dry ridges or leeward slopes, penetrated the forests and bogs as far as possible, and then walked out and down again when further progress was infeasible. Improved access today has greatly enhanced our ability to discover more of Hawaii's biotic diversity. The basic requirements however—an eye for patterns, long hours of observation, and careful organization of data–are still essential to make sense of the islands' multitudinous species.

GEOLOGY

The major controversy surrounding the origin of the Hawaiian Islands before the acceptance of plate tectonics was whether the islands had ever been connected to a major landmass by now-sunken land bridges. The theory of land bridges as a means to explain biogeographic patterns viewed on a static earth was a logical attempt to reconcile biogeographic and geographic patterns. Ever since botanist Joseph Hooker, after hearing the persuasive arguments of his friend Charles Darwin, rejected the idea of land connections among the southern landmasses, land-bridge enthusiasts had squared off against dispersalists to debate the origin of the Pacific Island biota. In Volume 1 Zimmerman first amassed evidence that the Hawaiian Islands are indeed oceanic in origin and thus all native flora and fauna must have originated from over-water—or underwater—colonization.

Much of the descriptive geology in Volume 1 is derived from Stearns (1946). The revised edition of his concise book (Stearns 1966) as well as McDonald et al. (1983) provide good overviews of the evolution of the islands' landforms. The Hawaiian Islands are among the best-studied geological formations on Earth, and a review of this subject is well beyond the scope of this preface. Below, however, I focus on several of the more controversial topics that have emerged as a result of advances in geology during the last quarter century.

In the 1940's, accepted thinking as to how the Hawaiian islands arose from the Pacific Plate involved a progressive weakening of the plate from northwest to southeast, producing sequential eruptions of basaltic magma that resulted in the formation of newer islands further and further to the southeast. This pattern of oldest to youngest islands—with Kaua'i being the oldest high island and Hawaii Island the youngest—was apparent to even the earliest students of Hawaiian biology. David Sharp, chief editor of *Fauna Hawaiiensis* and senior taxonomist on the project, wrote to R. C. L. Perkins on 24 January 1903 in a letter preserved in the Bishop Museum archives: "The Carabidae show that the things extend more from North to South than from South to North. This may be due to greater antiquity of northern islands or to currents." Sharp's conclusions were based exclusively on studying Hawaiian beetles, as his letter was posted from distant Cambridge and he never visited the islands.

Zimmerman based his discussion of the relative ages of the islands on assumptions about erosion rate and present-day topography of the islands. Using these criteria he suggested that the most eroded island, Oahu, might be the oldest, even though it is the southeastward neighbor of Kauai. Today we rely upon radiometric potassium-argon dating of specific lava formations to determine the ages of the various volcanoes making up the Hawaiian Island chain. Based on our knowledge of plate tectonics, the islands originated from two parallel tracks of volcanoes fueled by the energy from a geographically stationary thermal plume originating deep in the earth's mantle (Carson & Clague 1995). The plume's upwelling magma burns through the relatively thin, northwestwardly moving Pacific Plate, depositing magma first on the ocean floor. Subsequent flows overlie older deposits, culminating in a mature shield volcano much like Mauna Loa of Hawaii Island. The result is a nearly perfect pattern of younger volcanoes lying east of older neighbors (Table 1). The only exceptions—Hualalai and Niihau—represent instances in which the southwestern volcano of a pair erupted later than its northeastern counterpart. Zimmerman's incorrect hypothesis that Oahu

Table 1. Present and maximum heights and K-Ar ages of Hawaiian volcanoes (extracted from Carson & Clague 1995)

Volcano	Height (m)		Age (millions of years)
	Present	Maximum	
Hawaii Island			
Kilauea	1,247	1,247	0–0.4
Mauna Loa	4,169	4,169	0–0.4
Mauna Kea	4,205	4,600	0.38
Hualalai	2,521	2,950	0–0.2
Kohala	1,670	2,670	0.43
Maui Nui			
Haleakala	3,055	5,000	0.75
Kahoolawe	450	2,100	1.03
West Maui	1,764	3,400	1.32
Lanai	1,027	2,200	1.28
East Molokai	1,515	3,330	1.76
West Molokai	421	1,600	1.90
Oahu			
Koolau	960	1,900	2.60
Waianae	1,231	2,220	3.70
Kauai Nui			
Kauai	1,598	2,600	5.10
Niihau	390	1,400	4.89

originated earlier than Kauai arose from then unrecognized variability in the lava comprising each island and the impact of compositional differences on the subsequent rate of erosion. Kauai, composed of comparatively harder lavas, has been eroded to 60% of its original maximum height, whereas the younger Koolau volcano of Oahu has been reduced to only 50% of its maximum height in about half the time. James G. Moore and his colleagues at the United States Geological Survey have provided a dramatic explanation of this anomaly (Moore et al. 1989). Through extensive underwater exploration with side-looking sonar, they have shown that portions of volcanoes such as Koolau have been lost in enormous, cataclysmic landslides, the remains of which litter the Pacific Ocean floor. In this instance, an area estimated at 23,000 km^2 foundered in a single episode. Gazing at the Nuuanu Pali from the vantage point seen in Fig. 12 (p. 22), you might imagine that you are looking at a vista not unlike the summit caldera of Haleakala. In this case, however, the area behind you is ocean. A similar massive failure resulted in the dramatic sea cliffs of eastern Molokai.

In Volume 1 Zimmerman mentioned other phenomena associated with these failures. For one, he discussed the stature of the islands relative to their foundation on the Pacific Plate. The massive extrusions of magma have not only built substantial oceanic islands, but the weight of the islands themselves has depressed the Pacific Plate. For example (see pp. 12–13), the sea floor northeast of Mauna Kea reaches a depth of 5,500 m just 100 km from the 4,200-m summit of that volcano! Drilling near Hilo on the slopes of Mauna Loa has revealed that the boundary between Mauna Loa and Mauna Kea lies at a depth of 280 m, indicated by changes in trace element and isotopic ratios, and horizons of marine sediment and soil derived from earlier erosion of Mauna Kea (Hawaii Scientific Drilling Project Team 1996). Given the combination of extreme slope and the "layer cake" composition of the islands, with newer lavas separated from older underlying lavas by soil, water, and associated marine deposits, it is easy to understand the occurrence of slippage along these weaker "frosting layers."

Zimmerman also discussed the presence of a marine deposit at 365 m elevation on Lanai (p. 37). Both of his hypotheses concerning the origin of this deposit—substantial Pleistocene submergence of Lanai, or an anthropogenic origin—must be rejected. The Hulopoe Gravel deposit is now seen as the result of oceanic disturbances associated with a massive landslide along the Kona coast of Hawaii Island (Moore & Moore 1982, Moore et al. 1992). All the islands, in fact, are believed to have undergone an early period of rapid subsidence during the active shield-building stage when the volcano reached its maximum height and weight, thereby depressing the Pacific Plate. This would have been followed by a period of slower subsidence associated with lithospheric contraction as the island moved out of the area supporting active volcanism (Carson & Clague 1995). Thus the history of any particular Hawaiian island complex comprises five stages: 1, the initial, isolated origin of a single volcano; 2, coalescence of several volcanoes into a "big" island, the weight of which depresses the Pacific Plate; 3, erosional degradation of subaerial portions of the island complex through smaller landslips and prodigious landslides; 4, subsidence of the entire island complex due to the development of newer "downstream" islands as well as lithospheric cooling; and 5, ultimate degradation of the low islands to form submerged guyots through erosion and continuing isostatic subsidence of the ever thickening Pacific Plate as it cools.

PATTERNS OF DIVERSITY

Immense advances in our knowledge of Hawaiian insect diversity have been made since publication of Volume 1, in large part a result of contributions published in subsequent volumes of this series. Missing from Zimmerman's treatment of endemic insects in Volume 1 are several orders now known to include species endemic to Hawaii. The most significant of these is the entognathan order Collembola. The springtail fauna includes 169 species, of which 95 are Hawaiian endemics (Christiansen & Bellinger 1992). These endemic species are distributed among 33 genera, many of which are also represented in Hawaii by adventive species. Thus there have been numerous colonization events in Hawaii involving Collembola.

The Dermaptera, unrepresented in Volume 1 by endemics, includes at least eight Hawaiian endemic species: six species of *Anisolabis,* one or two of *Euborellia,* and *Paraflexiolabis ornata* (Nishida 1997). In addition, a single endemic flea (Siphonaptera), *Parapsyllus laysanensis,* has been described (Nishida 1997).

Therefore, Zimmerman's conclusions regarding attributes of orders not likely to diversify in Hawaii (pp. 69–70) need only minor modification. Among "the orders containing apterous, mostly delicate, minute, many blind, moisture-loving dwellers of damp soil," the Protura and Diplura have not colonized or diversified. However, taxa of the third order of Entognatha—i.e., Collembola—have repeatedly colonized the island chain, leading to the conclusion that they are more ecologically opportunistic than are the other two less abundant and less diverse orders. The parasitic order Siphonaptera can be attributed to the native fauna, but in this case colonization has not been followed by *in situ* cladogenesis; i.e., the colonizing taxon is most closely related to a non-Hawaiian relative. Finally, taxa of Dermaptera include a modest endemic species swarm, though monophyly of this group has not been demonstrated. Two more colonization events would be required to account for the *Euborellia* and *Paraflexiolabis* species. That a group of generalized feeders with good dispersal abilities has colonized the islands fits with Zimmerman's predictions. That they have diversified while other groups such as roaches (Blattaria) have not (see list item 10, p. 70) suggests that earwigs are more prone to isolation on an island system such as Hawaii, or that a colonist arrived much earlier than the colonizing, anthropophilic roaches.

Taxonomic advances within the endemic Hawaiian insect groups during the past 50 years are too numerous to list here. Still, even with the extensive taxonomic description of speciose radiations, the putative sources of the radiations, and the number of putative colonizing taxa, remain much the same. To aid the reader's understanding of the current knowledge of taxonomic diversity in Hawaii, I have recompiled Zimmerman's table (p. 93) in Table 2, listing genera of various diversity classes for the Hawaiian arthropod biota.

Several conclusions can be drawn by comparing this tabulation with figures compiled in the 1940's. The increased number of endemic species in certain genera, more than doubling to over 100 in some cases, reflects the industry of several taxonomists. Our limited knowledge of the Diptera at the inception of the *Insects of Hawaii* series is exemplified by Zimmerman's previous listing of *Campsicnemus, Drosophila,* and *Scaptomyza* as genera with only 26–50 endemic species. Since then, the contributions of Elmo Hardy and his colleagues have greatly expanded our knowledge of this order. The discovery and description of many new species of *Plagithmysus* cerambycid beetles and *Trigonidium* crickets were based on major research projects of J. Linsley Gressitt and Dan Otte, respectively. Other increases in numbers of species—e.g., *Hyposmocoma* and *Blackburnia*—reflect taxonomic decisions to combine genera when Hawaiian radiations were shown to be monophyletic. The relative representation of the less speciose genera has not changed significantly from the older figures. The 28% increase for species in genera of 10–25 species is partly due to an inclusive interpretation of "insects", whereby their arthropod brethren, springtails and spiders, are included. Removing these taxa reduces the increase in species for this class of genera to 20%. Even with our increased knowledge of the major radiations, genera including 10 or more endemic collembolan, insect, and arachnid species now account for 77.7% of all endemic species known from the islands, not much different from Zimmerman's figure of 79.3%. Among these 101 genera, the number of endemic species per genus averages 43 compared to Zimmerman's figure of 34 species/genus.

Comparing individual genera across the two tables shows an overall movement of genera upward through the size classes, with 14 genera added to the 10–25 species class, 9 moving up to the 26–50 species class, and 4 and 6 additional genera, respectively, now placed in the two largest size classes. Thus numerous new taxa have been described in genera of all levels of diversity over the past 50 years. Comparing Nishida (1997) and Volume 1, known endemic insect species have increased by 79% from 2,963 to 5,293. The downside to these numbers, unfortunately, is the unimpressive average rate of 47 new insect species described per year. To reiterate a consistent theme of Dr. Zimmerman's, systematists must be given better support in order to develop the taxonomic tools needed to characterize, manage, and conserve the incomparable biological resources of Hawaii.

Based on findings of the past 50 years, there is little reason to quarrel with Zimmerman's estimate of 233 to 254 original colonizing events to account for the entire endemic insect fauna. Few studies have included the multiple outgroups and comprehensive coverage of Hawaiian taxa required to corroborate monophyly of a Hawaiian radiation. Zimmerman's tabulation of the sources of various Hawaiian groups (pp. 71–92) remains the starting point for those interested in establishing the colonization history of Hawaiian insect groups.

DEVELOPMENT OF THE ENDEMIC FAUNA

That some components of the Hawaiian biota are older than the extant high islands is now commonly accepted. Given our knowledge of the sequential origin of the islands as the Pacific Plate moves west and north, and the relict species representing various radiations on the oldest islands (e.g., *Oodemas* and *Rhyncogonus* weevils endemic to Necker and Nihoa, *Agrotis* moths endemic to Laysan) this conclusion seems inescapable. The extensive diversity and highly derived anatomy, natural history, and behavior of individuals representing other radiations—e.g., Hawaiian *Drosophila* and predatory *Eupithecia* caterpillars (Montgomery 1982)—defy explanation if interpreted as end products of evolution taking place only on the present-day islands. Zimmerman's discussion of inter-insular segregate evolution (pp. 122–127) provides an apt explanation for how these groups have diverged

Table 2. List of genera containing ten or more endemic species (based on Nishida 1997, Liebherr & Zimmerman 2000); percent listed below generic names reflects increase or decrease in total numbers of species included in genera of each size-class compared to 1948.

10–25 species	26–50 species	51–100 species	>100 species
Odonata	**Orthoptera**	**Psocoptera**	**Orthoptera**
Megalagrion 24	*Laupala* 35	*Ptycta* 53	*Trigonidium* 130
Orthoptera	*Leptogryllus* 29	**Homoptera**	**Coleoptera**
Banza 11	*Prognathogryllus* 36	*Nesophrosyne* 60	*Proterhinus* 158
Psocoptera	**Heteroptera**	*Oliarus* 51	*Blackburnia* 129
Palistreptus 20	*Nysius* 28	*Nesosydne* 82	*Plagithmysus* 126
Thysanoptera	*Oceanides* 27	**Coleoptera**	**Lepidoptera**
Hoplothrips 13	*Nesiomiris* 50	*Mirosternus* 70	*Hyposmocoma* 345
Heteroptera	*Sarona* 40	*Xyletobius* 52	**Diptera**
Neseis 22	**Coleoptera**	*Mecyclothorax* 85	*Campsicnemus* 136
Nabis 24	*Cis* 35	*Oodemas* 62	*Drosophila* 337

(Continued)

Table 2 (continued). List of genera containing ten or more endemic species.

10–25 species	26–50 species	51–100 species	>100 species
Heteroptera (cont.)	**Coleoptera (cont.)**	**Lepidoptera**	**Diptera (cont.)**
Oechalia 14	*Rhyncogonus* 34	*Eudonia* 62	*Scaptomyza* 122
Homoptera	*Eopenthes* 33	**Diptera**	*Lispocephala* 101
Leialoha 12	*Dromaeolus* 31	*Eurynogaster* 55	**Hymenoptera**
Nesothoe 23	*Aeletes* 32	**Hymenoptera**	*Sierola* 179
Pseudococcus 10	*Nesopeplus* 31	*Nesoprosopis* 59	**Total: 10 genera**
Kuwayama 10	*Diestota* 29	*Eupelmus* 60	**1763 species**
Trioza 12	**Lepidoptera**	*Odynerus* 98	**+158%**
Neuroptera	*Carposina* 49	**Total: 13 genera**	
Anomalochrysa 19	*Mestolobes* 33	**849 species**	
Micromus 24	*Udea* 41	**+15%**	
Coleoptera	*Scotorythra* 37		
Holcobius 16	*Philodoria* 30		
Bembidion 17	*Agrotis* 28		
Apterocis 13	*Thyrocopa* 40		
Acalles 22	**Diptera**		
Dryophthorus 17	*Cephalops* 39		
Heteramphus 12	**Araneae**		
Labrocerus 17	*Tetragnatha* 28		
Itodacnus 11	**Total: 28 genera**		
Eupetinus 24	**795 species**		
Gonioryctus 22	**–4%**		
Nesopetinus 23			
Xyleborus 21			
Lispinodes 10			
Myllaena 11			
Lepidoptera			
Omiodes 23			
Orthomecyna 13			
Merimnetria 21			
Eupithecia 22			
Bedellia 14			
Cydia 14			
Eccoptocera 11			
Pararrhaptica 19			
Spheterista 17			

Table 2 (continued). Remainder of genera in size-class of 10–25 species

10–25 species			
Diptera	**Hymenoptera**	**Collembola**	**Araneae**
Dyscritomyia 25	*Scleroderma* 17	*Entomobrya* 14	*Lycosa* 11
Idiomyia 19	*Pseudodiranchis* 11	*Lepidocyrtus* 11	*Theridion* 11
Titanochaeta 11	*Enicospilus* 18	*Dicyrtoma* 11	**Total: 56 genera**
Scatella 15	*Spolas* 11		**915 species**
Trupanea 21	*Polynemia* 14		**+28%**
Limonia 13	*Ectemnius* 22		
	Nesodynerus 12		

from their extra-Hawaiian relatives. That the Hawaiian *Drosophila* are "older than the rocks" and were most likely present on the Hawaiian chain as long as 30 million years ago has been corroborated by both molecular and fossil data (DeSalle 1992).

Zimmerman's discussion of *kipuka,* the small fragments of forest isolated by surrounding lava flows, as a major factor in the isolation of limited populations is prescient, given what we have since learned about speciation in Hawaiian *Drosophila* (Carson & Templeton 1984). Zimmerman also notes the necessity of pluralistic acceptance of geographic and host-based isolation in promoting speciation among Hawaiian groups. This pluralism has a long tradition in Hawaiian natural history, as Perkins was the first to note that related *Plagithmysus* cerambycids are strongly associated with different hosts (Grant 2000). The taxonomic basis for studying these longhorned beetles has been established since publication of Volume 1. Pluralism is also required in viewing the bases for selection in speciation of Hawaiian species swarms. Taking the radiation of *Hyposmocoma* moths as an example, a group Zimmeman revised in Volume 9 of the series, both host-based isolation and sexual selection have played a role in diversification. The former is evident by the variety of hosts used across this radiation. Sexual selection is consistent with the bizarre male genitalic structures (Zimmerman 1980), in which setae on only the left valves of the male aedeagus have evolved from simple hairs to flattened paddles and, ultimately, to broad, scoop-like spatulae. This and many other examples make Hawaii the preeminent frontier for the study of evolutionary biology and speciation, regardless of the manner of diversification.

The existence of a highly derived lava tube cave fauna (Howarth 1973, 1993) was not known at Zimmerman's writing of Volume 1. Nevertheless, the extensive divergence that characterizes elements of this fauna could be used as a signal example in Zimmerman's discussion of the factors enhancing divergence of lineages. Lava tube caves represent "*New land open to colonization* [that] *is conducive to speciation*" (p. 122, emphasis Zimmerman!). Many of the troglobitic species appear most closely related to "sympatric" epigean relatives, suggesting that adaptive changes associated with cave life have evolved very quickly, at least during or subsequent to the last speciation event. Repeated origins of cave-inhabiting taxa across island radiations allow us to examine the results of parallel selection to cave conditions. In essence, we can compare the results of parallel evolutionary experiments involving closely related taxa.

To read this book is to understand how Zimmie passed along his infectious enthusiasm to so many students. His passion for biology is palpable on these pages, and this passion provides a clue as to how he has accomplished so much during his illustrious career. This book remains important to Hawaiian biology because so much of what is suggested in it has been corroborated. This also suggests that remaining unstudied subjects will be profitably pursued. Hawaii is not a place to which you go to complete a concise project and then move quickly on. The biotic complexity of these islands is staggering. This is due in part to the disharmonic nature of the biota, providing fewer and therefore more easily discernible connections among its diversified parts. The replication of taxa during radiation of Hawaiian lineages permits multiple comparisons of ecological, behavioral, biogeographic, and anatomical divergence. These multiplying avenues of inquiry satisfy the mind but do not provide the means to a quick exit. The *Insects of Hawaii* series was conceived as a means to open up these avenues. In our new editorial format, therefore, the series maintains the goal of a comprehensive and accessible characterization of the Hawaiian arthropod biota and its origins. We take up that lofty but important goal from Elwood Zimmerman. May we be up to the task.

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ELWOOD CURTIN ZIMMERMAN: AN UNCOMMON DEDICATION

J. O. Juvik

Reviewing the life and accomplishments of the indefatigable E. C. Zimmerman is like taking a long, arduous, but awe-inspiring transcontinental road trip with Sinatra's rendition of *My Way* reprising endlessly on the car's stereo. At present, in January 2001, "Zimmie" (to his friends) resides in working retirement, with his wife of 59 years, Hannah Louise (Bond) Zimmerman, on the coastal bluffs overlooking Tura Beach at Merimbula, New South Wales.

I had been a fairly indifferent student of geography and biology at the University of California in the mid 1960s, and but for two books that passed into my hands, I perhaps would never have seriously contemplated an academic career. In 1965 I chanced on a copy of Sherwin Carlquist's newly published and highly readable *Island Life.* Carlquist immediately replaced Frank Buck as the hero of my youth. It was a revelation. There actually seemed to be a real vocation of the likes I had only dreamed might exist: "island biogeographer"! Both in the preface and throughout *Island Life* there appeared laudatory references to a monograph entitled *Insects of Hawaii.* Quite fortuitously, I found a copy at a used bookshop in Berkeley, read it, and rashly decided to seek my own career in Hawaii. I made good on this pledge the following year. Upon arrival in Honolulu I found that Zimmie was by then more or less permanently based in England at the British Museum, where he continued his work on subsequent volumes of *Insects of Hawaii.* He later relocated to Australia in the early 1970s.

More than a decade would pass before I finally tracked down the elusive Zimmie in early July 1978. Braced against the cold of an early winter morning in Canberra, and clutching beneath my coat a well-worn copy of *Insects of Hawaii, Vol. 1,* I made my way across the Australian National University campus to the offices of the CSIRO Division of Entomology for our first encounter. My anticipation was tinged with apprehension, as I had heard stories: brilliant but irascible, a near-fanatical workaholic, suffering neither fools nor just about anyone else who might deflect him from his laser-focused, monographist mission. I was hoping only for a quick book autograph and a be-on-your-way-my-lad handshake. What I got was a long and wide-ranging discussion of evolution and systematics, and the beginnings of a personal friendship that has extended over more than 20 years. During this period Zimmie has shared with me many reflections on his life and career, some of which are included here.

At this first meeting in 1978, Zimmie was in the midst of proofing his 1900-page monograph on the Hawaiian Microlepidoptera (Zimmerman 1978), and I had a brief glimpse of his formidable ire, then directed at the University of Hawaii Press. He contended that the Press had sat on the manuscript for several years and then had the temerity to propose publishing it as a single, 120-mm-thick volume, rather than in a more manageable two volumes (a more efficient format for use on the taxonomist's lab bench). On this issue Zimmie prevailed, but I was made fully aware of the enormous struggles that burdened the lonely monographist's life. These included the obvious frustrations with editors, and petty administrative "bean-counters" who were unable to fully fathom or embrace the sublime objectives of the multi-decade and multi-volume systematist's quest. These are of course the inevitable trials of a driven and highly focused scholar confronted by the swarming distractions of a post-modern world. Zimmie's angst in such matters is best captured in his own words, which can be found peppered throughout the extended prefaces of his various works (see in particular Zimmerman 1978, xv–xvi).

THE OAKLAND HILLS

Zimmie was born to Ernst and Ethel Zimmerman in Spokane, Washington, in the midst of a severe storm on December 8, 1912. (His mother later recounted that the attending physician had been snowed-in for the night.) The family was of German, Swiss, French, and Scottish ancestry and had moved west from Tyrone, Pennsylvania, at the beginning of the 20th Century to settle in the thriving railhead and timber town of Spokane. His mother, later a nurse, contracted tuberculosis in 1916, and for health reasons the family relocated to Oceanside, California (near San Diego), where Zimmie's maternal grandparents were farmers. Soon after, his father found employment as a woodworker in Oakland and the family moved permanently to the San Francisco Bay area. Fortuitously, their Oakland residence lay on the outskirts of town, with a back door opening directly into the then undeveloped and beautifully wild Oakland Hills. Zimmie fondly recalls an idyllic childhood spent with his younger brother Harold amidst the Mediterranean scrub of surrounding ravines and ridgetops, where his penchant for insect collecting blossomed at an early age.

As a precocious high school student in the late 1920s, with a passion for entomology already well developed, Zimmie carried the nickname "Bugs" through grammar school. ("Zimmie" was an appellation coined by his colleagues years later on the Mangarevan Expedition.) During this period he was also influenced by the renowned "Bugsy" Cain, a Boy Scout naturalist in Oakland who organized and led summer camping trips with a heavy entomological focus. These summer outings influenced not only Zimmie but others among his boyhood fiends to seek careers in entomology, among them Robert L. Usinger, J. Linsley Gressitt (later head of the Entomology Department at the Bishop Museum), and E. Gorton Linsley. At this time Zimmie was also introduced to members of the entomology faculty at the University of California at Berkeley. The eminent professor E. C. Van Dyke was impressed by the boy's local entomological knowledge and enthusiasm for collecting. Viewing Zimmie's butterfly collection somewhat dismissively, however, the professor suggested that since far too many entomologists already worked on butterflies, the youngster should consider focusing his energies on a less charismatic but more scientifically interesting and largely unstudied group: weevils. History confirms that Zimmie took this charge quite literally to heart. During a Boy Scout camping trip in the summer of 1930 he collected a new weevil that was described in his first scientific publication (Zimmerman 1932). The vast majority of his subsequent published works authored over the intervening 68 years have also focused on the Curculionidae.

Zimmie entered UC Berkeley in 1931 along with Robert Usinger, who also was destined to become a distinguished systematist and Zimmie's occasional scientific collaborator. In late 1933 the Bishop Museum in Honolulu was organizing a comprehensive natural history expedition to the Southeastern Pacific and contacted the Berkeley faculty for recommendations on an expedition entomologist. Even before entering the university Zimmie already had some experience preparing and mounting Hawaiian and Pacific Island insects, having been employed as a technician by the Pacific Entomological Survey, which was then temporarily headquartered at UC Berkeley. In what was to prove the most far-reaching event of Zimmie's scientific career, he was selected to join the Bishop Museum's expedition, interrupting his undergraduate studies in the middle of his junior year.

THE MANGAREVAN EXPEDITION

Incongruously in the midst of the Great Depression, and employing a converted Japanese sampan (rechristened the *Islander*) poorly suited for Pacific circumnavigation, the Bishop Museum in 1934 launched the last of the ship-based, comprehensive, "natural history" expeditions reminiscent of those undertaken in the 19th Century. The expedition was under the able leadership of the Museum's malacologist, C. Montague Cooke, Jr. (scion of one of the Hawaii's elite business families who would later became Zimmie's revered mentor), who was also a trustee and benefactor of the Museum. The Mangarevan expedition took its name from a group of small, obscure islands lying near the southeast end of the Tuamotu Archipelago in French Polynesia. Years earlier a visiting anthropologist had collected spectacular shells of land snails there that fascinated Cooke, symbolizing the scientific *terra incognita* that characterized much of the remote Pacific at that time.

In February 1934 Zimmie sailed directly to Tahiti from San Francisco, where he was

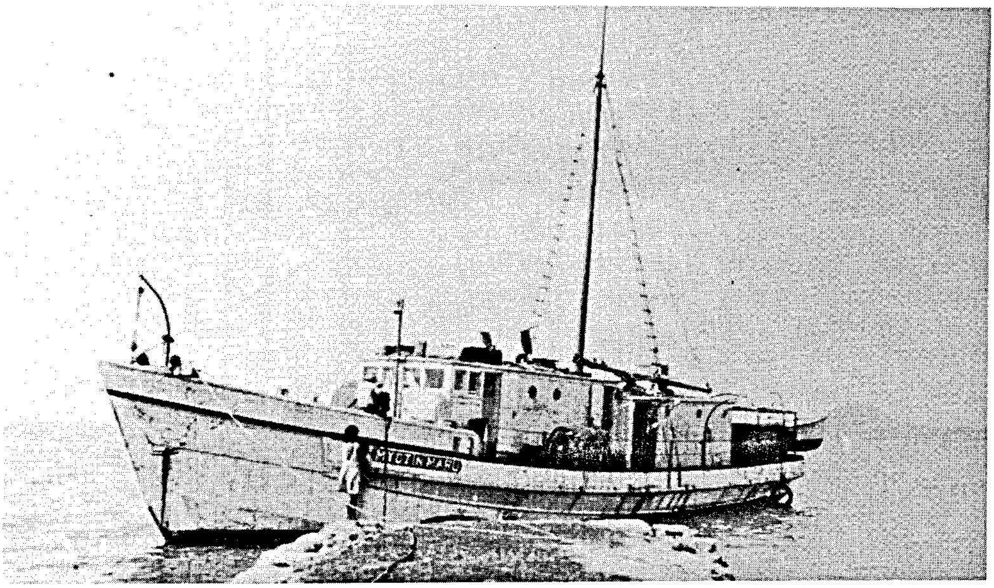

Figure 1.—The "*Islander,*" a converted Japanese fishing boat (Myojin Maru) carried the Bishop Museum's Mangarevan Expedition to more than 50 South Pacific islands between April and November 1934. (Photo by H. St. John, courtesy Bishop Museum)

scheduled to rendezvous with the expedition's main party from Honolulu. Delays in refurbishing the expedition vessel *Islander* resulted in the boat not leaving Hawaii until April 13, 1934. Thus Zimmie had some months in Tahiti on his own, but he recalled that torrential rains during much of this hiatus frustrated his collecting efforts. Though hampered by bad weather, he did manage to collect new beetles with links to both Australia and Hawaii, establishing a biogeographical connection not previously known for those taxa. When the *Islander* finally arrived at Papeete in May, Zimmie was shocked by the condition of the dirty, cramped, leaking, and questionably seaworthy craft. He immediately considered begging off the expedition to seek return passage to California. Implored and cajoled by the other expedition members, however, he soon relented and joined an adventure that would forever remain the high point of his life. At the age of 21, and still an undergraduate, Zimmie was thrown into close quarters for almost seven months with a group of exceptional men who, like himself, would rise to preeminence in Pacific science. In addition to the malacologist Cooke and his assistants Donald Anderson and Yoshio Kondo, the scientific party included University of Hawaii botanists Harold St. John and F. Raymond Fosberg. Anthropologists Kenneth Emory and the Maori–New Zealander Peter Buck (who later as director of the Bishop Museum became a nemesis for Zimmie) were also associated with the expedition but worked independently in the Tuamotus.

The expedition traveled throughout the scattered atolls of the Tuamotus and southeastward, finally reaching long-sought Mangareva. There the party was to face utter disappointment, as feral goats and fire had laid waste to virtually all of the island's native ecosystems. By contrast, farther westward on Rapa in the Austral Islands, Zimmie experienced the most exhilarating collecting days of his life. Although heavily modified by human use, there remained on Rapa's mountainous slopes pockets of largely undisturbed native forest, where almost every sweep of his collecting net yielded exciting new taxa (Zimmerman 1938). The expedition afforded Zimmie the opportunity to experience a breathtaking range of island types under different degrees of geographic isolation, each with their own exquisite evolutionary elaborations. The range and extent of anthropogenic impacts on insular ecosystems was also well exemplified during the voyage and would factor into Zimmie's deep and early commitment to conservation (Zimmerman 1948). Overall, the grand scale of this early Pacific experience was a rich source of biological questions and answers much larger than his tiny weevils. Figure 32 (in the present volume) is an oft reprinted and excellent example of exploiting his chosen taxa to illustrate the important biogeographic principal of "distance-decay" or "filter effect" in transoceanic dispersal.

Zimmie remained in Honolulu for some months at the close of the expedition, preparing at least a dozen publications that appeared later in 1935 and 1936. He then returned to Berkeley for the 1935–36 academic year to complete his undergraduate degree.

HONOLULU AND THE BISHOP MUSEUM

By mid-1936 Zimmie was back in Honolulu to assume the permanent position of entomologist at the Bishop Museum. In spite of substantial work remaining from the Mangarevan Expedition, he immediately conceived and launched an audacious plan to single-handedly monograph the entire native insect fauna of Hawaii, with a projected series running to more than a dozen volumes! He patterned the project after that of his Berkeley mentor, Professor Edward Essig's *Insects of Western North America* (1926). Zimmie's abiding interest in the history of entomology, nowhere better exemplified than in the literature review and biogra-

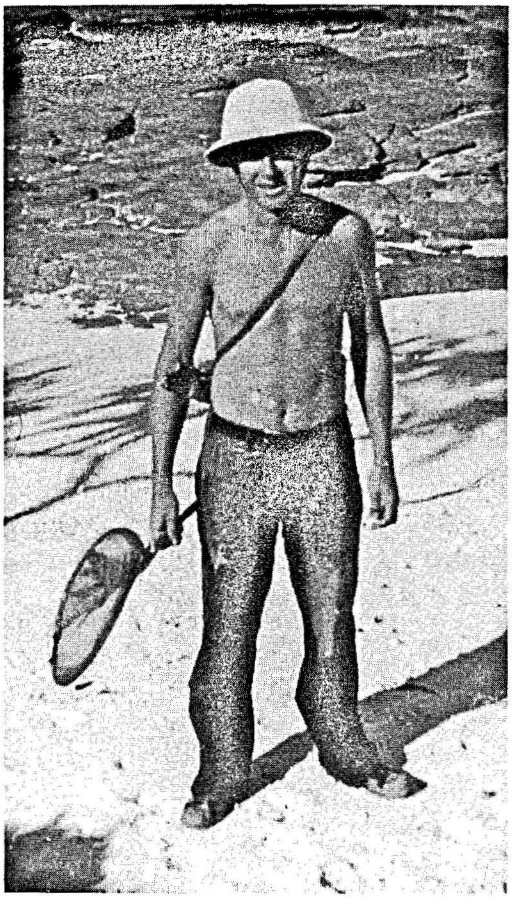

Figure 2.—Twenty-one-year-old Zimmie on Tauna Islet, Mangareva, 1934. (Photo by H. St. John, courtesy Bishop Museum)

phical vignettes of his *Australian Weevils, Vol. 3* (Zimmerman 1993), also owes much to the influence of Essig.

Concurrent with his newly conceptualized "grand plan," Zimmie continued to publish systematic works at a furious pace during the late 1930s (with 41 papers in 1938–39 alone) on topics covering Hawaiian, Pacific, and economic entomology. Zimmie's efforts during this period were actively encouraged by a cadre of talented local entomologists at the Hawaiian Sugar Planters' Association Experiment Station and the Pineapple Research Institute, in particular C. F. Pemberton and F. X. Williams. Zimmie's closest confidant in Hawaii, however, was Otto H. Swezey, an island resident since the early 1900s and a leading authority on the native insects. Swezey had worked with the legendary R. C. L. Perkins, who's late 19th and early 20th Century collecting and extensive entomological contributions to *Fauna Hawaiiensis* (1899–1910) form the foundation of Hawaiian entomology.

During a collecting trip to Samoa with Swezey early in 1940, a chain of events was set in motion that would impact Zimmie's personal and professional life on a scale exceeding even that of the Mangarevan Expedition. While on Tutuila, Zimmerman made the chance acquaintance of a United States naval captain whose ship was stationed in Pago Pago harbor. The captain offered to take Zimmie to collect on Rose Atoll. During the short trip the two struck up a friendship, and the naval officer suggested that Zimmie, should he ever visit the Boston area, contact his good friend Arnold Baker in Newton, Massachusetts. A year later, in the spring of 1941, Zimmie's research travels took him to the East Coast. While studying insect collections at Harvard he made a fateful call to the Baker family. After several social meetings, the Bakers were only too pleased to introduce him to an eligible cousin, Hannah Louise Bond. A courtship ensued while Zimmie continued work at Harvard, and the couple were married in October of 1941. By early December the newlyweds had returned to the West Coast via a circuitous route across the United States with Zimmie lecturing at various universities. At the onset of World War II, the Zimmermans were trapped in Berkeley for several months before being allowed to return to Honolulu in 1942. Zimmie must surely be one of the few wartime Honolulu residents with positive recollections of the era's "blackouts" and curfew years, when he could sit at night unmolested, usually sweltering (he tied ink blotters to his arms to keep sweat from smudging his manuscripts) in a shuttered, light-shielded home office, relentlessly advancing his *Insects of Hawaii.*

By the end of the war Zimmie had completed the first 5 volumes of *Insects of Hawaii* and had made substantial progress on several additional volumes. By this time Peter Buck had for some years been director of the Bishop Museum, where he sought to impose a stronger anthropological orientation. This meant that Zimmie's insect manuscripts were continually bumped down the publication queue as more favored anthropological treatises were brought into print. After several years of frustration, Zimmie took his manuscripts to Gregg Sinclair, President of the University of Hawaii (where Zimmie also taught courses in entomology and biogeography) and to Harold Lyon, Director of the Hawaiian Sugar Planters' Association Experiment Station (where in 1946 Zimmie had assumed a shared position with the Bishop Museum). The two organizations quickly agreed to co-sponsor the work for publication by the newly founded University of Hawaii Press. When Peter Buck became aware of this plan he threatened to withhold publication authorization unless other anthropological manuscripts were blended into the deal. Buck's scheme was rebuffed, but this meant that more seeds were sown for Zimmie's future marginalization and ultimate estrangement from the Museum. The first five volumes of *Insects of Hawaii* were finally published in 1948. These volumes met with immediate critical success both scientifically and with the Hawaii public (particularly the general natural history content of *Volume 1*). In a review of the first issued volumes, the distinguished Yale University professor G. E. Hutchinson described it as "one of the most ambitions works in descriptive zoology ever undertaken by a single investigator..." (*American Scientist,* 1949; p. 271). The volumes were awarded the 1948 annual Hawaii Literary Award for outstanding book by a local author. A storm of protest ensued (including irate letters to local newspapers) as some members of the local *literati* objected to the very idea of a "scientist" vying for literary awards that should clearly be reserved for novelists and poets. The following year the rules for the award were altered specifically to exclude scientific works!

Two other events in 1948 would also impact Zimmie's future career. That year, the young D. Elmo Hardy joined the University of Hawaii entomology faculty and Zimmie invited him to join the *Insects of Hawaii* project. Over the next 40 years Hardy would become a world-renowned dipterist and, among other projects, would monograph the evolutionarily important Hawaiian *Drosophila* for the *Insects of Hawaii* series. Both strong willed, Zimmerman and Hardy did not get along. Zimmie was fearful that Hardy would orchestrate a take-over of the series, since both Hardy and the Press were part of the University. For his part, Hardy apparently showed little interest in collaborating on Zimmie's Diptera work already in progress. In the end, however, Hardy completed the Diptera work to Zimmie's satisfaction, but the series was no longer the "one-man" effort originally conceived. It would be another fifty years, in the summer of 1998, before the two men would again meet and exchange pleasantries at a University of Hawaii Regents' award ceremony held in their honor.

Also in 1948, Zimmie received a Fulbright fellowship to work with the extensive Hawaiian insect collections at the British Museum of Natural History. The Zimmermans arrived in England in 1949 for an initial two-year residency that, with some interruption, would ultimately last for more than 23 years. Next to the Mangarevan Expedition, Zimmie considers his association with the Natural History Museum (London) and the eminent weevil expert, Sir Guy Marshall, to be the most influential experiences of his scientific career.

IN DEVON WITH R. C. L. PERKINS

One of Zimmie's first objectives upon reaching England was to drive to rural Devon, where at the edge of Dartmoor the 83-year-old R. C. L. Perkins lived in retirement. Perkins had

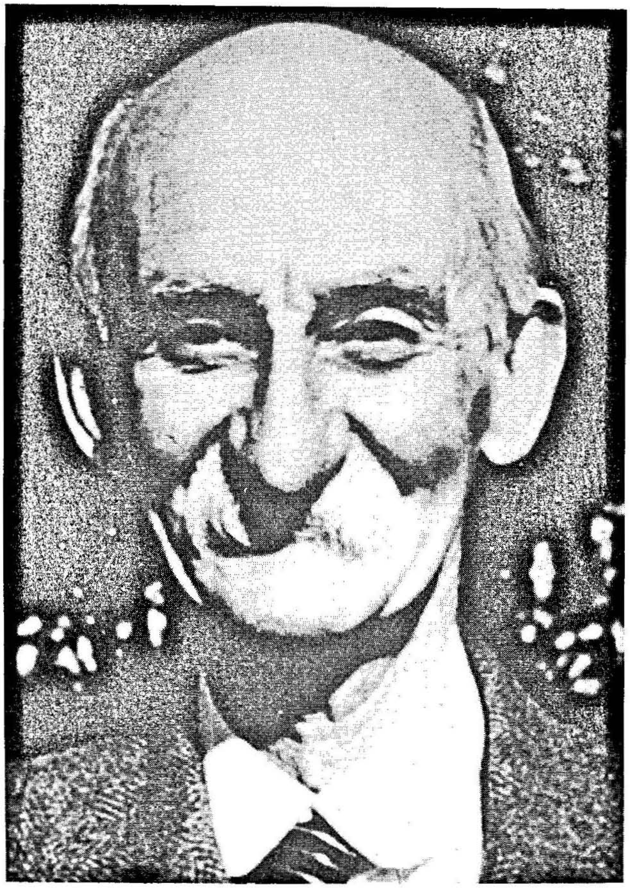

Figure 3.—This photograph of R. C. L. Perkins (age 83) was taken by Zimmie in 1949.

been sent out to Hawaii in the late 19th Century as part of a long-term research project undertaken by Cambridge University's "Sandwich Islands Committee." Perkins remained in the islands for more than 25 years, initially collecting and cataloging the Hawaiian fauna on behalf of his English patrons and later working for the Hawaiian Sugar Planters' Association. Even in old age Perkins retained an uncanny, near-total recall of his Hawaiian field collecting experiences, topics on which the two men had corresponded extensively throughout the 1930s and 1940s. At one of his meetings with Perkins in Devon, Zimmie recalls receiving precise directions from memory for a beetle collecting locality from the 1890s. The site involved a distinctive tree to be found some distance off a mountainous trail on the slopes of Tantalus, above Honolulu. Back in Hawaii in 1951, Zimmie was able to relocate this same tree, but in the intervening decades alien ants had come to dominate the area and the native beetle was no more.

Perkins arrived in Hawaii in the early 1890s, just at a time when the islands were poised on the cusp of a major extinction spasm that would devastate the native fauna. He was able to make extensive collections of Hawaiian birds and invertebrates, many of which would vanish completely within a few short years, ravaged by feral ungulates, expanding plantation agriculture, and the relentless arrival of new alien species (from ants to mongooses) and diseases. Collectively, these events led to the rapid disappearance of many endemic species and near obliteration of entire native ecosystems, particularly in the lowlands. Zimmie's heady collecting days on Rapa in 1934 were perhaps the closest he would ever come to savoring an entomological paradise such as Perkins had found in Hawaii more than 40 years earlier.

Zimmie spent most of the 1950s and 1960s working on his *Insects of Hawaii* monographs as an Honorary Associate at the British Museum of Natural History, and at his secluded home in Peterborough, New Hampshire, which allowed easy access to the library at Harvard's Museum of Comparative Zoology. For his Pacific work he received a DIC degree from Imperial College of Science and Technology, and a Ph.D. from University of London in 1956. During this period he subsisted on NSF grants and private funds. With his long absence from Honolulu, research funding became more problematic, as Bishop Museum personnel changed and more fashionable research priorities came to the fore. In 1957 and 1958, three further volumes of his *Insects of Hawaii* were published by the University of Hawaii Press (Zimmerman 1957, 1958a, 1958b). Also in 1958, Zimmie (who had done some earlier work on the Hawaiian *Drosophila;* see Zimmerman 1943) authored a short, provocative paper (Zimmerman 1958c) entitled: "300 insect species of *Drosophila* in Hawaii?—A challenge to geneticists and evolutionists." This paper helped stimulate one of the most outstanding and scientifically rewarding long-term, multidisciplinary research efforts in the history of evolutionary biology, encompassing systematics, genetics, ecology, and ethology of the *Drosophila* complex (see Williamson 1981).

By the early 1970s time was running out for the completion of Zimmie's *magnum opus.* Funding had dried up and Zimmie, never the politician, was no longer closely connected with the new generation of Museum and University researchers in Hawaii. In 1972 a rescuer appeared on the scene in London in the person of Douglas Waterhouse, Chief of the Division of Entomology of Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO). The rescue required a cruel Hobson's choice for Zimmie—continuing his lifelong but now unsupported work on *Insects of Hawaii* (with five volumes on the beetles and four on wasps and bees still in preparation) or moving to Australia to refocus his career on the Australian weevil fauna, with generous financial, technical, and clerical support beyond imagination on even the best days of his almost forty-year Hawaii campaign. His ultimate decision to sacrifice the completion of *Insects of Hawaii* would leave him emotionally scarred for life.

AUSTRALIA: SO MANY WEEVILS, SO LITTLE TIME

If Zimmie's plan to monograph the Hawaiian insects, conceived at age 22, seemed brash and audacious, what adjectives can be used to characterize his new initiative, begun at age 60 in 1973—arriving in Australia for a frontal assault on an impossibly large, Gondwana-aged, continental-scale weevil fauna! Apparently in need of additional outlets "to keep body in tone," upon settling in Australia the Zimmermans acquired a working cattle station near the rural town of Yass, 40 kilometers north of Canberra. For more than a decade, ranching was to occupy Zimmie's "after work" hours.

With but a few brief diversions to tie up loose ends on some of the unfinished Hawaii work [e.g., completion of the Microlepidoptera volume (Zimmerman 1978) and his more recent collaboration with J. K. Liebherr on Hawaiian carabid beetles (Liebherr &

Figure 4.—Zimmie and Hannah in Honolulu on June 24, 1998, at the University of Hawaii Regents' Award ceremony. (Regent John Hoag at left; photo by R. Chinn, University of Hawaii)

Zimmerman 1998, 2000)], Zimmie has devoted the last 27 years to the systematics of Australian weevils. By 1990, as manuscripts, illustrations, and color plates for the first five volumes of *Australian Weevils* were nearing completion, Zimmie again found himself confronting the same problems that had truncated his earlier Hawaiian efforts. Both Zimmie and his decades-transcending projects kept outliving their original benefactors and institutional supporters! Waterhouse was by this time long retired, and there seemed to be a new scourge underfoot at CSIRO: declining government support for science, and "professional administrators" chanting a perpetual mantra of down-sizing. In the end the Zimmermans were forced to liquidate their cattle ranch and personal effects, heirlooms, and rare books to subsidize publication of the initial five volumes of *Australian Weevils,* which appeared between 1991–1994 (Zimmerman 1991, 1992, 1993, 1994a, b). His cumulative publications now included more than 10,000 pages (and 20,000 illustrations). In addition, Zimmie and Hannah were able to endow a permanent position at CSIRO for ongoing and future Pacific weevil research. This position is now filled by Rolf Oberprieler, who continues to work actively in collaboration with Zimmie on new volumes of *Australian Weevils.*

In 1992 the Zimmermans relocated from their ranch to the New South Wales south coast at Merimbula. Here, in a home overlooking Tura Beach, ensconced with his extensive private library, large comparative collections, and a well-equipped laboratory, Zimmie continues to work with an uncommon dedication and passion. In his 89th year, with still steady hands, he continues to make dissections and illustrations of minute details of weevil morphology and internal anatomy.

In recognition of his lifelong scientific contributions to Pacific science, Zimmie was awarded a D.Sc. degree from London University in 1980. In 1983 he was awarded the Karl Jordan Medal for his work on the Hawaiian Lepidoptera. In 1995 he received both a special CSIRO medal and the Herbert E. Gregory Medal at the Beijing meeting of the Pacific Science Congress. In 1998 Zimmie was awarded both the Order of Australia from the Australian Government and the Regents' Medal of Distinction from the University of Hawaii.

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To My Friends and Counselors

CHARLES MONTAGUE COOKE, JR.
OTTO HERMAN SWEZEY

Keen Observers
Learned, Unselfish Servants of Science
By Whose Gleanings from Nature Men Will Prosper

FOREWORD

Need has long existed for an up-to-date and comprehensive work on the insects of the Hawaiian Islands—a work which would be of immeasurable benefit as a handbook for scientists, as a textbook for students, and as a reference for horticulturists, quarantine officers, and specialists in our sugar and pineapple industries and other branches of Hawaiian agriculture. Indeed, as agriculture of a highly specialized and scientific order is our basic economy, it is hard to visualize anyone in Hawaii who would not benefit, directly or indirectly, by the existence of a detailed monograph on the insects which each year cause damage amounting to hundreds of thousands of dollars.

Many insects of Hawaii are common to other Pacific islands and to many continental areas as well. A basic book on the insects of the Hawaiian Islands will serve as a solid foundation for studies of the insects of islands elsewhere in the Pacific Basin, and should in itself prove interesting and useful to investigators the world over.

Since 1934, when he returned from an expedition to the south Pacific, Elwood C. Zimmerman has been working on just such a study. He embarked upon his ambitious project as a young man who (perhaps fortunately for those of us who will benefit by it) was not fully aware of the enormity of the task nor of the obstacles and diverse activities which were to impede its progress during the succeeding years. Even without the inevitable interruptions, the project could never have been completed on a forty-hour-a-week basis; and it was only by dint of determination and a devotion involving very considerable personal sacrifice that the basic work on an anticipated twelve- to fifteen-volume set was done and the first five volumes completed for publication.

Mr. Zimmerman is eminently well qualified for this courageous undertaking, the comprehensiveness of which is staggering in this day of specialization. These first five volumes justify the confidence placed in him over the span of fourteen years which he devoted to this work—work which was interrupted by exploratory trips to many Polynesian islands and by the publication of more than one hundred papers.

It had been originally intended that *Insects of Hawaii* would be published by the Bishop Museum. The text expanded to such proportions, however, as to impose an excessive financial burden on that institution, and prospects for publication became indefinite. The Experiment Station of the Hawaiian Sugar Planters' Association, whose staff Mr. Zimmerman had joined in 1946, recognizing the great practical need for this work, encouraged the author to continue his labors. Early in 1948, the manuscript, accompanied by a grant-in-aid from the Experiment Station to the amount of one-half the cost of publication of the first five volumes, was offered to the University of Hawaii Press. This sum was matched by the University of Hawaii and the manuscript was accepted by the University of Hawaii Press. Through this cooperative arrangement, the early publication of the first five volumes of *Insects of Hawaii* was assured.

The University of Hawaii is proud to join with the other institutions in the publication of *Insects of Hawaii,* and wishes Mr. Zimmerman all success in the completion of his valuable contribution to the store of scientific knowledge.

GREGG M. SINCLAIR
President, University of Hawaii

PREFACE TO THE FIRST FIVE VOLUMES

This work was started soon after the completion of the Bishop Museum's Mangarevan Expedition to southeastern Polynesia in 1934. I arrived in Hawaii following that unique field experience filled with the enthusiasm and spirit of scientific research, fresh from exploration in some of the very islands which thrilled Charles Darwin, and instilled with the marvels of evolution and biogeography so vividly displayed by island life. I found Hawaii to be the most remarkable of any group of islands I knew, and I soon felt a great need for a revisional work which would contain essential facts about the Hawaiian insect fauna, would serve as a guide to all students, and would give workers here and abroad a better appreciation and appraisal of our accomplishments and our problems. The monumental *Fauna Hawaiiensis* is available, but is far out of date in many respects and is inadequate in many ways for our present purposes; it is largely the repository of original descriptions. Consequently, I determined to assemble a working outline of the Hawaiian insects. These five volumes represent a part of my results.

Plan of the Work.—These first five volumes include the "Introduction" and, in phylogenetic order, cover the groups of insects from the Thysanura through the Homoptera. I had hoped to include all this material in a single book, but the text increased until it was decided to divide it into five volumes. Thus, the volumes may be purchased or used separately, and many specialists no doubt will want to obtain only the volumes covering their special fields of interest.

There remain to be treated in subsequent volumes the following orders: Ephemeroptera, Neuroptera, Trichoptera, Lepidoptera, Coleoptera, Strepsiptera, Hymenoptera, Diptera and Siphonaptera. I want to prepare also a volume on the history of Hawaiian entomology and to issue a general checklist of the recorded species of all the orders. Most of the fact-gathering and bibliographic work for these future volumes is complete. Final preparation and publication rest largely upon time and facilities being made available for the work.

This work has been written to be used in conjunction with the *Fauna Hawaiiensis* and the *Proceedings of the Hawaiian Entomological Society*. It is assumed, therefore, that serious users will have these fundamental sources of Hawaiian entomology available and will use them as adjuncts to these pages. One or more of the leading textbooks of general entomology and a glossary should also be at hand.

The total number of insects listed in these first five volumes is about 1,100. The *Fauna Hawaiiensis* included about 500 in the same groups. Hence, these volumes show an increase of about 120 percent in the number of species known to occur in Hawaii. The proportion of native to immigrant species as listed herein is about 672 native species to 420 adventive species. There is a large number of endemic species yet to be described, and several recently immigrant species are not recorded here. The total number of known Hawaiian insects is approaching the 6,000 mark.

An attempt has been made to present in these volumes an enormous assemblage of information in compact form. Much time has been devoted to the preparation of keys (about 275 of them in the four systematic volumes) in the belief that they will, when used with the illustrations, take the place of individual descriptions. References are given to all original descriptions and to other pertinent literature, and these will have to be referred to when necessary.

There has been assembled a surprisingly large literature about Hawaiian insects. However, the more important bibliographies of particular groups of species usually are not very extensive. Thus, one learns quickly that R. L. Usinger's major work on the Hawaiian *Nysius* bugs was published by the Bishop Museum in 1942, and when the contracted reference "Usinger, 1942:60" is given, one will soon know what to look for without referring to the detailed bibliography for the complete title. I realize that this system has certain disadvantages, but I believe that its merits overshadow its faults.

Most abbreviations, including authors' names, belong in working notes. They have been kept to a minimum in this text, because I consider them confusing, particularly to foreign scholars and students, and not infrequently to the most skilled specialists.

No attempt has been made to compile complete data on the extra-Hawaiian distribution of all of the non-endemic insects, but the information which has come to hand has been incorporated. Many of the adventive species are found on more of the Hawaiian Islands than are recorded for them, but unless records have been seen in literature or specimens examined, I have been unable to complete the distribution lists. Specialized collecting will supply information to close many gaps, and it is expected that some readers will take pleasure in trying to supply new distributional data and annotating their copies of the text. The publishing of incomplete records should be a stimulant to such activity. Complete listings of synonymies have not been included under the adventive species, but those which have appeared in Hawaiian literature have been listed. Also, I have not included all of the misidentifications, the immigrant and introduced species which apparently have failed to become established here, or those which have been recorded by genus only, or those which belong to the quarantine records.

Inevitably, parts of this text are already out of date; the new discoveries and reports of the active group of Hawaiian entomologists will make it further behind the times as it goes through the time-consuming intricacies of publication. I plan, tentatively, to publish each year a supplemental paper in the *Proceedings of the Hawaiian Entomological Society* in which notes, corrections and certain additions will be incorporated—or perhaps someone else will undertake the task or carry on after me. Thus, one can keep his volumes annotated and corrected by referring to the *Proceedings*. This manuscript was closed with the year 1946, and only a few of the species which have come to attention since that year have been added.

Reference should be made to the *Proceedings of the Hawaiian Entomological Society* for pertinent information after the 1946 issue of that journal.

Before I began writing this text, I had not worked on any of the groups contained in these first volumes. They and their literature were generally unfamiliar to me. Obviously, this has been a serious handicap, for one of the greatest difficulties encountered when writing about unfamiliar groups is the proper evaluation to assign to various features. This deficiency will be, I fear, only too evident to my critics.

I have read the manuscript and proofs for this work many times, but there has not been a reading when I did not have some new material to add, or that I wanted to add, which had come to hand since the last reading. A few hours spent in the garden or on a field trip usually reveals some or many new things which I should write more about. There is no end!

This work has its share of errors—errors of omission and commission. What appear to be facts today may prove to be errors tomorrow; it is inevitably thus in science. Of course, there are also those many slips of the pen and the typographical errors that will escape notice until the printed page is done. My readers are encouraged to find, reveal and correct the errors, and the keenness of their criticism will be a measure of their interest in this work. This text can be made better only by use, revision and correction. Some sections of it are presented here more as working outlines than as completed projects; it will take years of study to perfect them. I urge my readers to send corrections and criticisms to me or to the Secretary of the Hawaiian Entomological Society so that they may be made available to all interested persons.

It is obvious that one of the major contributions of this work is its several thousand illustrations. These are of paramount importance in conveying clear opinions without excess verbiage. They speak for themselves. There are not enough illustrations here, and many of them are not as good as they should be. I hardly need to say that it is difficult and expensive to illustrate such a manual. One often has only imperfect specimens to work with (and, surprisingly enough, this applies to the common species as well as to the rare ones); or they do not lend themselves to good rendering in this technique or that; or there may be no specimens available to illustrate. I have been fortunate, however, in having the aid of some highly skilled artists who are responsible for the splendid reproductions offered here. (They are not to be blamed for the unsigned sketches made by the author, however.) I have encouraged them to render their skills in various ways, so that we could present a variety of types of entomological art work. It is regrettable that only a modest fund was available for the furnishings of drawings; hence, some of the sections are not illustrated as adequately as they should be. Here, again, we have compromised, but the artists have given us a set of illustrations of great and lasting value which would enhance the value of any text.

Acknowledgments.—To acknowledge the generous cooperation I have received is a pleasure. This work has been accomplished through the cooperation of many men and women in several institutions at home and abroad. Without their aid, *Insects of Hawaii* could not have been written.

First of all, I wish to thank the Director of the Bishop Museum, Peter H. Buck, and the Trustees of the Museum. Under their direction I have been given ample quarters and allowed to carry on this task as a principal project of the department of entomology. I particularly want to thank them for having trust in me as a scientist, for assigning me a quiet office, with appurtenances, where I could work, plan and think with a minimum amount of disturbance and outside interference while doing the job. Few men have had such an opportunity; perhaps this is one reason why such monographs are not common. To write such a long and complicated report, one must have a quiet retreat and be left undisturbed as much as is necessary to accomplish the task. Even under the best of conditions, such a work is extremely difficult and trying on one's physical resources. Interference, interruptions and lack of quiet make for errors and inefficiency. I wish to thank them also for grants-in-aid which enabled me to have many of the beautiful drawings made by leading entomological draftsmen, for many kind favors and for their interest in and patience with a long-term project.

The Experiment Station, Hawaiian Sugar Planters' Association, where I have been employed since the beginning of 1946, under the very able direction of Harold L. Lyon until March, 1948, and now in the capable hands of L. D. Baver, has assigned me the task of completing *Insects of Hawaii* as my major project. Although Dr. Baver has assumed the directorship since these first five volumes were completed, he has shown keen interest in the project and has been kind and generous in his support of my work. Dr. Lyon has shown a singular interest in the monograph and has made me feel that I was doing something worth while. He has been cheerful and generous with his aid, and I have been buoyed up by his continued encouragement. He has always given freely of sound advice and has championed the cause over the roughest of ways.

The Trustees of the Hawaiian Sugar Planters' Association have given the project excellent support. They are to be thanked especially for their broad-minded approach to the problems of basic research in an industrial institution. They are keenly aware that some projects which appear to be far within the realm of "pure" research frequently are ones which pay large dividends of lasting value. I hope that these fruits of my labors will repay the Hawaiian sugar industry for its large investment in these pages. There are few industries which can boast of such support to basic science, but this is a tradition of long standing with the H.S.P.A.

The Board of Regents of the University of Hawaii have contributed generously to the publication fund and have made it possible for the work to be issued by the University of Hawaii Press. The University's President, Gregg M. Sinclair, has given the enterprise his full support and has lent an encouraging and helpful hand.

There are two men to whom I owe more than I can express adequately on these pages. In the light of the knowledge of the natural history of Hawaii held by these learned, but all too modest, naturalists, my own learning appears meager and immature. I have written down much of what I know, but they have more information about the Hawaiian flora and fauna stored in their minds than I shall ever know. I refer to C. Montague Cooke, Jr., and Otto H. Swezey. They have been my close friends and advisors and my valued companions on expeditions to the south Pacific. They have been storehouses of knowledge from which I have drawn heavily. Such men are made rarely.

Dr. Cooke has been as a leading and guiding light to me for many years, and whatever success I may have achieved or shall achieve in my studies of the Pacific is in large measure because of him. I consider myself his very willing and fortunate protégé. He has been more than a friend and colleague—he has been as a father to me. I can never honor him enough.

Dr. Swezey has been a close companion ever since I came to Hawaii. He has guided me and introduced me to the intricacies of the Hawaiian insect fauna. He has aided me in ways too numerous to mention. His knowledge of the insects of our islands has been rivaled only by that of Dr. Perkins. For nearly half a century he has been responsible for more of the basic records in our entomological literature than any other person. I may try to follow in his footsteps, but I can hardly hope to catch up to him. I shall always be awed by the scope of his knowledge of Hawaiian natural history.

The entomological staff of the Experiment Station, H.S.P.A., took an active interest in this text many years before I was asked to join that institution, and the successful completion of this work is due in large measure to the interest and active participation of the Experiment Station. A large number of the photographs were made gratis by the Experiment Station before I was employed there, and the library, collections and other facilities were generously placed at my disposal. To C. E. Pemberton, Entomologist, in charge of the Department of Entomology, I am especially indebted. His interest, guidance, aid and encouragement have helped me carry on in the face of many difficulties. To him belongs much of the credit for seeing that these volumes finally have been published. F. X. Williams has been an ever-flowing spring of freely given knowledge. R. H. Van Zwaluwenburg read the systematic text in manuscript before I joined the Experiment Station, and his aid has been continuous and invaluable since I began the work. Unfortunately, I have had no personal contact with R. C. L. Perkins, distinguished retired member of our staff, but we have carried on through correspondence, and he has given me much help. Further acknowledgments to our staff appear in appropriate places in the text.

The artists whose illustrations appear in this work have made an outstanding contribution in supplementing the text. Nearly all the photographs were made at the Experiment Station by W. Twigg-Smith and J. T. Yamamoto, mostly by Mr. Yamamoto. Frieda Abernathy, now of the Division of Entomology and Parasitology, University of California, has produced a large set of beautiful ink and wash drawings which are a splendid contribution in themselves. R. L.

Usinger supervised her drawings of the Heteroptera, E. O. Essig those of the aphids and S. F. Bailey those of the Thysanoptera. We were fortunate in having Arthur Smith make a fine set of drawings, mostly of type specimens, at the British Museum (Natural History), where his work was supervised by N. D. Riley and W. E. China. G. F. Ferris took such an interest in the text that he supplied an unequaled array of plates of coccids. Professor Ferris's contribution calls for special comment in volume 5. F. X. Williams made a number of drawings especially for this work and supplied a large number of his original drawings used in previous publications and rearranged here. I am deeply indebted to all these artists who have given much to aid workers both in Hawaii and abroad.

It is a pleasure to acknowledge the aid given by several librarians who have done much to help with the difficult tasks involved in bibliographic work. Mathilde M. Carpenter, U. S. National Museum, and Mrs. M. A. Frazier, Museum of Comparative Zoology, Harvard, gave freely of their time during my research visits in 1941. The library facilities at the University of California and the California Academy of Sciences were used extensively during my visits to those centers. I am indebted to the Bishop Museum for making it possible for me to visit these institutions in 1941 to consult literature not available in Honolulu. In Hawaii, Mabel Fraser, Experiment Station, H.S.P.A., and Margaret Titcomb, Bishop Museum, have contributed much to this work. For more than a dozen years Miss Fraser has borne cheerfully the brunt of many of the most difficult of the bibliographic problems encountered. During the past few years her assistant, Jean Dabagh, has helped in many ways.

Harold St. John, University of Hawaii, and Marie Neal, Bishop Museum, have helped with the identification of hostplants for many years, and I am grateful for their aid.

To C. F. W. Muesebeck and his competent staff of the Division of Insect Identification, U. S. Bureau of Entomology and Plant Quarantine at Washington, I am deeply indebted for favors too numerous to mention in detail here. Although he and his staff are continuously overwhelmed by work, not one of my many requests for aid has been ignored. They were particularly helpful during my visit to Washington in 1941, and they were joined by E. A. Chapin and R. E. Blackwelder of the National Museum, who also did much to make my research successful. Additional acknowledgments will be found in succeeding volumes.

Likewise, N. D. Riley and his associates at the British Museum (Natural History) have contributed much to the molding of this series of volumes.

My close friend and colleague since school days, R. L. Usinger, has taken an active interest in *Insects of Hawaii* and has given whole-hearted aid and encouragement.

There remains to be thanked a group of people who all too frequently remain as anonymous contributors to published works. I am deeply grateful to Juliette Wentworth, editor, University of Hawaii, who has shown unusual understanding in the preparation of this technical manuscript for the printer. It has been a rare pleasure to work with her, and her broad-minded approach to editorial complexities and her understanding of the author's problems has been most gratifying. She has done much to make these volumes better for the users. She has had the able association of Margaret Blegen, and Jean Kangeter, Helen Matthews and Richard S. Cowan have given aid in the reading of proof. Typing of most of the manuscript was done by Mrs. S. Austin, Patience Wiggen Bacon and Violet Sumi at the Bishop Museum. Thomas Nickerson, head of the Office of Publications, University of Hawaii, has taken a keen interest in the work and is largely responsible for the facility with which it has been issued from the University Press, and I am deeply indebted to him for many kind favors. Leonard Tuthill, Editor of *Pacific Science* and Associate Professor of Entomology at the University, has been an active participant in the editorial and publication details. The printing and engraving departments of the Honolulu Star-Bulletin have given excellent cooperation, and these printed pages and the illustrations they bear speak for them and the care they have taken in setting the type and making the engravings.

E.C.Z.

Honolulu, Hawaii
June, 1948

INTRODUCTION TO VOLUME 1

The text of this volume of *Insects of Hawaii* was read, in abstract form, as the address of the retiring president of the Hawaiian Entomological Society, December 14, 1942. It is premature, for it would have been better to have written the discourse after this proposed series of volumes had been completed and after many intricate problems had been investigated more thoroughly. But the completion of such a task as this involves many years of study, and who knows whether conditions will enable the author to finish his work? However, this presentation is justified as stimulation to further study, as a foundation upon which to build and as a review of pertinent problems.

The foundations for this essay were laid during the Bishop Museum's Mangarevan Expedition to southeastern Polynesia in 1934, and from then until the outbreak of the recent war most of the remaining data were assembled. It was not thought that so many years would pass between the presentation of the manuscript in 1942 and its publication. Much has been accomplished in the Pacific since this paper was read. Thousands of new soundings have been made, the "guyots" of Hess ("sea mounts" of some observers) have been described, deep holes have been drilled on Bikini, thousands of specimens and a large amount of new information have been assembled and some notable papers have been published. The pressure of other work made it impossible for me to revise the entire manuscript to include many of the new facts, but I have not seen any reports which would change the conclusions put forth here. This thesis remains, then, essentially as it was presented to the Hawaiian Entomological Society in 1942.

I fear that my "insular isolation" in some ways has had a delimiting effect upon my work, and perhaps many of the errors and weak points in this volume could have been avoided had I been exposed to the "rigorous competition" of a "continental environment" during the preparation of the final draft. One's work is bettered by association with students keenly interested and actively engaged in the same and bordering fields of endeavor, but many authorities have not been available for personal consultation, nor has it been possible for them to have seen the manuscript. However, I have been fortunate especially in having close and stimulating association with several leading students of Polynesia who are resident in Hawaii. C. M. Cooke, Jr., has been particularly interested in the text for this introductory volume and has been a source of constant aid, enlightenment and encouragement. Dr. Cooke read much of the manuscript, and his constructive criticism has been most helpful. He and his assistant, Yoshio Kondo, have given me much help with problems concerning Polynesian land molluscs. O. H. Swezey has aided in many ways with several sections. C. K. Wentworth and W. O. Clark read the section on geology, H. E. Gregory gave aid on various problems, and F. X. Williams read the chapters on dispersal and development. Harold St. John and F. R. Fosberg have given valued aid on Polynesian botany. Ernst Mayr and Dean Amadon of the American Museum of Natural History have given much help during our discussions of problems of Polynesian birds. Dr. Mayr has been a constant source of encouragement, and his well-known publications have been a source of inspiration. R. H. Van Zwaluwenburg has read all the proof sheets, and I am much indebted to him for his aid and interest in the work. I owe these men many thanks.

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INSECTS OF HAWAII

CHAPTER 1

GEOLOGICAL HISTORY OF HAWAII

> *Time is a sort of river of passing events, and strong is its current; no sooner is a thing brought to sight than it is swept by and another takes its place, and this too will be swept away.*
>
> —*Marcus Aurelius*

Although the gross features of the geology of the Hawaiian Archipelago are comparatively simple, I might wisely hesitate to enter into a discussion of a field so far outside my own. However, there are those who still persist in looking for the mystical in the islands of Oceania and who insist upon vast and ancient Pacific continents or great land bridges that are supposed to have vanished beneath the waves to account for the development and distribution of the particular groups of organisms composing their special fields of research. At the risk of repetition for those few workers who have studied the geology of some Polynesian islands, a discussion review of the geological foundations of Hawaii is essential for the proper understanding of the subjects that follow. Moreover, even the rudiments of the established geological facts regarding these islands are not wholly familiar to the majority of biologists.

As a result of geological study, it is known that the Pacific Basin is underlain by heavy basaltic rock; that in the continents generally lighter or metamorphosed rocks rest on heavier under-layers; and that continental shelves extend for various distances under shallow coastal waters and then terminate rather abruptly at the edge of the deep water which is of remarkably uniform depth of about 12,000 to 15,000 feet and more in the true Pacific Basin; that the volcanoes now above sea level have risen from great depths and have been built of basic rock, and that in no islands in the central Pacific Basin have true continental rocks been found. So far as it is known to geologists, the only pre-existing extensive land masses in the tropical Pacific, since the rise of modern floras and faunas, are those west and north of Australia and on the New Guinea–New Caledonia–New Zealand axis, possibly extending eastward to near the Tongan Trough in the neighborhood of Fiji. There is no geological evidence to indicate the existence of any large land masses east of Tonga and Fiji.

However, in spite of the carefully recorded geological data, some biologists continue to raise great masses of millions of square miles of sea bottom 12,000–18,000 or more feet, and then sink them into oblivion without a trace of the requisite diastrophic action, to account for the distribution of a few organisms whose presence on certain islands constitutes a puzzling problem to the worker in question. Thus, Jeannel (1937), to account for the presence of two tiny ground beetles in Hawaii, believes that the islands once formed a part of a great land

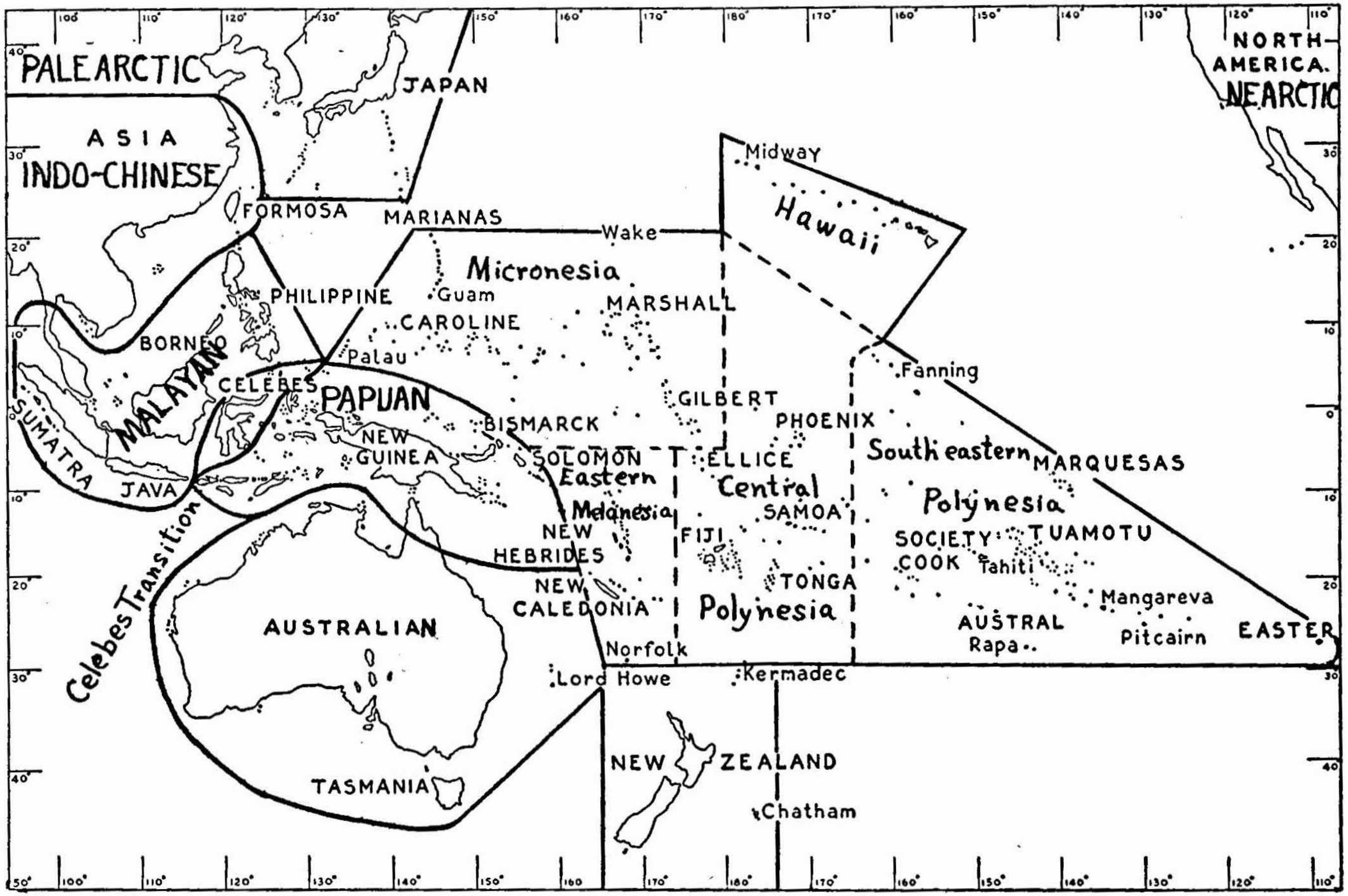


Figure 1.—Map of the central and western Pacific showing zoogeographical divisions. The five provinces of Polynesia are connected by broken lines and labeled in lower-case letters.

mass connected to "Gondwana" and that the beetles migrated to Hawaii in Jurassic times. The fact of the matter is that these two beetles were recently accidentally introduced with plants imported into Hawaii and are now established in the soil at the Sugar Planters' Experiment Station in Honolulu! Crampton (1932, and recent discussions) would "create" a great land mass extending from the Marianas and Palau Islands over 5,000 miles to southeastern Polynesia to account for the distribution of a single genus of land snails and gives no heed to many other land snails of the same area whose distributions are quite the opposite of his proposed land mass, to say nothing of other genera of plants and animals. It is difficult to conceive that such a great continental area would founder and leave only the few organisms now used for support by the "continentalists" as evidence of its existence. All our continents have developed great and distinctive floras and faunas, and the partial submergence of any of them would leave on isolated areas abundant evidence of the characteristic biota, not just a few snails.

As said elsewhere (Zimmerman, 1942:282):

> So many continents and land bridges have been built in and across the Pacific by biologists that, were they all plotted on a map, there would be little space left for water. Whenever a particularly puzzling problem arises, the simplest thing seems to be to build a continent or a bridge, rather than to admit defeat at the hands of nature, or to consider the data at hand inadequate for solving the problem. Most of the land bridges suggested to account for the distribution of certain plants and animals in the Pacific create more problems than they solve. If the central and eastern Pacific ever included large land areas and bridges, there would be some indication of the consequent peculiar development of the fauna and flora, but there is no such evidence.

WHAT IS HAWAII?

Hawaii is a great chain of 18 islands, several satellite islands and various islets, reefs and shoals extending on a northwest–southeast line from about 178° 29′ to about 154° 51′ west longitude between about 18° 5′ and 28° 25′ north latitude, an extreme length of over 1,500 nautical miles (1,660 nautical miles has been given as the extent from Hawaii to an unnamed shoal 280 miles from Kure) and a maximum spread of a little more than 600 miles in latitude. The northwestern island is a coral atoll; the southeastern island's volcanic summit rises to the maximum Hawaiian elevation of 13,784 feet. The islands are "north sea" islands, for the southernmost island is about 1,100 miles north of the equator. This line of islands may be divided into two groups. Those islands extending southeast from Niihau and Kauai to Hawaii are spoken of as the main or windward group; the remainder to the northwest, called the leeward group, consists of small reefs, islets or rocks which support only a small number of indigenes. In this paper, then, the entire chain of islands will be considered, and the two groups will be referred to as the main, or high, islands and the leeward islands. The main group consists of eight islands and several satellite islets. However, two of these islands, Niihau and Kahoolawe, were so completely denuded by grazing animals and their native products brought so close to extermination so many years before

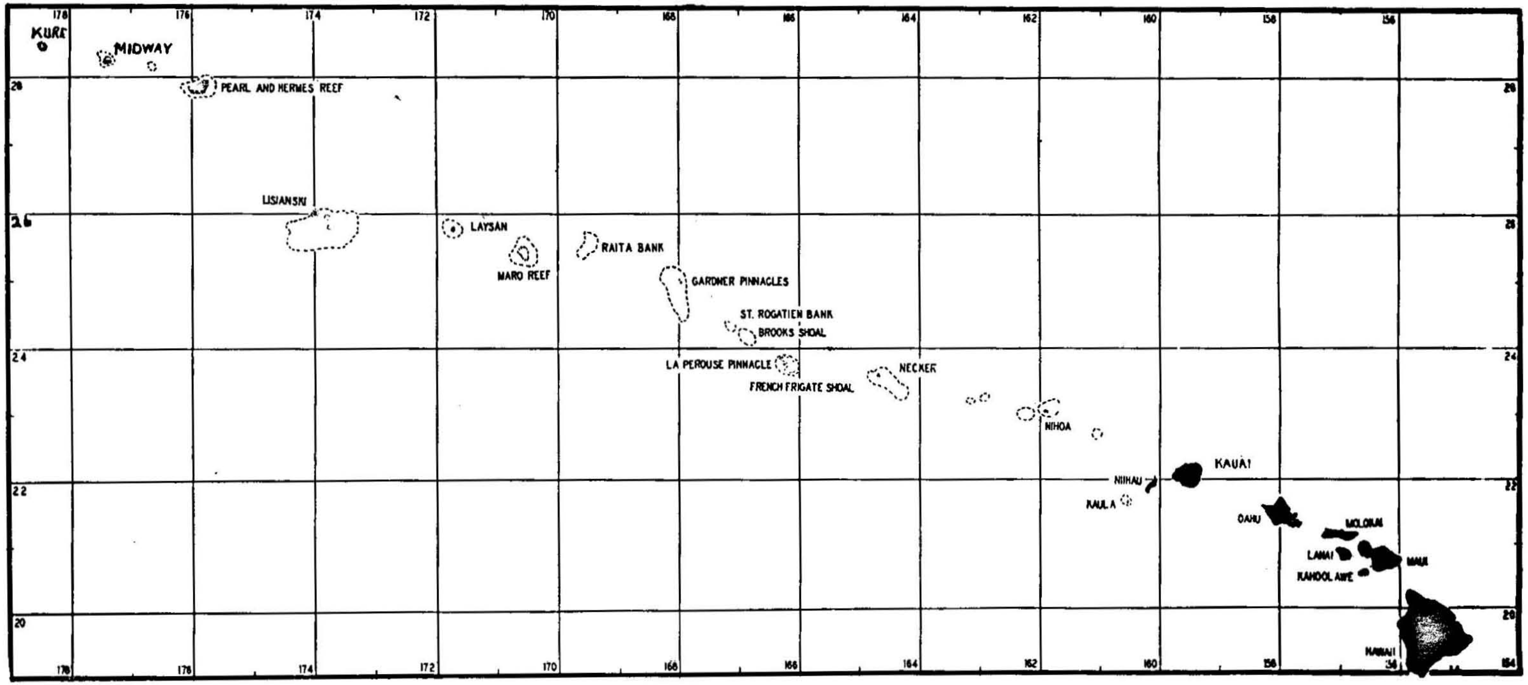


Figure 2.—The Hawaiian Archipelago. The shoal areas in the leeward islands are outlined at the 100–fathom line. Compare the sizes of these areas with those of the main islands.

natural history surveys were begun in Hawaii that they are mostly omitted from the discussion because we have almost no knowledge of their native floras and faunas. Therefore, the biota of the six main islands of Kauai, Oahu, Molokai, Lanai, Maui and Hawaii forms the foundation of our work.

The northernmost island of the leeward group is about as far north as the mouth of the Mississippi River, or about 200 miles south of Shanghai; the southernmost island is as far south as Mexico City, or approximately at the same latitude as the most northern tip of the Philippine island of Luzon. The north and south spread of the main islands in latitude is about equivalent to that of Cuba, and the length of the group of main islands is somewhat more than one-half the length of the island of Cuba. The length of the entire chain is about equal to the distance between Montreal, Canada, and Havana, Cuba, or between London and Moscow. The length of the main group of islands approximates the distance between Boston and Washington, D. C., or from Dover to Belfast.

The islands lie in the mid-Pacific. The nearest continental land is the coast of California to the east, or the Aleutian Islands to the north; both of these areas are about the same distance from the main islands. San Francisco is 2,091 nautical miles from Honolulu. Dutch Harbor, Unalaska, is somewhat closer. The nearest high islands (volcanic, that is) to the main islands are the Marquesas, the nearest of which is approximately 2,000 miles from the southern tip of the island of Hawaii. If we use Honolulu as a reference point, the following distances are significant:

Yokohama, Japan	3,394 miles
Hongkong, China	4,857 miles
Manila, Philippines	4,767 miles
Sydney, Australia	4,420 miles
Auckland, New Zealand	3,840 miles
Suva, Viti Levu, Fiji	2,783 miles
Pago Pago, Tutuila, Samoa	2,276 miles
Papeete, Tahiti, Society Islands	2,381 miles
Panama Canal	4,685 miles

The nearest island to any of the Hawaiian islands is the coral atoll of Johnston Island, which is about 600 miles from the nearest main island, Niihau, and about 450 miles from the nearest leeward island, French Frigate Shoal. Directly to the south of the main islands, a string of atolls, known as the Line Islands, connects with the Society Islands and the Tuamotu Archipelago. This line of coralline islands begins at Kingman Reef, which is about 850 miles south of the island of Hawaii, and continues southward through Palmyra, Washington, Fanning, Christmas, etc. The nearest islands to the southwest, beyond Johnston, are the coralline Gilbert and Marshall Archipelagos, which average about 2,000 miles from Honolulu (some of the Marshalls are 1,200–1,500 miles from the most leeward Hawaiian islands), and the Phoenix Islands, the nearest of which are 1,600–1,700 miles from the nearest main island; Howland and Baker are about 1,500 miles from French Frigate Shoal, the nearest Hawaiian island. To the west lies the isolated coral atoll of Wake, about 2,000 miles from Honolulu, or about 1,100 miles from the nearest leeward island (Kure). Then come the Marianas, which are all over 3,000 miles from the nearest main Hawaiian island and over 2,000 miles from the most westward of the leeward islands. There is no land to the north of Hawaii until the Alaskan Peninsula and the Aleutian Islands are reached. The nearest of the Aleutian Islands are about 1,400 miles from the most northern Hawaiian island, Kure, and nearly 2,000 miles from the nearest main island; and there is no deep-sea island between Hawaii and the North American continental shelf.

AREA, ELEVATION, ETC.

The present areas of the small leeward reefs, rocks and islets are negligible, for they total only a few square miles, and for comparative purposes may be omitted from this discussion. The accompanying table has been compiled from data assembled by Wentworth (1939).

Only two of the United States, California and Washington, have greater ranges in elevation. Only California, Washington and Colorado have mountain peaks more than one foot higher than Hawaii's 13,784-foot Mauna Kea.

The total area of 6,435 square miles may be compared with some other areas with advantage to the discussion farther along in this paper. This area is equivalent to about 1/1,243 part of North America, 1/470 of continental United States, 1/457 of Australia, 1/24 of the state of California, 1/16 of the combined North and South Islands of New Zealand, 1/5 of Ireland, or 4/5 of the state of Massachusetts. The following areas of other islands, in approximate areas in square miles, may be compared:

New Guinea	312,329
Borneo	285,000
Sumatra	164,480
Philippine Islands	114,400
Luzon 40,814; Mindanao 36,906	
Celebes Islands	69,255
Java	50,000
South Island, New Zealand	58,525
North Island, New Zealand	44,468
Solomon Islands	16,975
Formosa	13,892
New Caledonia	8,500
Fiji Islands	7,070
New Hebrides Islands	5,700
Samoan Islands	1,200
Society Islands	600
Marquesas Islands	400
Tonga Islands	385

HAWAII: OCEANIC OR CONTINENTAL?

This problem involves the evaluation of both geological and biological criteria. In the following commentary, some of the salient facts regarding the building of the islands from the ocean floor, and the life supported by them, will be discussed.

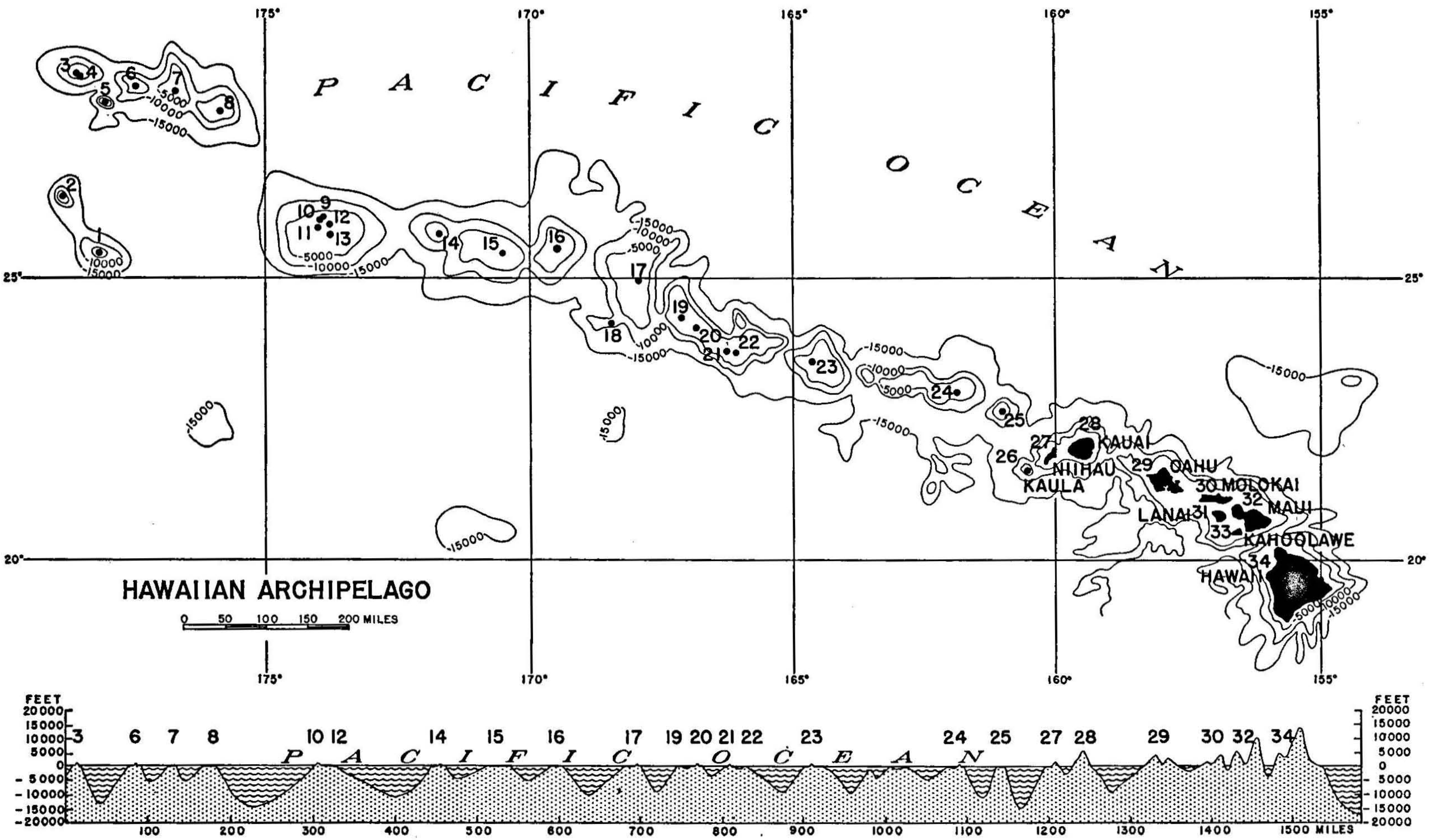
The Hawaiian Islands are oceanic; there is no evidence whatsoever to support the contention that they are of continental origin or character, or that they were ever joined together in an elongate subcontinental land mass or even in a continuous subaerial mountain range. The great body of evidence amassed from the study of both geology and the biota supports the oceanic opinion; "... the eastern oceanic insect faunas could not have become what they are with any great land areas or bridges in the central Pacific; their very character precludes those possibilities. The known groups are the results of overseas sifting; there are too many groups lacking for any other means of dispersal to have been involved." (Zimmerman, 1942:282.)

SIZE AND LAND AREA OF MAIN ISLANDS OF THE HAWAIIAN ARCHIPELAGO

ISLAND	EXTREME LENGTH	EXTREME BREADTH	PERIMETER	EXTREME ELEVATION	AREA (TOTAL = 6,435)	AREA OVER 20 MILES INLAND	AREA 10–20 MILES INLAND	AREA 5–10 MILES INLAND	AREA 0–5 MILES INLAND	GREATEST DISTANCE FROM COAST
	miles	*miles*	*miles*	*feet*	*sq. miles*	*sq. miles*	*sq. miles*	*sq. miles*	*sq. miles*	*miles*
Hawaii	93	76	319	13,784	4,030	346	1,365	1,110	1,209	28.5
Maui	48	26	160	10,025	728		2	172	554	10.6
Oahu	44	30	190	4,025	604		1	126	477	10.6
Kauai	33	25	112	5,170	555		6	177	372	10.8
Molokai	38	10	104	4,970	260				260	3.9
Lanai	18	13	53	3,370	141				141	5.2
Niihau	18	6	47	1,281	72				72	2.4
Kahoolawe	11	6	37	1,415	45				45	2.4

The breadths of the channels between the islands are roughly as follows in land miles:

Niihau–Kauai	17	Molokai–Lanai	9
Kauai–Oahu	73	Maui–Lanai	9
Oahu–Molokai	26	Maui–Kahoolawe	6
Molokai–Maui	9	Maui–Hawaii	29


175°
170°
165°
160°
155°
25°
20°
PACIFIC OCEAN
HAWAIIAN ARCHIPELAGO
0 50 100 150 200 MILES
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
KAHOOLAWE
HAWAII
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
-5000
-10000
-15000
FEET
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500 MILES

THE PACIFIC BASIN AND THE DEPTHS OF THE SEA IN THE HAWAIIAN AREA

The Pacific is the oldest, largest, broadest and deepest of the oceans; it has many characteristic features of its own; but it is the least known of the oceans. In spite of the lack of detailed surveys of many of the ramifying fields of oceanography, there are known some pertinent and dominant data regarding the gross features of the Pacific Basin which are fundamental to any research on the distribution and development of the biota. These criteria are all too frequently overlooked or are neglected by biologists. But they are basic—they cannot be ignored. Any theory concerning the distribution of plants and animals which fails to take these data into its primary scope has its foundations built upon unsound blocks—its very beginnings spring from error. Certain workers in the past have been prone to substitute daydreaming and wishful thinking for the less exciting, more laborious tedium of routine research when attempting to solve their individual problems of biogeography. Also, more often than not, some workers develop a theory to account for their particular problem and fail to take into consideration the all-important implications of such a theory on the study of the entire biota and on the sum total of the geology of the region included.

In describing the Pacific Ocean, I can do no better than to quote the summary of topographic relations written by H. E. Gregory (1928) after a number of years of intimate association with all phases of the study of the Pacific as Director of the Bishop Museum. Gregory says:

> The Pacific Ocean is a huge affair: it is long and wide and deep. From Bering Sea to Wilkes Land on the Antarctic Circle the distance is 9,300 miles, and along the equator the distance is 10,000 miles—two-fifths of the circumference of the earth—and more than three times the width of the Atlantic. These great stretches of water form the axis of an area comprising more than 55,000,000 square miles—the area of the United States is about 3,000,000 square miles. The Pacific is nearly twice the size of the Atlantic and greater in area than all the continents and islands combined. The volume of Pacific water is incomprehensibly great. If all the lands above sea-level—plains, plateaus, and mountain systems—were piled into the Pacific they would sink to the bottom and be submerged at a depth of about 12,000 feet. If the water were drained from the Pacific the descent from the present shore line to the floor of the deepest valley would be greater than the present ascent to the loftiest Himalayan peak.
>
> In a geological sense this vast water-filled basin comprises two parts: (1) The Pacific continental border and associated continental islands; (2) oceanic islands, which have no genetic relation to continental masses. The line separating these two parts extends from New Zealand past the Kermadecs, Tonga, and Samoa, and continues northward in an undetermined position. West of this line the islands, shoals, and intervening spaces have been structurally parts of

---

Figure 3.—Map and profile of the Hawaiian Archipelago showing the submarine contours in feet. 1, unnamed shoal; 2, Bensaleux Reef; 3, Kure or Ocean; 4, Green; 5, Nero Bank; 6, Midway; 7, Gambia Shoal; 8, Pearl and Hermes Reef; 9, Lisianski; 10, Fisher Reef; 11, Minor Reef; 12, Neva Shoal; 13, Springbank Reef; 14, Laysan; 15, Maro (Dowsett) Reef; 16, Raita Bank; 17, Gardner Pinnacles; 18, Two Brothers Reef; 19, St. Rogatien Bank; 20, Brooks Banks; 21, La Pérouse Pinnacle; 22, French Frigate Shoal; 23, Necker; 24, Nihoa; 25, unnamed shoal; 26, Kaula; 27, Niihau; 28, Kauai; 29, Oahu; 30, Molokai; 31, Lanai; 32, Maui; 33, Kahoolawe; 34, Hawaii. (After Stearns, 1946. Cut loaned by U. S. Geological Survey, Honolulu.)

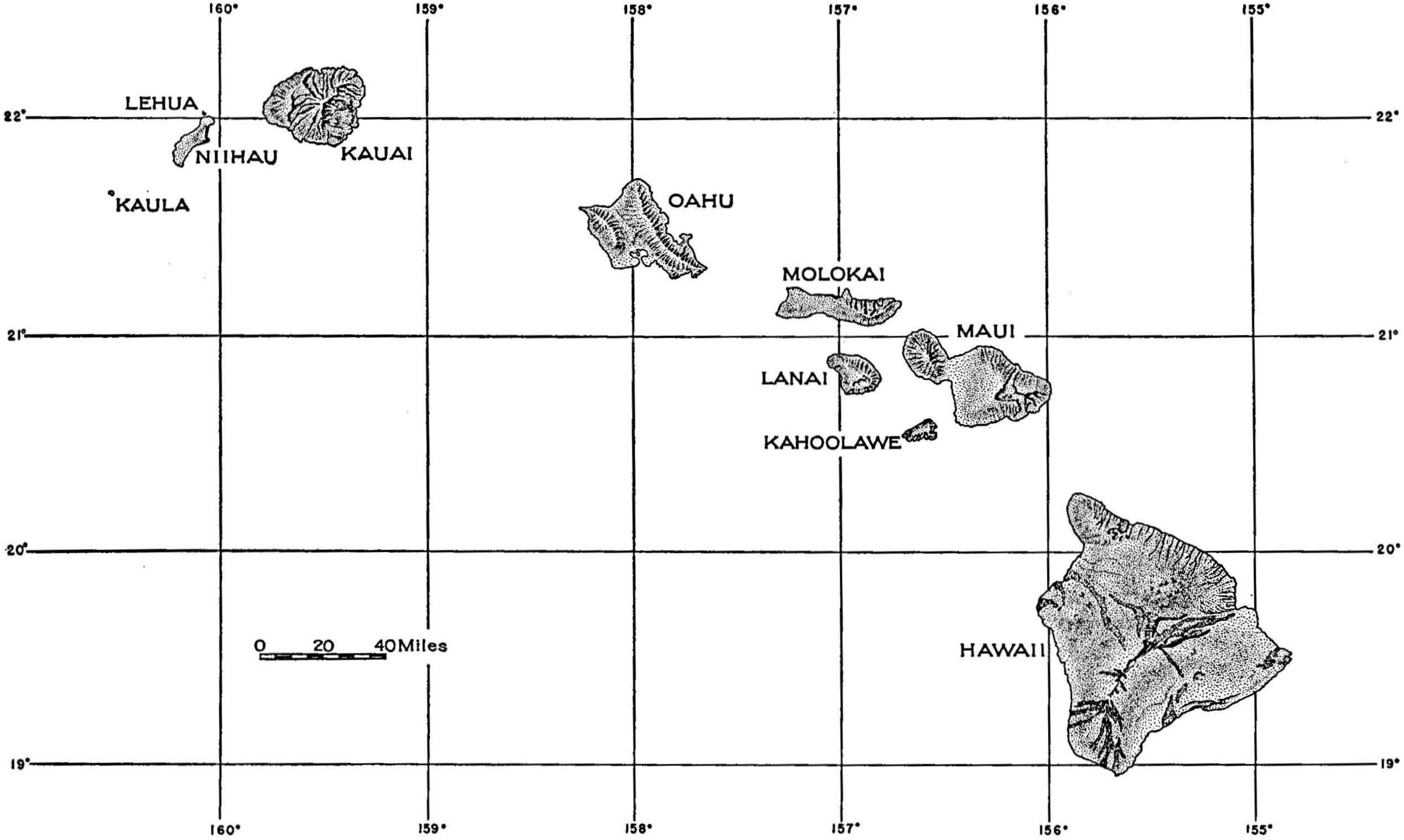


Figure 4.—The main islands of Hawaii. (After Stearns, 1946.)

large land masses. They have been submerged and emerged, connected and disconnected, in various combinations at several periods during geologic time. They occupy a region of general crustal unrest.

East of this changing border of an Australian-Asiatic continent and extending nearly to the American shores is the true Pacific depression, a submerged region of plateaus and intervening broad valleys from which rise mountain masses with relatively small areal bases. The general arrangement is a floor at profound depth from which rise volcanic masses as individual mounds or combined to form ridges or long, narrow submarine highlands. Most of these peaks and ridges terminate below sea-level and are revealed only by soundings; some of them terminate above sea-level and stand as islands. But they are true oceanic islands; they have never been parts of the continents of Asia, Australia, and America. They are all volcanic masses with outer slopes descending steeply to great depths. Some of them retain their original form;

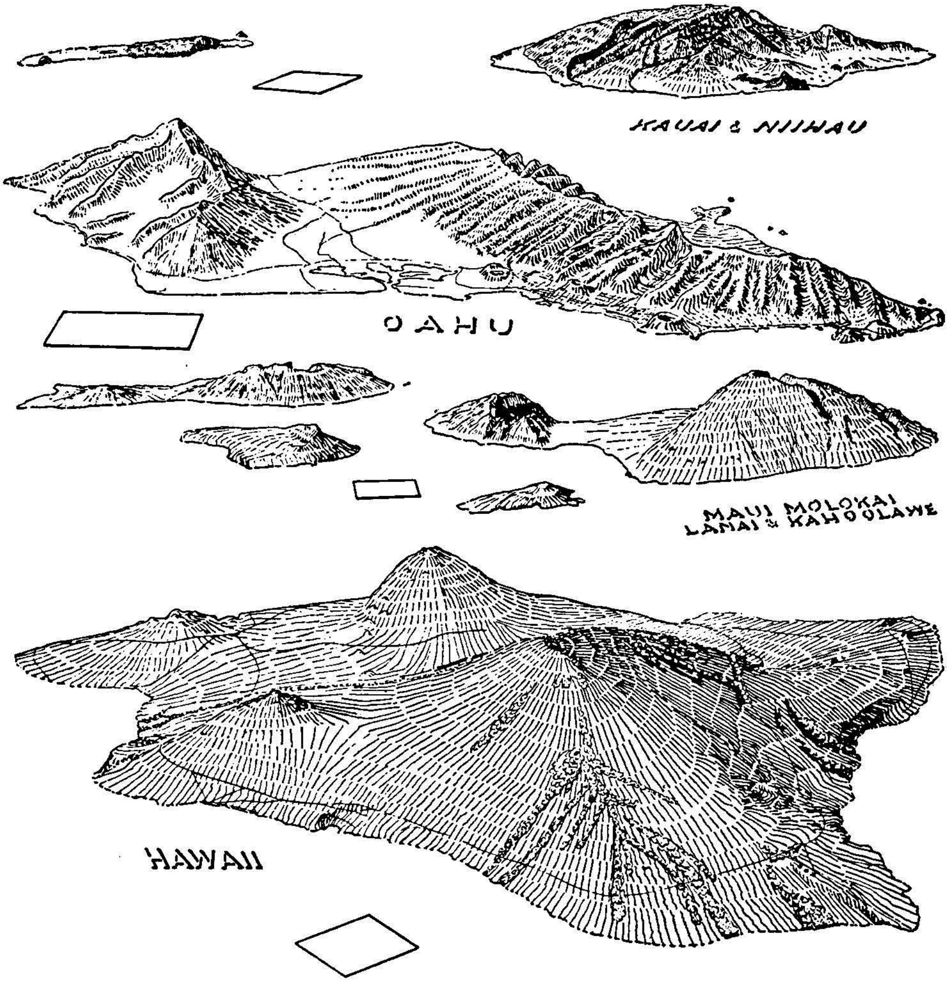


Figure 5.—The main Hawaiian Islands separated into four groups and arranged in perspective. The horizontal scale is indicated by quadrangles 5 miles square. The vertical scale is somewhat exaggerated. (Rearranged from Wentworth, 1939.)

> others are much eroded, and still others have worn down to submarine platforms on which grow coral reefs.
>
> Unlike the western Pacific, the eastern Pacific has experienced relatively few changes. Its present depth and position of islands are essentially those of past geologic times. The evidence shows that most Polynesian oceanic islands have experienced uplift and subsidence at different times, at different rates, in different amounts, at different places. So far as known, the extreme range in oscillation is something like 1,200 feet, so that islands now separated by less than 500 feet of water may have been nearly or quite joined, but islands now separated by as much as 1,000 feet probably were not joined, and parts of the sea floor at greater depth doubtless have never felt the air. There is no geographic evidence for greatly enlarged islands, vanished archipelagoes, or "lost Pacific continents."
>
> For the Pacific as a whole perhaps the most significant feature of land distribution is the extension of Asia southeastward through the Malay Peninsula and on through Sumatra, Java, Celebes, Ceram, Papua—five big islands associated with many small islands in such manner as to form nearly continuous land. And beyond Papua as far as Fiji the Ocean is packed with islands. In essence this great region of Indonesia and Melanesia is a suburb of Asia. In age and composition its rocks are those of the continent; its animals and plants predominantly are those which now live or once lived on the larger land mass.

Gulick (1932:421) ably emphasized the disproportionate amount of open sea in the Pacific when he wrote ". . . any part of the ocean where the proportionate area of fairly deep sea falls as low as 98 per cent, and the area above water becomes as great as 0.2 per cent is treated by geographers as dense archipelago. It is, geologically unlikely, therefore, that this vast area could ever have been actually continuous land, as that would involve a considerable alternation in the isostatic balance of a whole major region of the earth, although faunistic arguments favoring such a supposition have been brought forward. . . ."

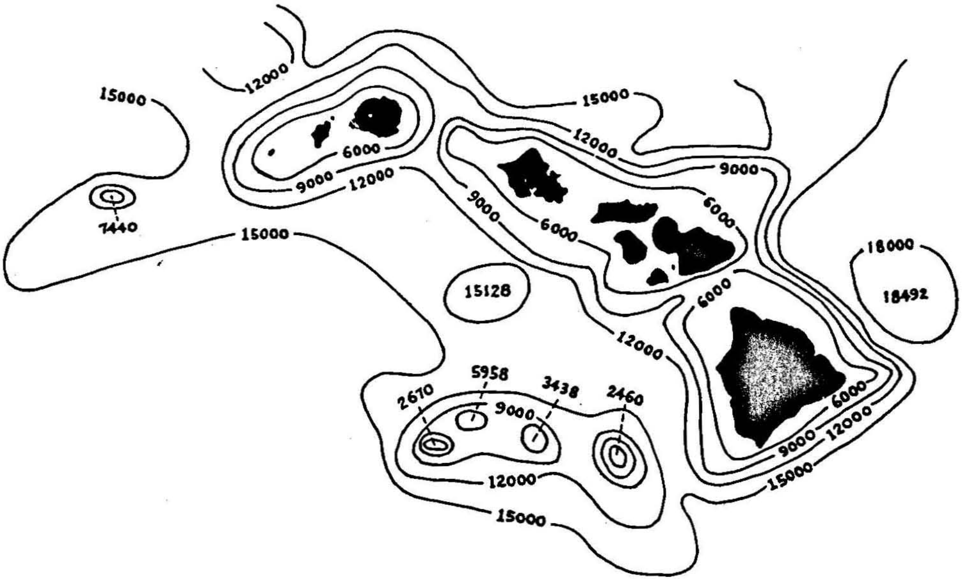


Figure 6.—Submarine contours around the main Hawaiian Islands. Depths in feet.

E. H. Bryan, Jr., has tabulated (in manuscript) the islands of Micronesia, and he has informed me that in the Marshalls, Carolines and Marianas there are 77 coral islands and 20 islands with exposed basalt. These units contain 2,148 individual islands whose combined land area is only 903 square miles, about a quarter of which is made up by the island of Guam alone.

The area of the Pacific is variously given with great discrepancies, but according to one source (National Encyclopedia) the area is about 71 million square miles, or more than the combined areas of the Atlantic (40 million) and the Indian (29 million) Oceans. The average depth of the Pacific is said to be about 15,000 feet. The greatest depths recorded are along the northern and western sides. South of the Aleutian Islands the Albatross Deep is recorded as 24,012 feet. Ramapo Deep, southeast of Yokohama, is 34,626 feet deep. Mindanao Deep, close to the northeast coast of Mindanao, Philippines, is 35,400 feet deep. Aldrich Deep in the Kermadec Island region is 30,930 feet deep. Other "deeps" occur along the South American coast.

According to information given by the U. S. Coast and Geodetic Survey chart 4000, the Hawaiian Island chain from Hawaii to Kure, within about 75 miles on either side of the islands, is surrounded by depths between 15,000 and 17,000 feet. In some localized areas irregularities are indicated. For example, within 30 miles of the east coast of the island of Hawaii a depth of 18,876 feet has been recorded (thus, the continuous slope between the top of Mauna Kea and this deep is 32,660 feet within 60 miles!). Farther out to the south there are depths that exceed 18,000 feet between Hawaii and Kingman Reef. There is no suggestion whatsoever of extensive submarine ridges or banks which might indicate shallow-water connections with any other archipelago extending outward in any direction from any part of the Hawaiian Archipelago. There is positive evidence to indicate that here and there within 500 miles, for example, there are areas shallower than 15,000 feet which are indicative of local volcanic activity that stopped before building any great underwater masses which approached the surface. On the other hand there is said to be a submarine volcanic mass that rises as much as 13,000 feet from the ocean floor about 140 miles SSW of Honolulu. Also, there is said to be a submarine range of "high mountains" about 200 miles southwest of Necker Island. More detailed soundings will reveal additional irregularities. The floor of the central Pacific Basin is studded with hundreds of submarine volcanic masses of varied sizes and elevations which have never felt the air; some of them rise for several thousands of feet above the ocean bottom. This is as we should expect it to be in accordance with the basic theory which governs our present conclusions. It is probable that more adequate mapping of the ocean bottom will reveal that there are many more submarine volcanic cones in the basin than the number whose tops appear above the surface today.

If there were ever continental masses in the true Pacific Basin, various methods of physical measurement would reveal them. The study of seismological data alone brings to light some fundamental facts concerning the Pacific Basin. One need not send equipment to the bottom of the Pacific in order to sample the rock to know its basic nature. Earthquake waves travel at different rates through rocks of different densities and the differences in speed are indicative of the nature of the rocks. Thus Gutenberg (in Vaughan, 1937:41–44) notes that the speed of a wave in Recent, unconsolidated sedimentary rock is about 1 km./sec., but in basalt it is 5.00–5.75 km./sec. Using this method of analysis, he found a "difference in structure between the Pacific basin and all other regions of the earth." It was found that

> In the Atlantic and Indian Oceans, the total thickness of the crust is only a fraction of that on the continents; ... but in both oceans there still is a well-marked discontinuity between the crustal rocks and the mantle.... In the region of the Pacific basin no marked discontinuity

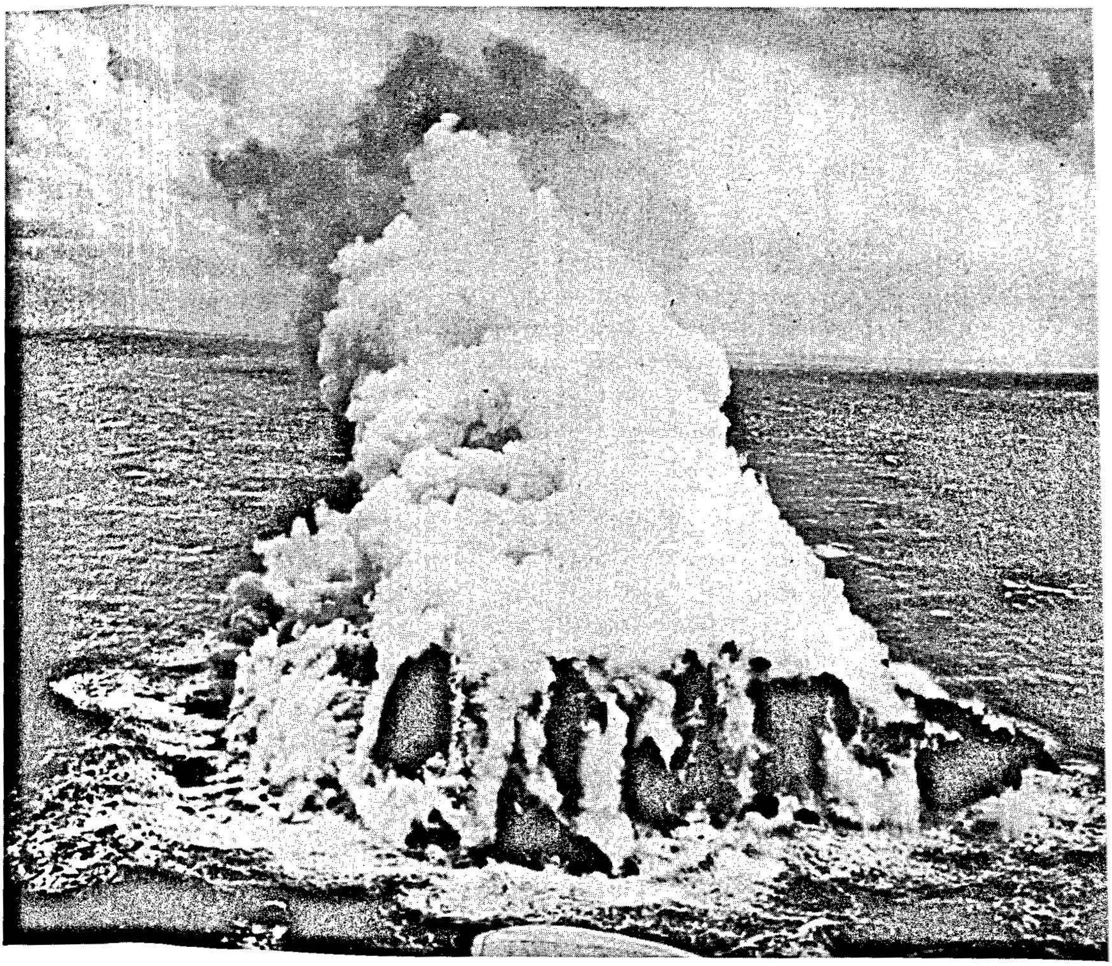


Figure 7.—A new Pacific island building up from the depths of the sea (31 degrees 58.5 minutes north latitude, 139 degrees 57.75 minutes east longitude). Our present Hawaiian Islands may have appeared similar to this when each first appeared above the surface of the sea. (Official U. S. Navy photograph, Pacific Fleet, 1946.)

> between crust and mantle exists; except for local accumulations of erupted basaltic material, it does not appear that the elastic constants neaı the rock surface differ significantly from those of the mantle.... It seems to be very probable that the continental layers consist of granite at the top, and rocks with increasing basicity at greater depths, that the bottom of the Atlantic Ocean is formed by the same type of rocks, the layers being noticeably thinner, and that the entire bottom of the Pacific Ocean and all regions of the earth at depths of more than 50 kilometers consist of very much more basic material than is characteristic of the uppermost part of the continents.

The following is Gutenberg's summary:

> ...we find that the region comprised within the limits of the Pacific Ocean...has one kind of structure and all other regions of the earth, perhaps excluding a part of the arctic basin, another. In these latter parts of the earth (non-Pacific area) there is a continental layer which consists of several shells. Its thickness is about 40-50 kilometers under the continents but decreases towards the Atlantic and probably the Indian Ocean, where its thickness is of the order of 20 kilometers. There is no indication that the continents have broken during any geological time and drifted apart; however, our findings would be in agreement with the assumption that in early geological times the thickness of the continental crust was different in many localities from what it is today and that plastic flow in the continental crust may have changed the distribution of land and sea in the area including all continents and the Atlantic and Indian Ocean.
>
> The basin of the Pacific Ocean proper is a unique element of the earth's crust and its boundaries affect the layers down to many hundreds of kilometers. As it is not evident how the continental crust could have been removed in a gradual way from the Pacific Ocean the conclusion seems to be probable that the Pacific Ocean either never had such a crust or that it was removed by a cosmic event.

Gutenberg and Richter in their paper "Seismicity of the Earth" (1941:82) say, "The Pacific basin is the largest of all the stable masses. Except for the single interval zone of the Hawaiian Islands, and for possible volcanic shocks in some other island groups, it is an area of complete seismic calm. This is particularly well established for the north Pacific."

Fleming (in Vaughan, 1937:52), in discussing magnetic ocean surveys, says that "under the Pacific Ocean the basic surface of the Earth's mantle is practically exposed. There then we may expect different geological and geographical properties from those found elsewhere," and he notes that there is a difference in magnetic variation over the Pacific "as witness the moderate rates of annual change over the Pacific as compared with those over the Atlantic and adjoining continental areas."

Unfortunately, detailed gravity research has not been conducted in the mid-Pacific, but such needed investigation should supply many pertinent facts. The incomplete gravity data available for Oahu indicate that the volcanic mass rises from an unbroken crust. Betz and Hess (1942) quote the following material from the work of Meinesz, who, in discussing gravity anomalies for Oahu, says, "As far as this scanty material allows a conclusion, we have seen that it points to the island being a volcanic load on an unbroken crust. There seems to be no root at the lower boundary of the crust or, if there is one, it cannot have great dimensions, for else the regional anomalies ought to show stronger deviations than they actually do. So we may conclude that the present material points to a crust which has undergone no shortening at all. This would determine the islands as huge volcanoes piled on the ocean-floor and pressing down this floor by their weight."

Even du Toit, that indefatigable student and advocate of continental drift, evidently finds the foregoing conclusions consistent with his basic ideas of the Pacific Basin. He says (1940:182), "The current idea of a subbasic to basic ocean floor finds support from earthquake waves, gravity anomalies, and volcanicity.... The ocean appears to have developed from a larger Mesozoic basin through the pressing-in of its framework in the manner pictured under the hypothesis of drift.... The intra-Pacific region remained neutral, though put in slight tension latterly, and is characterized by youthful basalts and nepheline-basalts emitted largely from vents. The circum-Pacific compression girdle is, from the Mesozoic onward, marked by recurrences of andesites and granodiorites."

Betz and Hess (1942) in preparing their recent paper on "The Floor of the North Pacific Ocean" have had available numerous new data including recent gravity studies and results of more than 35,000 sonic soundings made by the

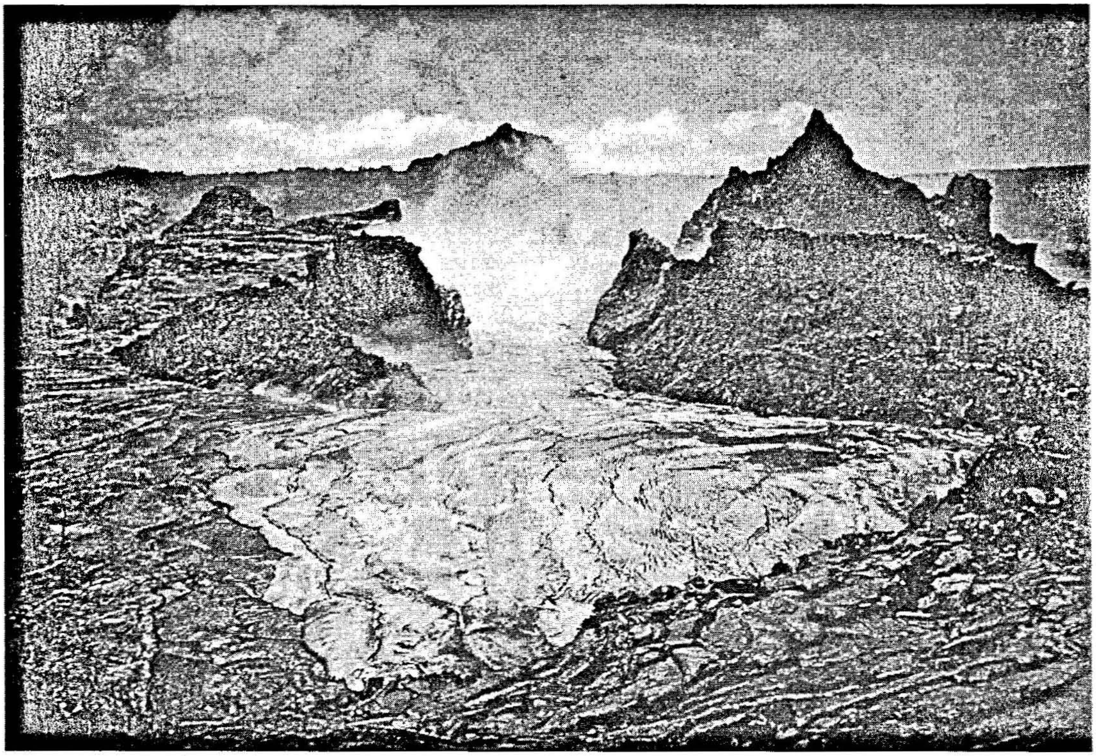


Figure 8.—An example of a principal feature in the upbuilding of the Hawaiian Islands: the outpouring of molten lava at Kilauea. (After Stearns and Macdonald, 1946. Photograph by T. A. Jaggar. Cut loaned by U. S. Geological Survey, Honolulu.)

United States Navy. Their careful weighing of the evidence leads them to conclude that the data now assembled do not support Chubb's conclusions (1934) that the mid-Pacific island chains arise from submarine ridges of fold origin. They agree with Williams (1933) that, if the volcanoes were removed, no submarine ridges would exist. They say (p. 108), "If the volcanic peaks are disregarded, the region of the islands would seem to be a hardly perceptible swell, not a ridge. ... Considering the probable strength and thickness of the crust, a fold of 600 miles wide (width of the Hawaiian Swell) seems improbable. In cross section, the configuration of the swell does not suggest folding." In place of the fold and ridge theory, Betz and Hess (1942:109) conclude that "A hypothesis that would entail the opening of fissures—perhaps tension cracks—on the floor of the ocean and the extrusion of large amounts of volcanic material to build up the gentle rise of the swell would seem to agree with present observations." Also, in reviewing the conclusions of Chubb, Williams and Powers, Betz and Hess say (p. 110) that "the opening of fissures to permit the extrusion of volcanic material is generally postulated, but the manner in which they developed is not agreed upon." They conclude that "Fissuring and volcanic eruption suffice to account for the Hawaiian Islands and similar island chains in the Pacific Basin...." Chubb (1934:295)

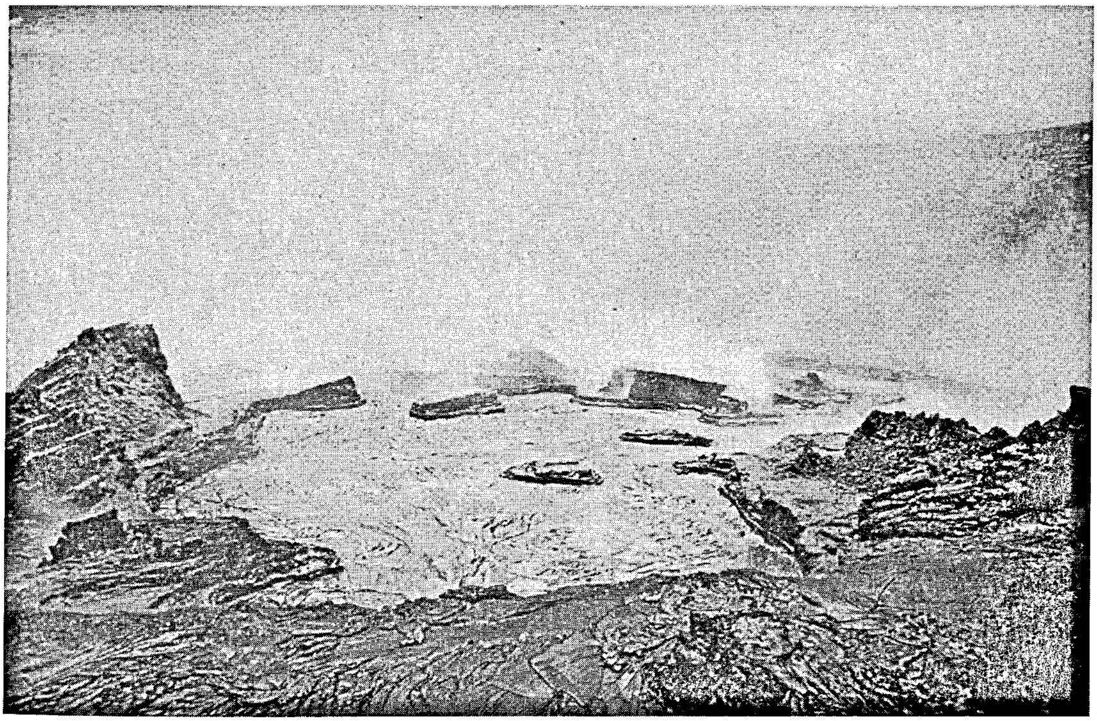


Figure 9.—Islands in the molten lava lake in Halemaumau, Kilauea. (After Stearns and Macdonald, 1946. Photograph by T. A. Jaggar. Cut loaned by U. S. Geological Survey, Honolulu.)

calls for strike faults and dip faults resulting from folding, and moving anticlines to account for the formation of the island chains. Williams (1933:7) suggests that the island chains "are located along lines of fracture, that they represent the summits of great volcanic cones developed on a more or less flat ocean floor by the outpouring of lava from crescentic fissures determined by the outcrop of thrust-planes with the curved surface of the globe." The findings of Betz and Hess do not support those of Chubb, and these authors do not recognize the crescentic thrust faults of Williams in the data at hand. They believe that "Any fault to be considered in the formation of the Hawaiian Swell was probably of such a nature that great vertical displacements did not occur generally along its course. This suggests to us the possibility that the swell may lie in a zone of trans-

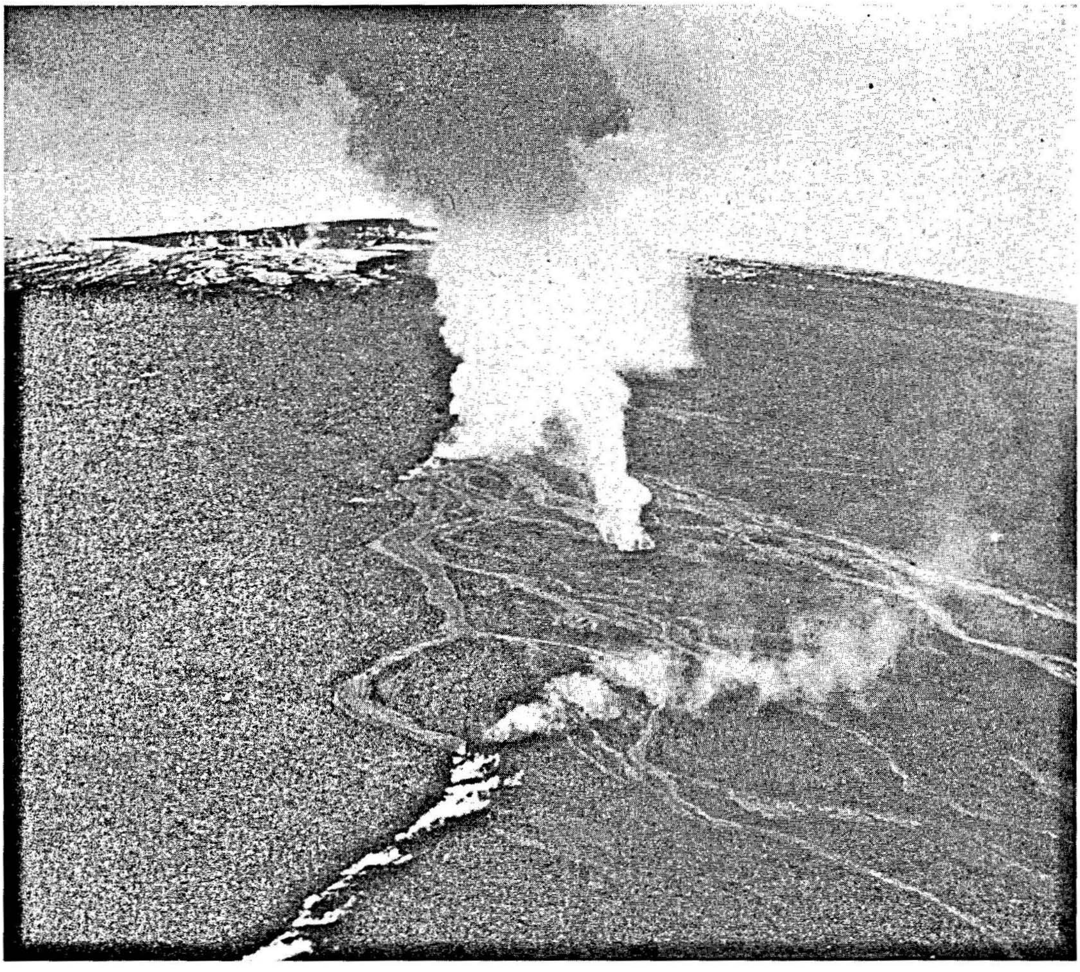


Figure 10.—The 1935 flank eruption of Mauna Loa. Photograph by U. S. Navy showing the fiery streams of lava flowing down the slopes. (After Stearns, 1946. Cut loaned by U. S. Geological Survey, Honolulu.)

current, or strike-slip, faults, such as the San Andreas fault [in California], with its dominant movement horizontal. The relative straightness of the Hawaiian trend, as well as of similar island trends in the Pacific Basin, implies that the probable fissures along which the volcanic material ascended were vertical or nearly so." The map prepared by Betz and Hess is significantly instructive.

DERIVATION AND CHARACTER OF THE ROCKS

The rocks of the Hawaiian Islands are derived from two basic sources: (1) basalts or related rocks from the molten magma of the earth's interior; (2) from the deposition of calcareous and organic materials by marine plants and animals. There are also minor deposits of calcareous and siliceous materials from solution. There are no earthy materials naturally present other than these or their derivatives. There are no commercial mineral resources available other than water, building stone, road metal, recent reef limestone, sand and similar products. There are no deposits of gold, silver, copper, precious gems or other such minerals or elements. There are no ceramic clays with the exceptional occurrence of some small, aberrant pockets of almost negligible commercial value found in a few restricted mountain areas. There are no glass-making sands. There is no coal. There are no metamorphic rocks. The rocks are characteristic of average, normal, isolated, oceanic islands.

THE BUILDING OF THE ISLANDS

Because of stresses set up in the earth's crust, a linear zone or zones of weakness developed along the north–west south–east line beneath what is now the Hawaiian Islands. Along this line, great submarine volcanoes burst through the weakened crust and poured forth uncounted cubic miles of lava. Broadly speaking, it appears that it was along the northern part of the line that the magma first broke through. How long ago this process of relieving tension began, no one knows; but it is known that the Tertiary—especially during and since the Miocene—was a period of extensive volcanism, and the beginnings of the Hawaiian Islands probably were during that period of the Cenozoic era. There appears to be no evidence of pre-Tertiary volcanism in the Hawaiian part of the Pacific Basin. At this early part of our discussion, therefore, we have dated the birth of the Hawaiian Archipelago as post-Cretaceous.

By a gradual process, the first islands were built up beneath the sea. Their beginnings were at great depths—between 14,000 and 18,000 feet below sea level. Unless the speed of upbuilding was greatly accelerated during the submarine period, the length of time required for the volcanic mass to reach the surface was far greater than its subaerial activity. This conclusion is obvious, because each of these islands has many times the bulk beneath sea level that it has exposed above the sea. There appears to be no good reason for supposing that the rate of outflow was extraordinarily accelerated at the beginning, although it is probable that it was somewhat more rapid than near the maturity of the volcanoes. The almost universal thinness of the lava flows supports this view.

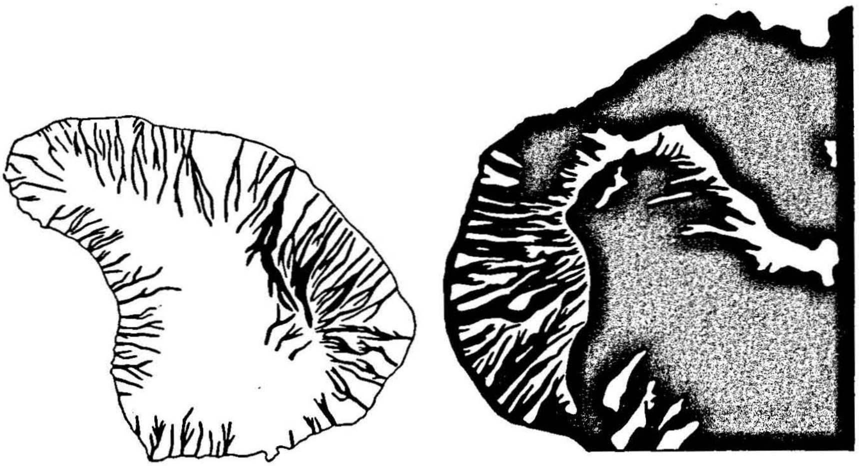


Figure 11.—Maps of comparatively young and old island areas to show amounts of the original surfaces which have been eroded away. The areas from which the original volcanic surface has been removed are shown in black. Lanai, one of the younger of the main Hawaiian Islands, is at the left. The greatly dissected southwest part of old Kauai is shown at the right. (After Wentworth, 1928.)

To some workers, it appears that the volcanic activity, or speed of upbuilding, is greatly retarded at the present time. However, such a conclusion may be misleading. The constructive processes of Mauna Loa during the past century of recorded eruptions indicate that enough material has been poured out of that mountain to raise its dome between three and six feet in one hundred years! It has poured out an estimated five to ten billion cubic meters of lava in the last century. The flow of 1859 added 600 million cubic yards alone. Mauna Loa is so huge that if Mount Rainier, Mount Hood and Mount Shasta in North America were placed within it, there would be space left over for ten more of any one of them, it is said. The smaller, visible part of the mountain contains more than 1,000 cubic miles of lava. If the construction rate of between three feet and six feet per century be taken not as fact but only for the purpose of illustration, a mountain 13,000 feet high could be built in about 225,000 to 450,000 years. The great volcanic mass that is the island of Hawaii appears to be the product of about a half a dozen separate major conduits whose combined action may have resulted in the construction of the mountains of that island in less eruptive time. On the basis of estimates of upbuilding of island areas in Hawaii, it is suggested that the constructive period for a 13,000-foot mountain might conceivably be as rapid as 45,000 or even 22,500 years! (But I am not intimating that such a spectacular speed has been attained, although it is theoretically possible.)

The history of Falcon Island in Tonga has been fairly well recorded, and a few notes taken from the United States Hydrographic Office "Pilot" no. 166, vol. 2, 1933, regarding it as an example of rate of growth may be of interest and not altogether out of place here. The island was discovered in 1865 as a reef;

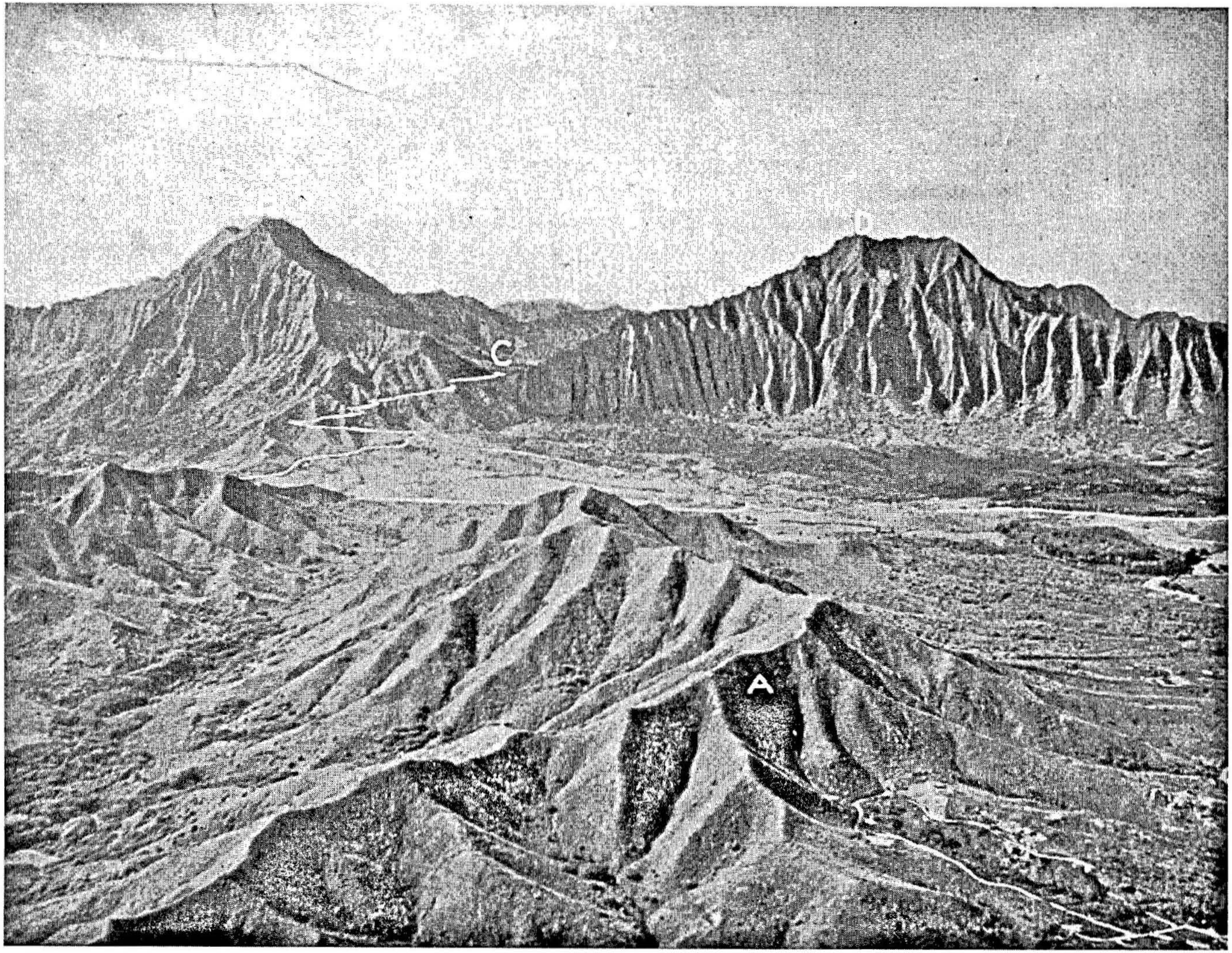
it was seen as an island above water in 1885; in 1889 it was 1.3 miles long, 1 mile wide and 153 feet high, and was estimated to have been two-thirds washed away since 1885; in 1894 it was almost entirely washed away; in late 1894 it was found to be 3 miles long, 1.5 miles wide and 50 feet high; in 1898 it had washed away again to a shoal about 100 yards long; in 1900 it was 9 feet high; in 1913 it was under water; in 1921 there were about 3 feet of water over it in its shallowest part; in 1927 it was steaming and found to be 1,739 by 1,430 yards in extent; in 1928 it was in eruption and reported to be about 2 miles long, 1 mile wide and 600 feet high; in 1930 it was reported to be about 1.2 miles long and 475 feet high. The average rate of growth between 1921 and 1928 was about 86 feet in elevation per year. However, this island is composed of cinders and ash, and its growth rate must be interpreted in the light of that fact.

There have been recorded enough soundings, around our main islands at least, to enable us to understand the gross underwater contours and extent of the islands. Each is a typical volcanic dome arising either from the floor of the ocean or breaking through the underwater slopes of a neighboring island. Their base is the floor of the sea—not an underwater platform which in any way can be called a "continental" type. However, the main islands are so close to one another that their bases have merged and all are united at depths from a few hundred feet, as between Maui, Kahoolawe, Lanai and Molokai, to more than 11,000 feet between Kauai and Oahu. They are true oceanic islands.

DEGRADATION OF THE ISLANDS

As soon as the islands were built, submarine and later subaerial activities—chemical and mechanical—began to tear them down. At the beginning, the rate of construction exceeded that of degradation and the islands rose out of the sea. However, as volcanism abated, the less spectacular but nevertheless gigantic forces of erosion took the forefront, and, with the exception of only parts of the island of Hawaii building up with its contemporary volcanoes, these islands are in the process of being torn down and flung back into the sea. In fact, most of the leeward islands have been completely worn away and have suffered subaerial removal as well as being cut off as far below sea level as the action of the waves and currents could abrade their tops, or they have been submerged to lower levels by subsidence of the land or rise in sea level. But some of those islands have entered into another constructive phase—a biological one—for today they are capped with coralline products. Again they have risen out of the sea as the waves have torn at the reefs and hurled the plant and animal skeletal and shelter material as high as the limit of storm action or tsunami ("tidal" waves), and winds have swept it farther upward. However, unless and until volcanism should break out in them again, or until they should rise in relation to sea level by diastrophism or climatic change, they are doomed to eons of time in the monotonous existence that is the fate of atolls.

These processes are not ended; they are in continued full force all around us. The land upon which we now stand is by natural law willed to the sea. Eventually,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all these majestic islands will meet a similar end—a burial at sea and a headstone of biological lime.

RATE OF DEGRADATION

The speed of erosion is the direct result of the action and combination of the destructive forces and the nature of the substratum involved in the given region. Weathering in the Hawaiian Islands needs to be interpreted in the light of the special conditions characteristic of the islands.

The topographic features of the islands above marine action are principally the results of chemical and fluvial erosion acting upon particularly susceptible strata. The bedding of lava flows of different porosity and resistivity, the enclosed lava tubes, cracks and weak zones, together with the other characteristics of the mountains, make for unusual permeability and are of major importance in the denudation processes and results.

In the words of Wentworth (1928:385,387) the erosional features of the islands

> ...are mainly the product of the normal erosional processes of the region, of which the conditions differ somewhat markedly from those of most temperate, humid, parts of the earth. The principal factors are the high porosity of the rock and its susceptibility to chemical weathering, the high mean annual temperature and the rarity of great ranges of temperature, the absence of frost and the high annual rainfall of certain parts of the group. As a result, chemical weathering at elevations near the low water table dominates the development of the deeper valleys and is a controlling factor in determining their configuration.
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> . . . .
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> The major structure of the rocks of the Hawaiian Islands is simple and uniform. The entire land mass above sea-level is made up of thin basaltic flows lying one on another to form cones some of whose bases are as much as 40 or 50 miles in diameter and whose summits rise to maximum elevations of nearly 14,000 feet above sea-level. The submarine dimensions of the cones are enormously greater. The individual lava flows are in the main from 5 to 20 feet thick, very few so far as known exceeding the latter figure over any considerable area. Most of the individual flows are limited to one side of the cone of which they form a part, and, in general, probably have a width of considerably less than the radius of the cone. The lengths of the flows vary from a few yards up to a few miles, and the areas of historic flows on the island of Hawaii range up to 20 or 25 square miles. It is apparent that unless the old flows which have formed the various islands were of far greater extent than the historic ones, there are great numbers of slight unconformities between over-lapping flows, but the exposures are so limited and the identification of key flows so difficult that the structure gives the impression of great uniformity and parallelism.

EROSION

Because of the tropical climate, frost action is a negligible factor in the degradation processes over the islands as a whole and is significant only on certain of the highest peaks (see section on glaciation). Eolian erosion probably had little

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Figure 12.—An extensively eroded landscape—the precipitous Nuuanu Pali, Koolau Mountains, Oahu. According to some investigators, Kokokahi Peak (**A**, in the foreground) is a root of the ancient firepit of the Koolau volcano. The highest peak in this range is Konahuanui, 3,105 feet, at **B**; Lanihuli is at **D**, and the Pali gap at **C**. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

to do with the principal erosional features of the islands before the advent of man and, more particularly, his grazing animals. However, the overgrazing of the dry island of Kahoolawe has resulted in an island that has been blowing out to sea for many years. Therefore, chemical, marine and fluvial erosion, together with the action of plant growth, are to be regarded as the prime factors of erosion in prehistoric Hawaii.

The sea and land have shifted and reshifted in reference to one another, and the attack of the sea at any given temporarily stable level has not been geologically great. There are peneplains on the windward sides of the older islands. Evidence is widespread around the seaward parts of the islands to show conclusively that much marine erosion has taken place. It appears reasonable to believe, therefore, that the soundest approach to the subject of erosional time would be based upon subaerial erosion and the comparative amounts of material removed.

There are a number of special conditions in these islands which account for their characteristic topography. Of these, the nature of the rocks, their composition, porosity, reaction to mechanical and chemical weathering, structure and formation are contributing parts, but there are other factors. One of the most important is the climate. Owing to the heights attained by the main islands, the mean rainfall is great (about 100 inches for the entire group). Also, in certain areas exceptionally wet conditions are the rule. On Mount Waialeale on Kauai (elevation 5,080 feet) the average rainfall is the greatest recorded over a period of years of any place on earth. The mean annual rainfall for a 30-year period to 1942 was 462.7 inches, but the more complete and accurate records for the 12 years between 1930 and 1942 show an average of 537.5 inches per year. In the year ending July 24, 1942, 618.75 inches (51.56 feet!) of rain were recorded. However, only 15 miles away from that rainfall station is a lowland one whose annual mean is between 15 and 20 inches. On the island of Maui a station at 5,000 feet recorded 562 inches of rain one year, and a lowland station only 8.5 miles away recorded as little as 2.5 inches for one year. These large amounts of water falling in the highlands have left a spectacular topography in their wake. Moreover, much of the weathering and erosion here may be compared to that of limestone areas; this is a significant feature.

Unlike the water table of much of the continental United States, for example, the water table in Hawaii does not cling close to the topographic outline of the land, but is deep down and is controlled by the character of the rocks, the depths of the valleys and the saturation of the lower rocks with sea water. Wentworth's figures (1928:395) graphically present this and are reproduced here (fig. 15). Stearns (1935:236) found the water table to slope from 1.6 feet to 3 feet to the mile in certain sections of Oahu, and said, "Such flat gradients are also charac-

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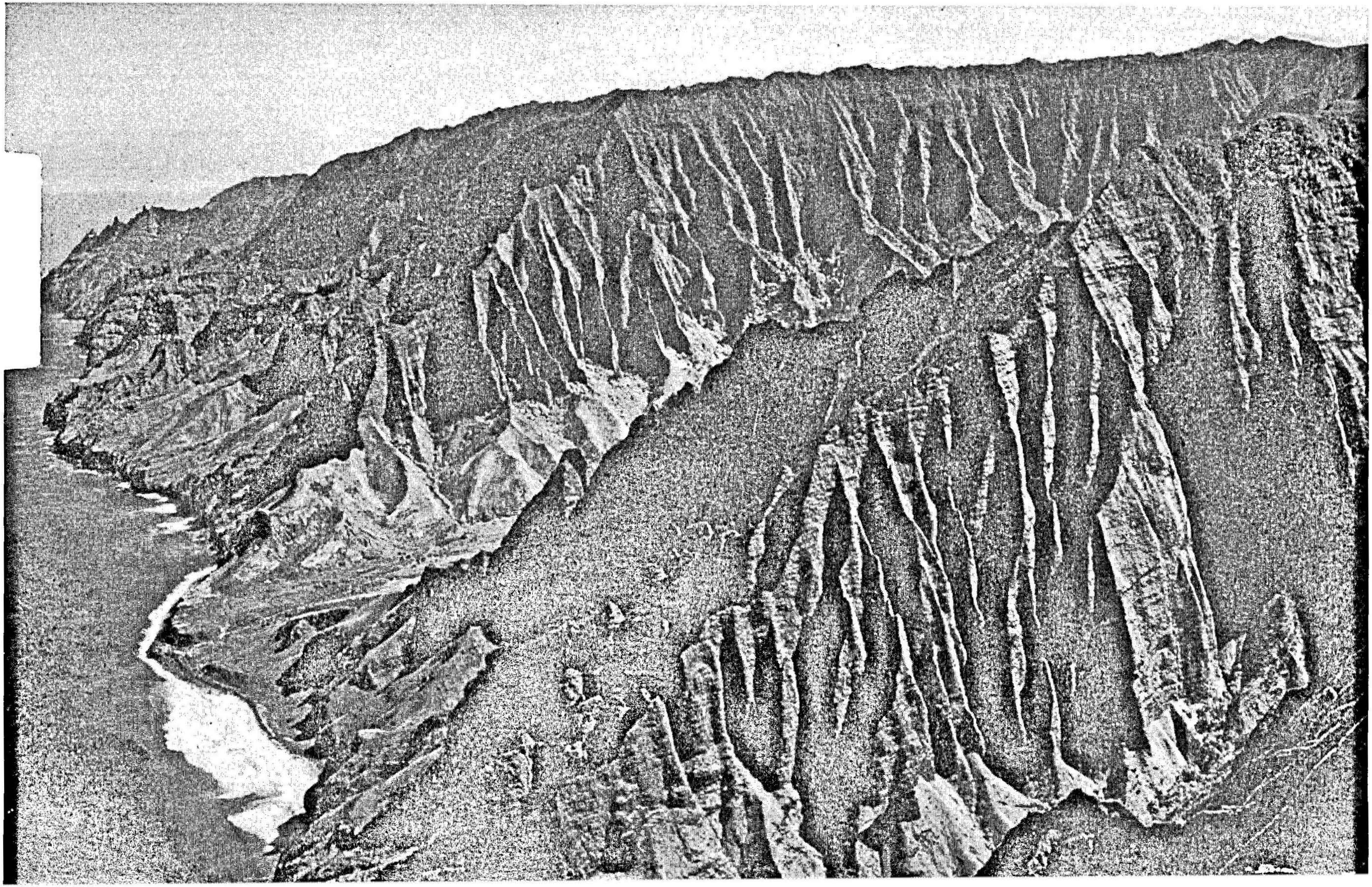
Figure 13.—Waimea Canyon on Kauai. This great canyon is cut through 3,500 feet of old lava flows and runs from an area of extremely heavy rainfall to the dry coast of the island. The area in the foreground is dry and has been extensively grazed over, especially by goats. Note the bedding of the lava flows, particularly in the background. (After Stearns, 1946. U. S. Navy photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



teristic of the basal water table in the other islands and indicate that the rocks are exceedingly permeable."

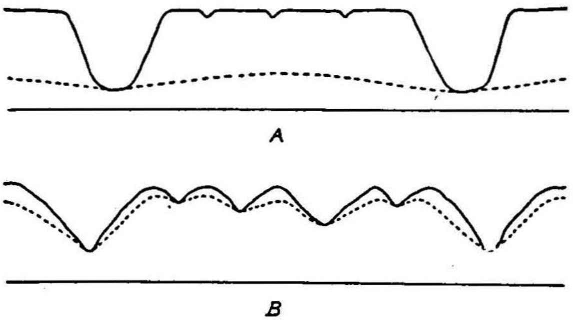


Figure 15.—Diagrams of water tables to show the relation of ground water to the topographic surface in Hawaii (**A**), and the same relation in a humid part of the United States mainland (**B**). (After Wentworth, 1928.)

The chemical weathering that accompanies heavy rainfall and the subsequent dense vegetation cover is, according to Wentworth, the paramount weathering activity. The low water table results in the most active weathering not upon the heights, but low down near the water table. This conclusion is the reverse of what many casual observers are likely to believe, but is ably elucidated by Wentworth. Thus the rugged topography of the islands is produced by these special and, to many observers, cryptic processes. Wentworth (1928:396) says:

> The greater activity of weathering near the water table and hence at low altitudes, and the capacity of the rock partially weathered chemically to stand at high angles when physical weathering is inoperative, combine to produce slopes of great uniformity and steepness. The declivity of the slopes is the angle of stability for the unweathered or moderately weathered material of the cliffs. The uniformity of steepness to the very top of the slope is a result of nearly uniform wastage from the base of the cliff, either by weathering or by stream transport. In most regions [continental] the upper parts of slopes are affected by weathering processes of a type which are progressively more active at higher altitudes, and the higher slopes have also been longer subject to such action. Both of these factors tend to produce gentler slopes at the top of any given profile and hence convexity of the upper part of the profile. On the contrary, agencies which are more active at lower levels are responsible for the forms of the deeper parts of valleys which are of necessity concave. In most parts of Hawaii the processes which promote more rapid wastage at lower levels are dominant, and the wastage at the lower levels is shown in the nearly uniform slopes of cliff faces.

Many readers will immediately recall that these conclusions are the reverse of the classroom principles of geology which they received in their continental university or college training. Valleys which might be classed as glacial valleys in North

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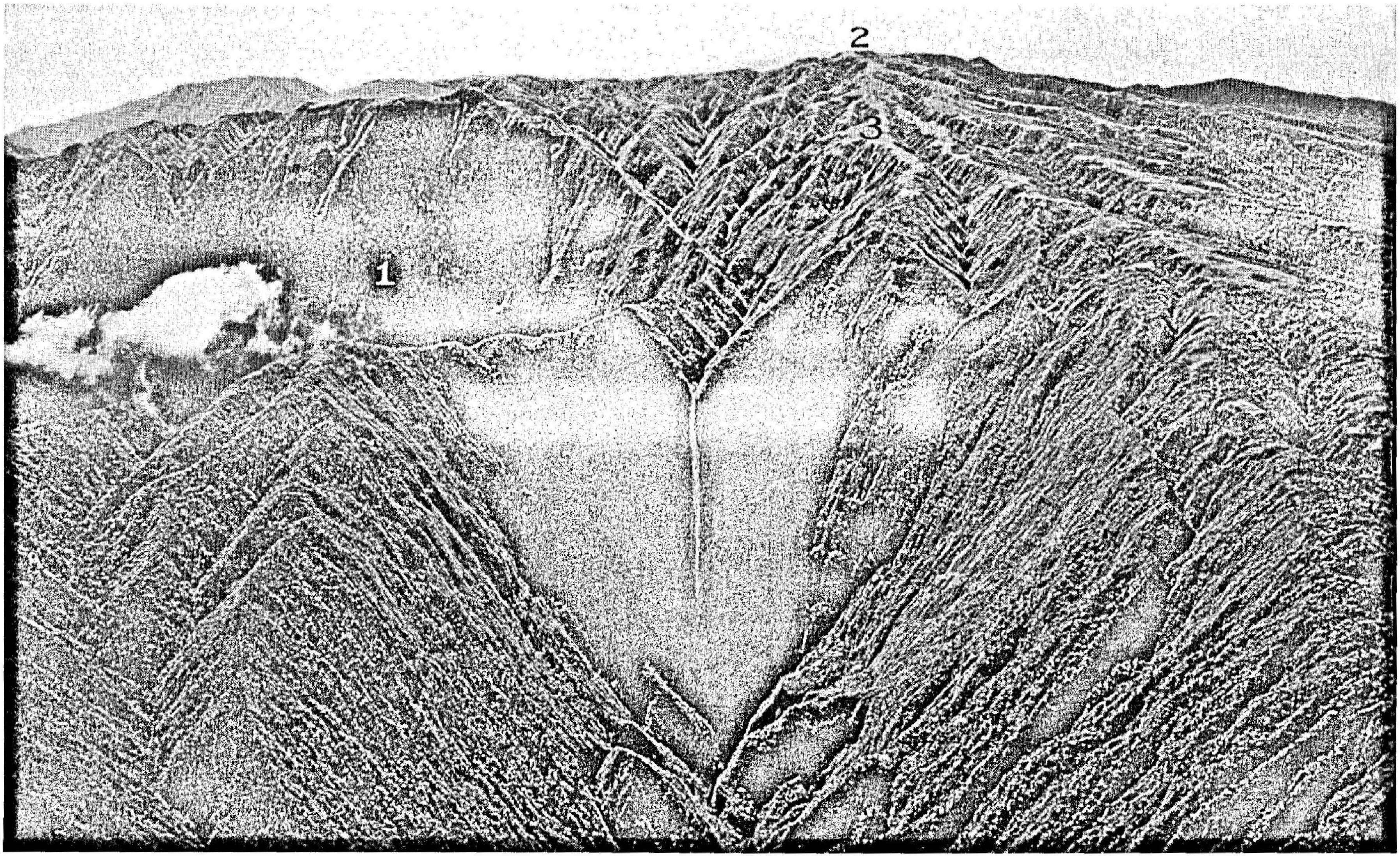
Figure 14.—Looking northeast along the Napali Coast of Kauai (the large valley is Kalalau), showing the erosion patterns typical of some of the wet, seaward faces of old areas. Note the gentle slopes of the ancient lava flows, best seen toward the top of the ridge in the foreground. The ridge in the background rises to more than 4,000 feet at the right. The sea cliff is about 2,700 feet high. I need not emphasize the difficulties one encounters in attempts to explore this type of terrain. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)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America are normal products of chemical and fluvial erosion in Hawaii. Conditions on Pacific islands are not the same as those existing in North America or Europe and they must be studied geologically and biologically with this fundamental point constantly in mind.

Stearns's theory (1935:24) is based upon "(1) the original slope of the surface, (2) the presence of alternating resistant and nonresistant beds dipping downstream, (3) high rainfall at high altitudes and low rainfall at low altitudes on a conical surface, thereby inducing active piracy in the upper parts of the drainage basin and (4) plunge-pool action and landslides removing the divides between tributaries."

A combination of both these points of view is justified; there are many factors which must be taken into account. Some of these are the rapid disintegration of the basaltic lavas as a result of the acids released from large accumulations of decaying vegetation of the dense rain forests; the weight of masses of vegetation on steep slopes, the common resultant landslides and the great spalling effect they have; the rapidity of stream erosion on the steep slopes; the large numbers of waterfalls; the spectacular cutting through of mountain ranges and stream piracy. The spalling effect of landslides appears to play a dominant role in the configuration of higher slopes. Landslides may tend to form new water courses which may, in part, influence the spectacular fluting of cliff areas and steep slopes. Forbes (1885:115) was struck by the action of landslides in Java and wrote,

> During the rainy season the thunder of slopes laden with forest trees and shrubs crashing down, often for hundreds of feet into the valleys, was a daily sound, which impressed me with the supreme potency of rain as an agent in planing down the mountains and widening the valleys. I have often been astonished at the rapidity with which even a small stream will carry away the *débris* of a great landslip. When a heavy gale accompanies continued rains, the fall of giant trees on the narrowed ridges of mountains is very often the cause of extensive landslips into both the adjacent valleys, which lowers down by very perceptible degrees their barrier ridges.

More emphasis needs to be placed on the action of plants in mechanically breaking up the rock by their root growth. The mass action of a dense rain forest in breaking up rock, thus enabling the resultant soil and finely broken rock to be carried away more rapidly by fluvial means, is enormous.

Since this was written, Wentworth's paper on soil avalanches (1943) has appeared. He concludes that the knife-edged ridges so characteristic of our topography are formed largely by slides. He concludes (pp. 62–63) that

> If 1 foot be removed from one slide area and if the next slide be assumed to consist of 1 foot of nearly loosened decomposed rock from beneath it, a slide every 1000 years in each spot would be rapid erosion. In checking over possible rates, it is thought that in the past 8 years,

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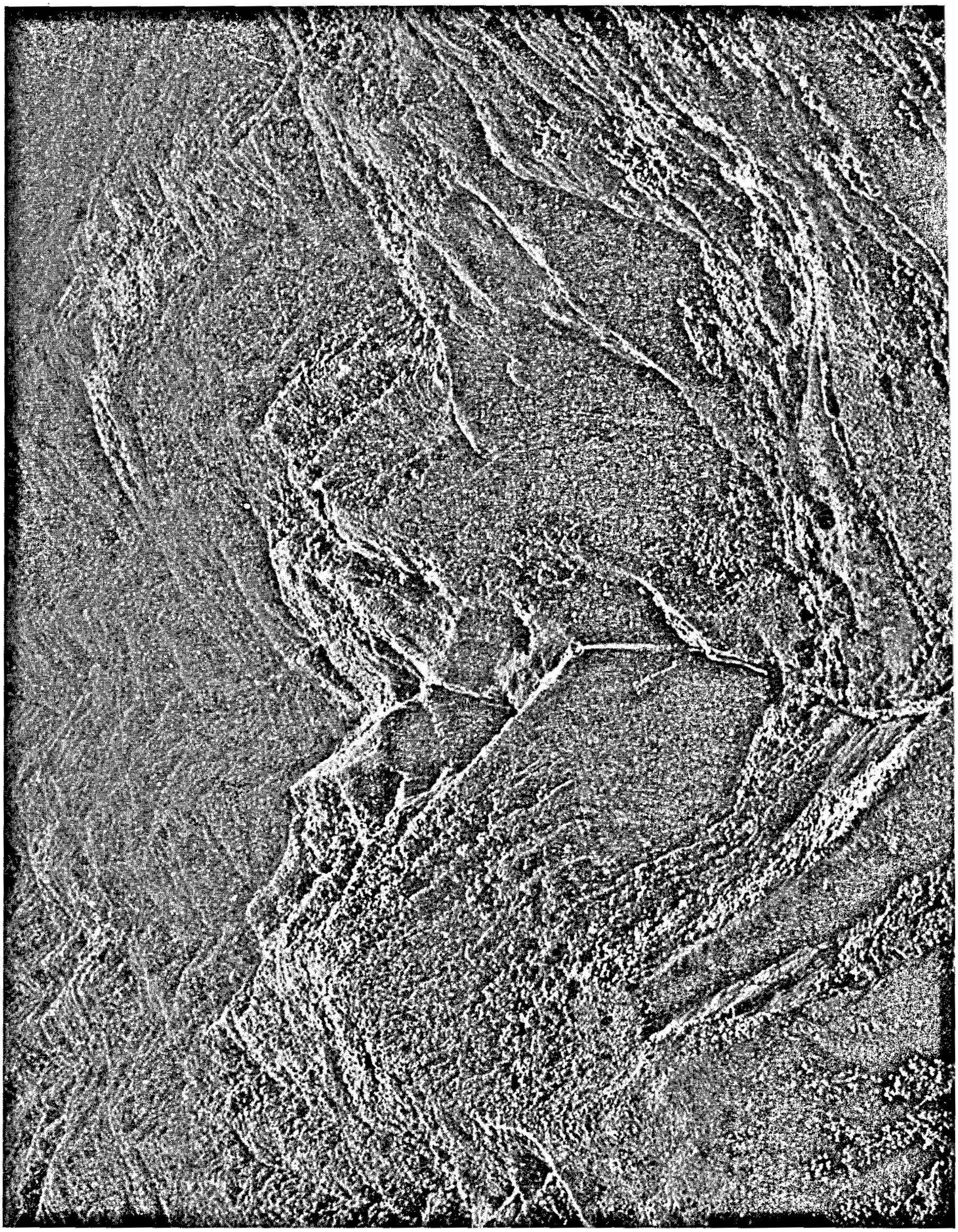
Figure 16.—Head of Honokohau Canyon, West Maui, 2,300 feet deep, nearly captured by Waihee Canyon (1); Puu Kukui (2) is the highest and wettest peak on West Maui; the pale-colored flats (3) are peat bogs. (After Stearns, 1942. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



in an area of about 15 square miles, in the part of the Honolulu watershed best known to the writer, there have been the equivalent of 200 slides involving an acre each. If it can be assumed that the material removed is eventually carried downslope and to the ocean by streams, the removal of 1 foot of average thickness from these areas is equivalent to a rate of about 1 foot in 400 years for the whole area. Even if these assumptions favor too high a rate, the process can be very significant in land reduction.

GLACIATION

A unique feature of Hawaiian geology is the glaciation of the great mountain, Mauna Kea. On this mountain is displayed the only evidence of glaciation on any island of the Pacific Basin. Interested readers are referred to the detailed accounts of the study of the ice action on the summit of Mauna Kea by Gregory and Wentworth (1937), Wentworth and Powers (1941), and Stearns (1945).

The final story of the glaciation of Mauna Kea has not yet been told, and geologists are not in agreement as to the age and extent of glaciation. The most recent study has been made by Stearns (1945), and he concludes that the top of the mountain is all of late Pleistocene or Recent structure, and that there was a small ice cap present which extended down to about the 10,500-foot level in the most recent glacial epoch—the Wisconsin—about 25,000 to 30,000 years ago. The ice cap which might have extended over about 20 square miles of the summit and reached a possible thickness of 150–350 feet was smaller in extent than the present-day ice cap of Mount Rainier (45 square miles) in the state of Washington.

It would not take much lowering in the mean annual temperature to bring about permanent snow fields on Mauna Kea today. Freezing temperatures are thought to occur there every night in the year, and during some years snow lies on the ground in patches throughout the year. It was estimated by Stearns that if the mountain were extended upward an additional 1,000 feet or more, the permanent snow line would be at about 14,000 to 15,000 feet today. Known shifts in sea level that are now recorded in the seaward parts of the islands probably played a part in the formation of the snow and ice fields.

INFLUENCE OF GLACIATION ON THE BIOTA

The ice age apparently played a more important part in influencing the marine than the terrestrial life of the islands. Reef-building corals grow in Hawaii in a narrow and critical temperature range. It is thought that if the mean minimum water temperature should drop 3° C. or more, the reef-building corals could not flourish. The drop in temperature during the Pleistocene is considered to have been 3° to 10°. Therefore, Gregory and Wentworth conclude that while "Mauna Kea was capped with ice the waters about its base held no reef building organisms." Anyone who has seen the flourishing coral reefs that grow on many islands

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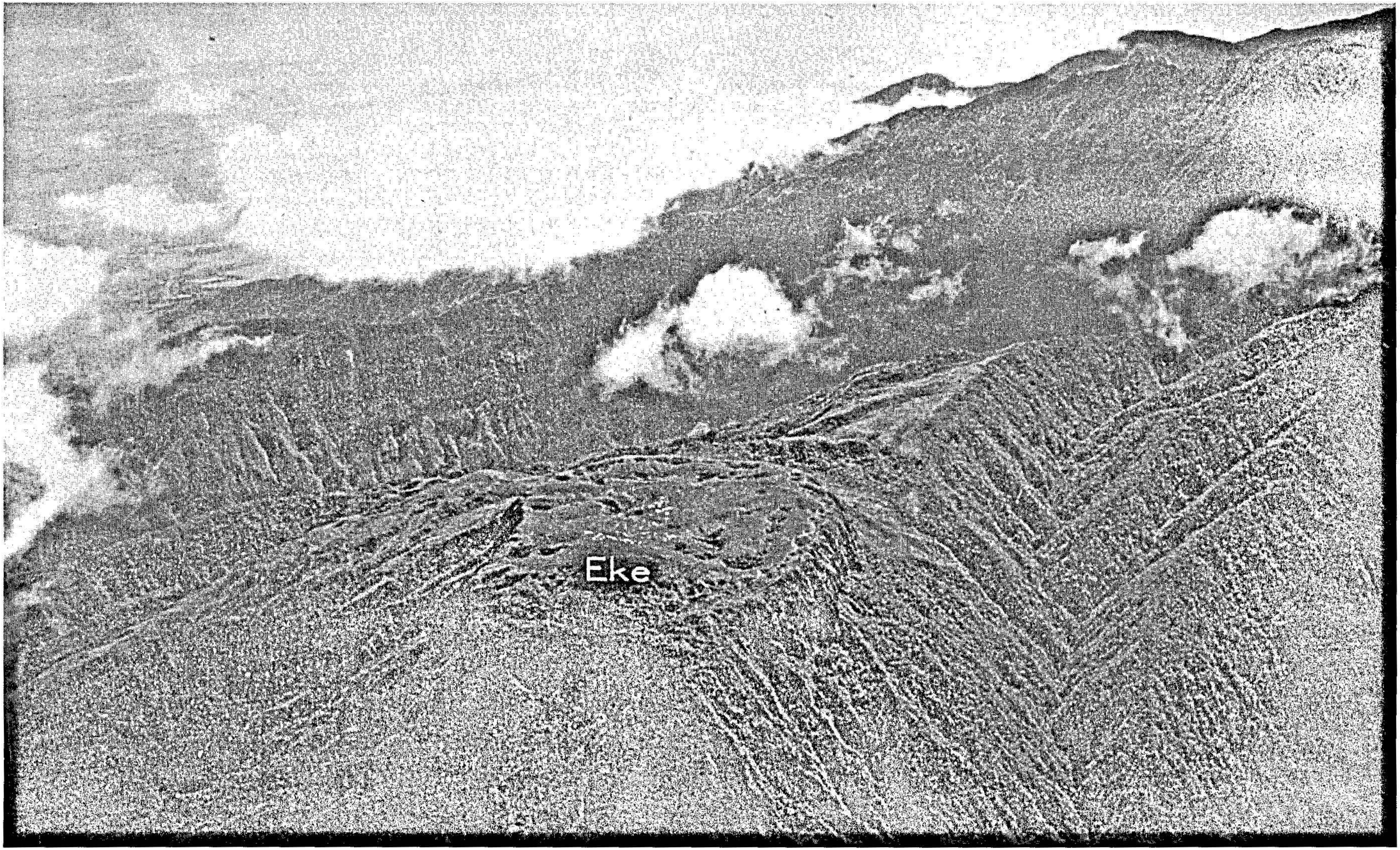
Figure 17.—Halawa Valley, Molokai. (After Stearns, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)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nearer the equator, realizes that the Hawaiian reefs are not growing in optimum conditions even at the present time. However, the decadent condition of at least some of the Hawaiian reefs is evidently correlated with food supply, water polution and recent changes largely brought about by the influences of man.

As Vaughan (1910) points out in his study of Hawaiian corals, "reef corals can endure a range in temperature from 68° F. to 85° F., but the annual mean must not be below 70°; the summer temperatures would be higher. The lowest summer surface temperature recorded by the 'Albatross' was 73°.... The greatest abundance of forms is between temperatures 73° and 78°, depth 0–40 fathoms; ... All the strictly reef building genera live at a temperature of 73°–78° F." Vaughan found that 77 of 121 species of Hawaiian corals studied lived in the 78° to 73° F., 0 to 40 fathom, zone. The number of species dropped to 19 in the 73° to 60° F. zone. Vaughan also notes that the Hawaiian reef fauna exhibits a peculiarity worthy of further notice, in the absence of some of the common reef-building genera of other areas. "There are no species of Oculinidae, Eusmiliidae, or the Astrangiidae; there are very few Orbicellidae, none of the large, massive, meandrinoid Faviidae, nor of the Mussidae."

"The known rate of coral growth shows that post-glacial time is ample for the building of Hawaiian reefs, and also the much greater barriers and fringing reefs about tropical Pacific islands." (Gregory and Wentworth, 1937:1740).

Ostergaard (1928:32) speaking of marine Mollusca said,

> In view of the fact that many species now found thriving best in the warmer Indo-Pacific are represented in Hawaii by fossils only and others by species on the border of extinction, it is reasonable to assume that at the time when the limestone of Oahu was formed Hawaii had a higher ocean temperature. A more prolific representation of fossil than of living Madreporarian coral on the reefs of Oahu supports this conclusion. Worthy of note also is the presence of well developed coralline algae, which form compact encrusting layers over dead coral boulders and substantially aid in reef building by preventing a breaking up or dissolution of these coral boulders. The efficiency of these corallines in reef building is well exemplified in the reef at Apia, Samoa, where these algae are seen to encrust and cement together coral masses into a firm compact reef, forming a barrier about a mile from shore.

He also states that "On the basis of percentage of extinct forms a geological age greater than the Pleistocene should not be assigned to the emergent limestones of Oahu."

It is probable that the glacial stages in Hawaiian geological history did not have the same drastic influences on the terrestrial flora and fauna that they are thought to have had on marine forms of life. Plants and animals have the ability to move upward or downward or sideways along mountain slopes and can more

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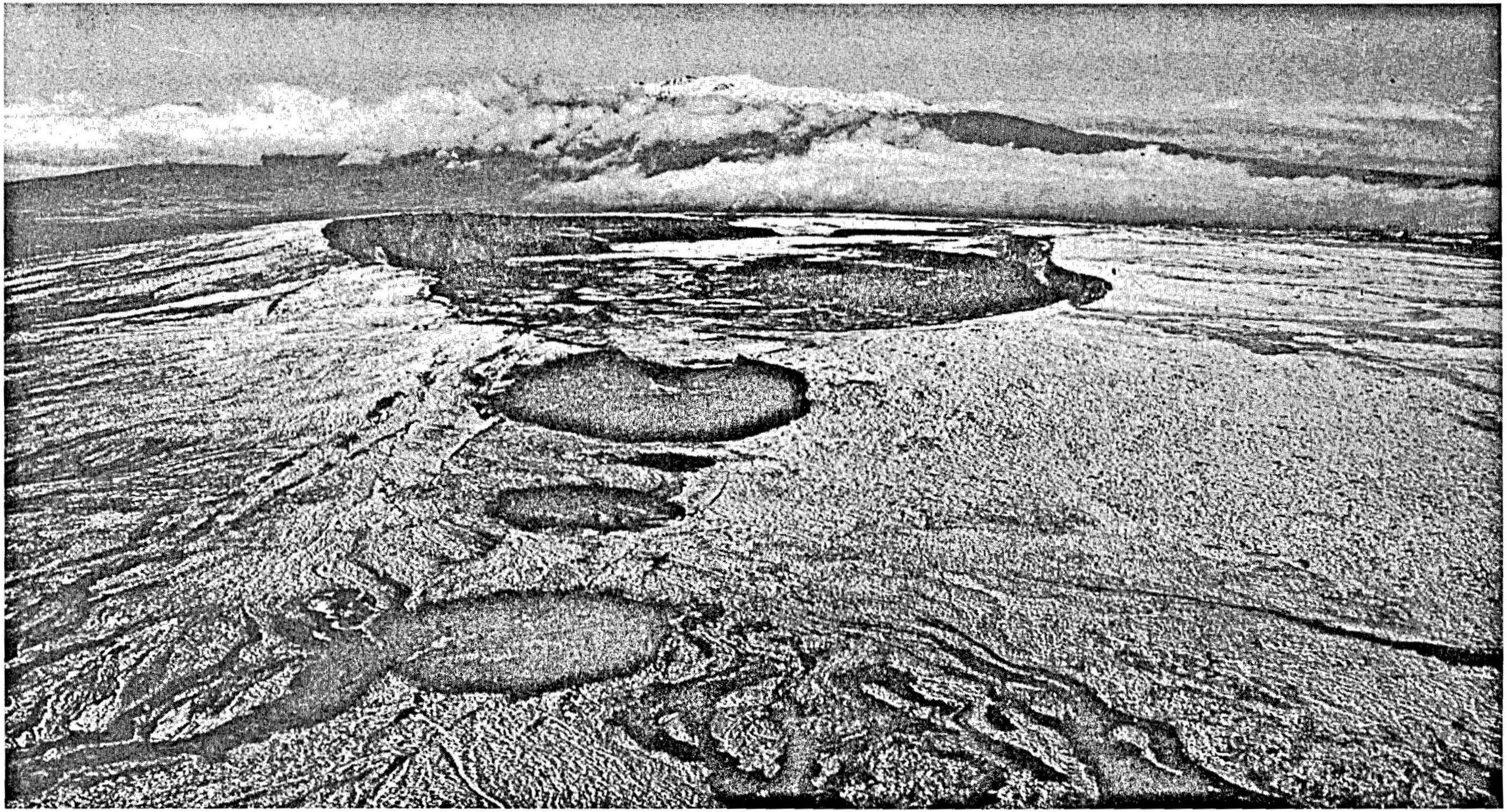
Figure 18.—Mount Eke, 4,500 feet high in the wet mountains of West Maui. Its top, about one-half mile across, is a cold, windswept boggy region, with an average rainfall of about 250 inches a year. The mountains in the background rise to 5,788 feet, and rainfall up to 523 inches has been recorded there in one year. Under the clouds in the background the rainfall is only about 20 inches per year. (After Stearns and Macdonald, 1942. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



or less choose more favorable environments, within limitations, during times of climatic changes such as those which have taken place on Hawaii. The zone of local migration of reef organisms is, however, a greatly restricted one, and the effect of climatic change is amplified. It is difficult to ascertain how the colder climate affected the Hawaiian terrestrial biota as a whole. There appear to be no markedly significant features about it that can be attributed conclusively to climatic change within the islands. During glaciation, however, precipitation over the islands may have been greater than at present, and the rate of erosion may have been increased with its consequent influence on species formation as discussed below under Geographical Metamorphosis and Evolution. Today insects follow the plants to tree line and above with no apparent ill effects, and we find "tropical" forms living in regions of frost and snow and apparently getting along as well as those found at middle elevations. However, it is common knowledge that dead insects can be seen by thousands on the barren, wind-swept, arid, mountain-top deserts of the highest peaks where they have been driven from lower elevations by winds and have perished on snow fields or by freezing in those unprotected places. There is nothing in the character of the fauna to indicate large-scale climatic extermination or long-maintained cold climate.

SUBMERGENCE AND EMERGENCE

There is abundant and indisputable evidence of considerable shifting of sea level in relation to land surface in the Hawaiian Islands. The data of such movements have been assembled from the logs of wells sunk to as much as 1,500 feet below sea level, from exposed fossil reefs, from dunes, sandstone, marine-worn boulders, ancient shore lines, well shafts above sea level, drainage canals, road cuts, quarries and similar sources.

The evidence at hand shows that Oahu, at least, now has a sea level in the neighborhood of 1,000 feet higher than it was during earlier periods of its life. Data from wells and the extent to which subaerially cut valleys have been filled or drowned amply support this conclusion, and geologists are in agreement on this point. It is of interest that Recent fossil forest trees have been uncovered in tunnels extending below sea level on Oahu. Also, there is evidence to show that a number of Recent fluctuations of small magnitude have moved the shore line above and below its present level several times over. Because of isostatic balance, major shifts of sea level on one island safely may be assumed to have occurred also on the other islands of the main group, because, except for possible local minor fluctuations of relatively small magnitude, the main group of islands apparently acts as a unit in large-scale movements, and it cannot be considered that any one island has ever acted in major shifts independent of the entire

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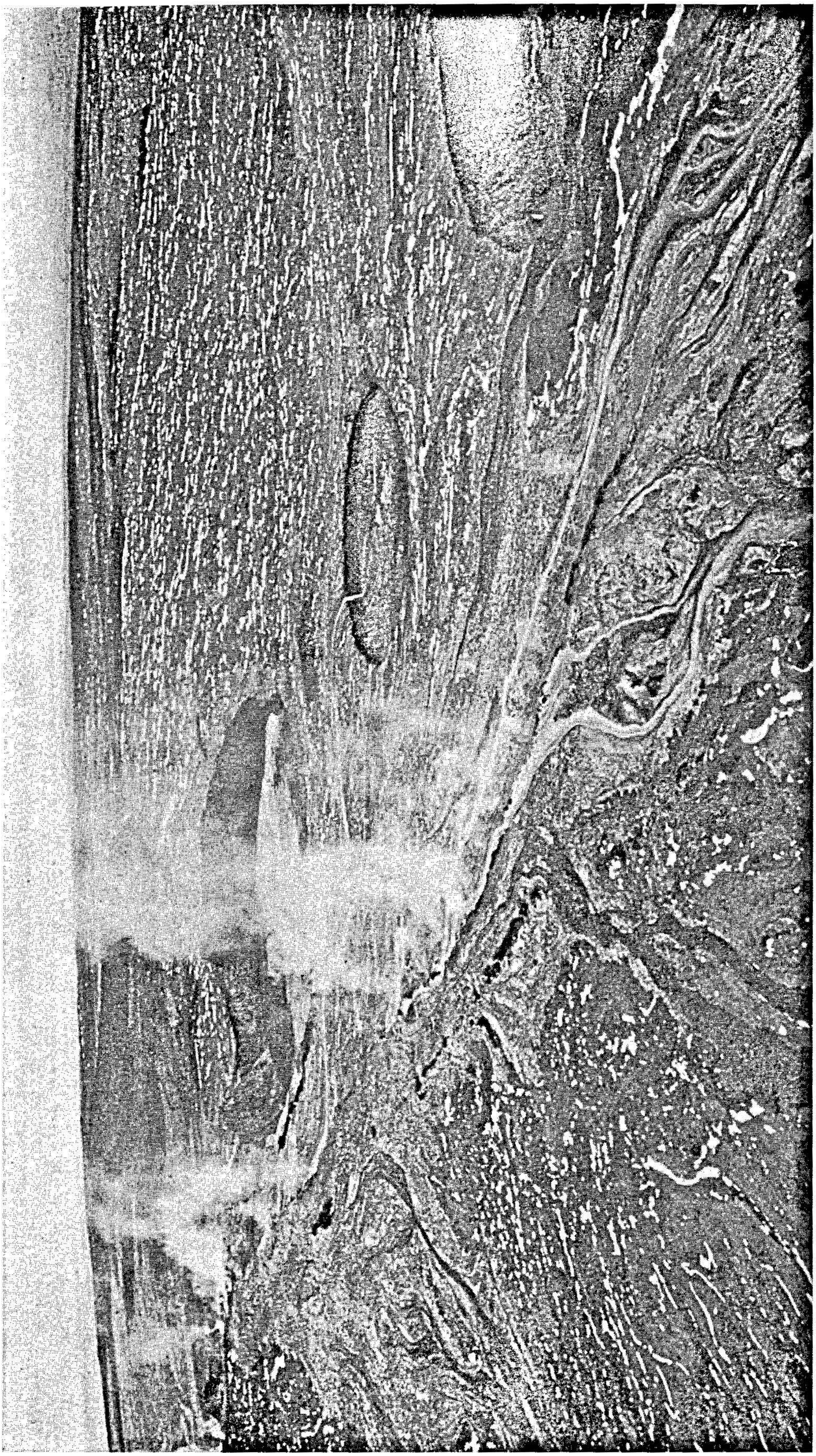
Figure 19a.—Summit of Mauna Loa after a flurry of snow showing Mokuaweoweo Caldera and pit craters on the southwest rift and Mauna Kea in the background. The highest elevation in the foreground is 13,679 feet. Note the dark lava flows in the foreground. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut courtesy U. S. Geological Survey, Honolulu.)



anastomosed mass. Similarly, the drawing away or adding of water during glacial or interglacial epochs would result in sea-level marks at similar elevations on all of the islands (provided, of course, that they were all above water at any given time). It is significant that the known or postulated shifts in sea level in Hawaii are dated as Pleistocene.

The maximum suggested emergence of any island in the Hawaiian group is indicated by a shore line described by Stearns (1938:618) at about 1,200 feet above the sea on Lanai. According to Stearns, an outcrop of fossiliferous marine limestone is "in place" at an altitude of 1,069 feet, and he says that in his opinion there is no reason to believe that the material has been man-carried to the locality. These marine fossils are recorded from a site at an elevation greater than recorded for any other such Hawaiian fossils. Stearns says,

> Evidently considerably more limestone formerly cropped out at this place, but weathering and livestock have nearly destroyed the exposure, leaving only the vein-like deposits. These outcrops are only a quarter to half an inch wide and 2 to 3 feet long. They contain, however, distinctly recognizable coralline algae and gastropods. Some fragments of coral are discernible. Paul Bartsch and H. A. Rehder, of the United States National Museum, found one pelecypod—*Pinctada* sp.— and three gastropods— *Modulus tectum* Gmelin, *Triforis* sp. and *Strombus hellii* Rousseau—in fragments of fossiliferous limestone from this locality. All these forms are now living in Hawaiian waters, which fact indicates that the deposit is probably not older than Pleistocene.

According to Stearns, unstudied indications on Oahu, Molokai and West Maui suggest to him that these islands may also have remnants of an ancient shore line at about the 1,200-foot level which may correspond to that found on Lanai. Other geologists have evidently not seen such indications.

Wentworth's survey of Lanai was made about ten years prior to Stearns's researches, but Wentworth did not find the highly elevated indications of prior stands of the sea that were recorded by Stearns. He says (1925:33),

> Coral fragments and shells are found widely spread over the central plateau in association with Hawaiian stone artifacts, but these are clearly of human distribution. In a talus mass at a place northeast of Manele and about 150 feet above sea level shells and coral fragments were found to be so abundant that a natural origin seemed reasonable. Subsequent search in other gulches failed to reveal similar evidences and I have concluded that the deposit must be in part of artificial origin. It is impossible to believe that the sea has stood more than 10 to 15 feet above its present level at any time since Lanai was formed. Had it done so, it seems certain that there would be clear indications at more than one place and of more than one sort.

Such opposite points of view are surprising and somewhat discouraging to the biologist seeking knowledge of the land. Of course, small outcrops of fossiliferous materials might easily be overlooked by the pioneer observer of the gross geology

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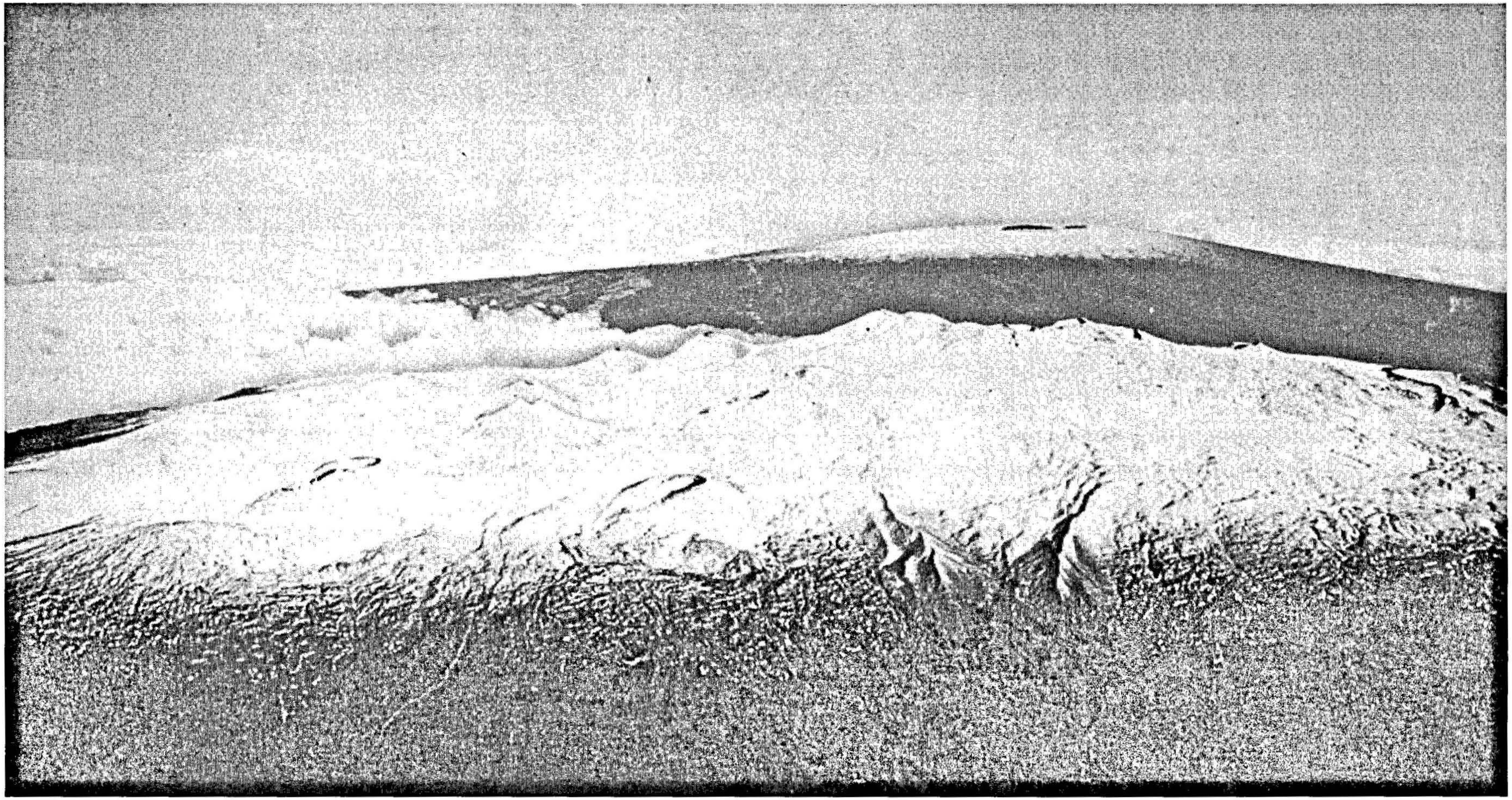
Figure 19b.—Lava flowing from fissure along the southwest rift at the top of Mauna Loa, April 8, 1940. Note the lava river cascading into the pit crater and the irregular courses of the other flows. Snow lies in depressions in the older lavas. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)



of such a region, but later on may be pointed out to a specialist who can develop an entirely new interpretation after getting a cryptic key to his special field of interest. However, the interpretations given by Stearns evidently have yet to be verified by other geologists. It is regrettable that our knowledge is in such an incomplete stage. For the present, we must give due consideration to the findings of more than one geologist regarding such great shifts of sea level. Moreover, we must not overlook the activities of the old Hawaiians who carried coral and other beach material high into the hills to build their shrines. Materials from the beaches have been carried up the sides of Haleakala, Maui, to about 9,000 feet and used as building material for shrines. Also, ethnologists and others report an abundance of shells and coralline materials scattered over wide areas in the uplands of Lanai—the results of the activities of the Hawaiian people. The Lanai record should be checked carefully. The Hawaiians might have carried coral to the area several hundred years ago, and its subsequent change and burial may make it appear to be "in place."

Assuming, for purposes of argument, that the more recent estimate of Stearns might be approximately correct, and that there might have been a stand of the sea at about 1,200 feet above present sea level, what influence upon the extent and relative positions of the islands would result? And, on the other hand, what were the results of the downward shift of sea level to about 1,000 feet lower than it stands today?

EFFECT OF SUBMERGENCE

If the sea stood 1,200 feet higher than its present level (so that the lower 1,200 feet of the main islands' present subaerial topography were drowned), roughly about 40 percent of the combined areas of the main islands would be drowned. It would result in all of the main islands being separated by wider channels of ocean than now separate them, but, surprisingly enough, the distances between any two islands would be increased by only a few miles. The greatest increase between any two islands would be between Oahu and Molokai, and that increase would amount to about five or six miles. The flooding of the lower 1,200 feet would result in the dividing of the islands of Oahu, Molokai and Maui each into two islands. Thus, on Oahu the Koolau Mountains would be an island separated from the Waianae Mountains island by a channel about three miles across at its narrowest point at the north, to about eight miles across at its broadest point at the south, and the shallowest part would be about 250 feet deep (the Koolau island would be nearly twice as long as the Waianae island). Molokai would be split into east and west islands separated by a channel about 775 feet deep at its shallowest part and about nine miles broad at its narrowest point, but the west island would be only about two or three square miles in area and only about 150 feet high at its highest point. Maui would be split into east and west islands

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Figure 20.—A view of the snow-covered summits of Mauna Kea (foreground), 13,784 feet, and Mauna Loa (background), 13,679 feet. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

Figure 21.—The middle figure shows the main Hawaiian Islands at the present stage of level of the sea. The top figure illustrates the islands at 1,000 feet above present sea level. The lower figure indicates their appearance at 1,000 feet below present sea level. View figure from side.

separated by a channel about 1,075 feet deep at its shallowest part and about 10 miles wide at its narrowest point. Kahoolawe and Niihau would be reduced to small rocks.

A present-day submergence of between 125 and 200 feet would divide Maui into two islands; submergence of 425 to 500 feet would separate Molokai into two islands; and submergence of 950 to 1,000 feet would divide Oahu into two islands.

EFFECT OF EMERGENCE

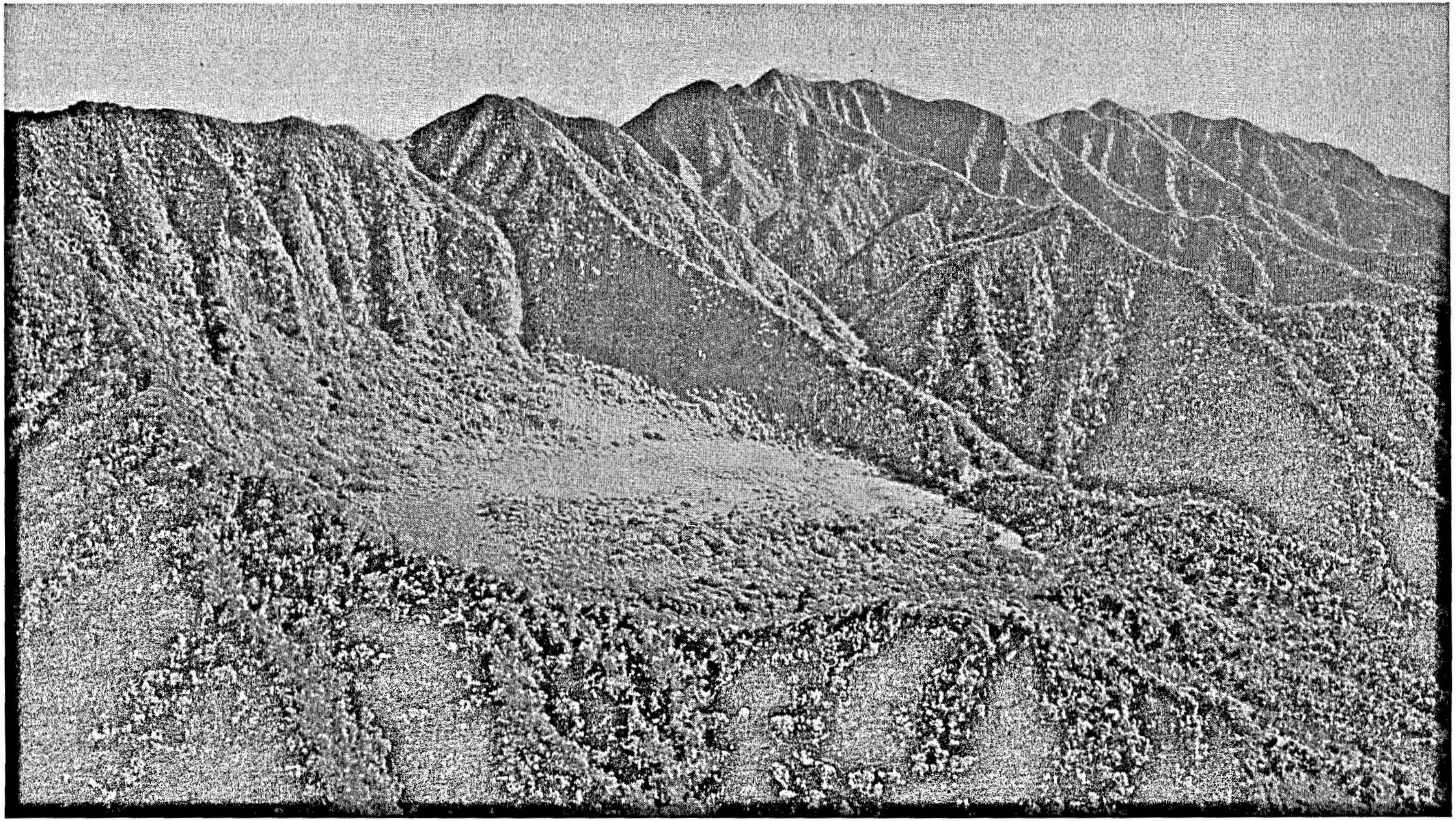
An emergence of 1,000 feet would have a greater effect on the area and disposition of land than has been indicated by an analysis of the results of submergence to 1,200 feet above present sea level. The total dry land would approach twice what it is today (about 11,100 compared to 6,435 square miles as determined by rough planimeter measurements). All the islands would be larger and closer together, and Molokai, Lanai, Maui and Kahoolawe would all be anastomosed to form one large island about eight-tenths as great in area as the present island of Hawaii. Niihau would be separated about 10 miles from Kauai with more than 1,000 feet of water in the channel; Kauai would be about 55 miles from Oahu with more than 10,000 feet of water in the channel; Oahu would be five or six miles from Molokai with more than 1,000 feet of water in the channel; Hawaii would be about 18 miles from Maui with more than 3,000 feet of water in the channel.

THE AGE OF THE HAWAIIAN ISLANDS

The dating of these islands in numbers of years is difficult, if not impossible. The rocks are so young that they appear to fall within the range of error of the radioactivity method of age determination, and fossil evidence is meager. However, it appears that it is possible to assign the ages of at least the main islands to geological epochs, and that is about all that is needed for our purposes. Early in this essay, we noted that the islands are of Tertiary origin. The Tertiary covers an enormous period of time—some 70 million years. A special committee of the National Research Council has recently calculated that the durations of the subdivisions of the Tertiary were about as follows:

Pleistocene	1 million years
Pliocene	11 million years
Miocene	17 million years
Oligocene	11 million years
Eocene	20 million years
Paleocene	10 million years
Total	70 million years

It is obvious that we do not know exactly when these Hawaiian volcanoes first broke out beneath the sea, but we can see, in a broad way, what happened to them after their exposure to the air. It is possible to estimate roughly how much of the islands has been worn off and arrive at an approximate rate of erosion.



It is also possible to ascertain roughly the rates of upbuilding. However, the attempts to date various islands or parts of islands in numbers of years have not been very successful.

Wentworth (1925) studied the island of Lanai in detail and estimated the age as between 131,000 and 200,000 years. His method was as follows: The amounts of outflow of historic lava flows in Hawaii were ascertained and their character fairly well understood; the average volume of Lanai basaltic flows was estimated at 200 million cubic meters; the subaerial volume of the island is equivalent to 580 such flows; on the basis of the frequency of lava flows on Hawaii and elsewhere, and the presence of evidence to indicate that outflow was so regular that no decided erosional intervals were interspaced in the upbuilding period of Lanai, it was estimated that the lava flows "probably succeeded one another at an average interval of not less than ten or more than 100 years." Thus the subaerial upbuilding of Lanai was estimated to have taken from about 6,000 to 60,000 years. (It is worth-while to note here that the historic flows of Mauna Loa during the past century have been estimated at between five and ten billion cubic meters—or enough lava has poured out of that mountain to raise its gigantic dome three to six feet higher in the past one hundred years.) The rate of erosion based upon subaerial removal was estimated at one foot in 2,900 years for Lanai, and the erosional age was thus estimated at 125,000 years. Wentworth concludes that "the first appearance of Lanai above sea level dates from a time well back of the Wisconsin stage of the Pleistocene but not so far back as early Pleistocene if recent estimates of the duration of that subdivision of geologic time are correct. Moreover, if the terrace building epoch indicated by certain features of Oahu be correlated with one of the more pronounced advances of glacial ice in North America, Lanai, which . . . postdates these features, will be at least somewhat younger than early Pleistocene." (1925:55–56.)

It may appear that such a method of age estimation might be applied to all the islands. However, there are many complicating factors that enter into the problem, and such estimates can only be applied to certain restricted areas where a great body of information has been assembled and where the underlying framework is completely understood. It is thought that in some areas of high rainfall the rate of degradation may be as great as a foot in 400 years. Thus most areas in Hawaii are now excluded from such age estimation, for too few data have been collected.

Geologists may be asked what they know about what is hidden beneath the islands, and the good and logical question is advanced, "How do you know that there are not ancient islands buried within the interiors of the present islands which you maintain are young islands?" As a matter of fact, it is known that at least on the islands of Hawaii, Maui and Kauai, and probably on all the islands,

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Figure 22.—Kaau Crater, a youthful volcanic outburst on the rugged, deeply eroded slopes of the Koolau Mountains behind Honolulu. (After Stearns, 1946. Photograph by U.S.A.A.F. Cut loaned by U. S. Geological Survey, Honolulu.)

there are considerably older dissected areas buried beneath the more recent lavas making up the bulk of the islands, and this evidence extends the ages of the islands far back beyond the ages suggested by the much younger surface lavas. The evidence at hand, however, appears to be good enough to enable us to conclude that there are no significant, ancient, unknown islands buried or hidden within or below our mountains. Great canyons like Waimea on Kauai have exposed several thousands of feet of strata which show conclusively what has gone on in past ages of lava flow and erosion. (Newer flows, in which the river is now cutting, have filled part of the bottom of Waimea Canyon to about 800 feet. Nuuanu Valley on Oahu has similar recent flows, as do other valleys.) Also, we have numerous, carefully logged well shafts that have been sunk to as much as 1,500 feet below sea level, and water tunnels have been driven far into, or entirely through, mountains and mountain ranges. Such data are indisputable. These old dissected areas buried by later lavas have been taken into account and are thoroughly considered here.

Wentworth considers that there is no reason to believe that any existing land surfaces in the islands are over 5,000,000 years old, and he said ". . . physical evidence does not appear to indicate the emergence of any part of the Hawaiian group above sea level before the later part of the Tertiary period." (1927:133.) Both Wentworth and Stearns believe that the main islands are Pliocene or more recent and that the bulk of the land of the main islands is largely of Pleistocene age.

Too much assumption and too little actual knowledge are behind much of the reasoning that prompt some authors to voice opinions regarding Pacific island geology. It seems that the only logical course to pursue is that based upon concrete evidence uncovered by the more careful and conservative of geologists who have actually done extensive and critical field work in the islands, rather than to rely upon the imaginative flights of those who conjure up, from fertile imaginations, continents, continental islands, land bridges and ancient islands of great extent for the purpose of solving what appear to be particularly difficult problems of biogeography.

Hereinafter, therefore, this discussion will be based upon the ages of the main islands as is generally agreed upon by geologists. That is, that they are of late Pliocene and Pleistocene age, and the bulk of the erosional and topographical features are largely Pleistocene.

THE COMPARATIVE AGES OF THE ISLANDS OF HAWAII

It has been generally agreed by geologists and biologists that, roughly speaking, there is a progression in age of the islands from west to east—that the older islands are to the west, the younger ones to the east. In the leeward islands are found shoals, reefs, atolls, rocks and volcanic stacks, but the main islands terminate to the east with the young lavas and active volcanoes of the island of Hawaii. Also, in the main islands of Oahu, Molokai and Maui, each of which is formed from the fusion of two major volcanic masses, the western segment of each appears to be older than the eastern part. However, the picture is not so orderly and simple as it may at first appear. Nothing is known regarding the order of events in the leeward group, but the windward islands present features which lend themselves to at least partial interpretation. Much of what has been said regarding the leeward islands is conjecture—we actually know very little about them. Powers (1917:514) said, "Along the Hawaiian rift the volcanoes have arisen not in exact order from west to east, but in a somewhat irregular manner, with a general migration of the lava in an easterly direction. Furthermore, the order of extinction of volcanic activity has not always been the same as the order of initiation."

Of the various leeward islands, Kaula, Nihoa, Necker, Gardner and French Frigate Shoal have exposures of volcanic rock—the other islands, reefs and shoals are coralline. According to Edmondson (1929), there are no coral reefs on Kaula, Nihoa, Necker or Gardner. The leeward islands appear to be the remnants of high islands, some of which may have been about the size of Molokai, Kauai or Oahu, others larger, while still others were apparently smaller. They appear to be the relics of a decadent mid-Pacific island chain, and there is no reason for otherwise considering them. A knowledge of the island chains of the south Pacific indicates that the usual trend of events in the metamorphosis of such chains has been carried on in Hawaii as elsewhere in the mid-Pacific. Moreover, all evidence shows that this metamorphosis from high islands to rocks, reefs and shoals is vigorously active today, and that it will continue until the main islands assume the general form of the most completely altered of the leeward islands.

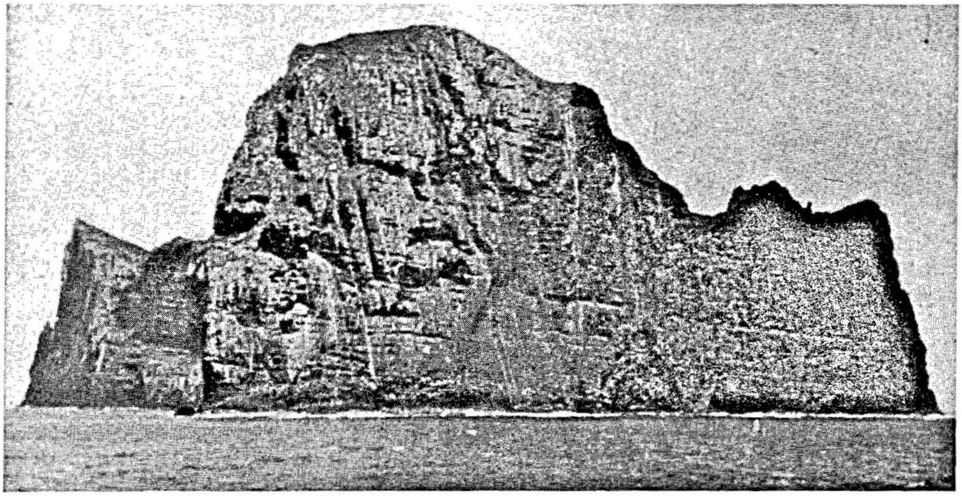

Figure 23.—Nihoa Island, a remnant of an extensively eroded, old Hawaiian island. This craggy mass (895 feet high) of only about 156 acres is all that remains of a former majestic high island many square miles in extent. Note the gentle dip of the lava beds. An extensive shallow bank surrounds the island. (Photograph by E. H. Bryan, Jr.; courtesy of Bishop Museum.)

Palmer has made the most complete survey of the geology of the leeward islands, and he concludes (1927:5) that "It seems logical to believe that the islands and shoals of the northwestern segment were formerly high, volcanic islands much like the present islands of the southeastern segment, but that wave action has completed the truncation begun by wind and running water. The truncated volcanic cones now form submarine platforms, some of which are simple shoals and others are reefs built by marine organisms and enclosing sheltered lagoons above which rise sand islets ten to twenty feet high."

It appears reasonable to conclude that the ancient leeward islands were, at the peaks of their subaerial developments, capable of supporting diversified floras and faunas as typically oceanic in composition as those of the main islands are today. There appears to be no evidence available to use in dating the ancient leeward islands. By way of a guess, and perhaps no one is in a position to do more now, it might be suggested that some of the leeward islands may have been at their zenith in Pliocene or possibly earlier Tertiary time. Obviously, we do not know! Also, I do not now see how it is possible, with our present information, to ascertain the order of emergence, development and degradation of the leeward islands. For the main islands, the problem perhaps is less difficult because we can see the islands in their present subaerial condition. But the task of interpreting their history is not easy. There are a number of complicating factors—geological and biological. As said before (Zimmerman, 1940:273), speaking very broadly and in generalized terms, "The islands are successively

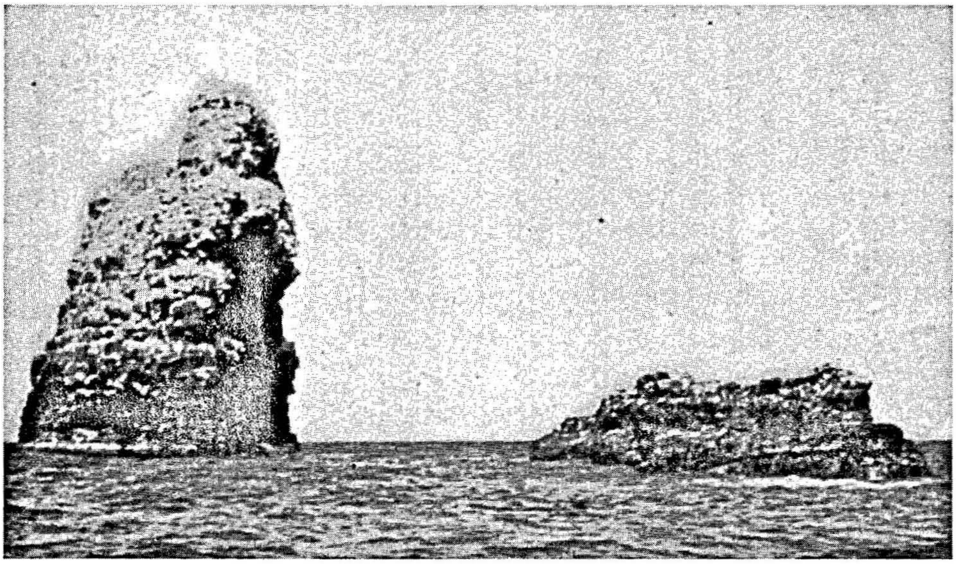

Figure 24.—La Pérouse Rock, vestiges of a decadent leeward Hawaiian island at French Frigate Shoal. Note the flat bedding of the lava flows. The large rock is 122 feet high, the small one 10 feet high. This area is surrounded by a shallow platform 15 miles or more in diameter. (Photograph by E. H. Bryan, Jr.; courtesy of Bishop Museum.)

younger from Kauai on the north to Hawaii with its active volcanoes on the south." However, I do not believe that it has as yet been conclusively shown that Kauai is older than the Waianae Mountains of Oahu, or that part of Molokai is not as old as part of Oahu, or that the Kohala Mountains of Hawaii are not as old or older than West Maui or East Molokai. It appears possible that future evidence may be gathered that would indicate Oahu to be older than Kauai, and Hinds (1931:203) concluded that "The long series of events involved in the development of the Oahu domes and their present landscapes, together with the extent of fluvial and marine removal, lead me to consider both of these domes older than Kauai." Hinds (p. 204) says, "The relative ages of the landscapes of the high old domes appear to be: (1) West Oahu, (2) East Oahu, (3) Kauai, (4) East Molokai; West Maui and Kohala are younger, but their sequence is yet to be determined." Lanai appears to be nearly the same age as West Maui; Kahoolawe may be older than East Maui. Hinds considers the Penguin Bank at the northwest end of Molokai as "... the oldest landscape in windward Hawaii ..." and that it "... may be approximately the same age as [that] of the leeward islands." This bank is about 16 by 30 miles in extent and lies under about 25 to 70 fathoms of water. It is doubtful that the data on this bank are complete enough for conclusions to be drawn from them. However, we should keep them in mind in our studies. What appears to be a rather simple problem thus turns out to be a complex one. However, if we keep these facts in mind, I believe that our interpretations of the developments of the biota will be based upon sounder footing than if they are ignored.

PALEONTOLOGICAL EVIDENCE

Fossil insects would probably tell us interesting tales—if there were any fossils! From all the Pacific Basin, I have but one record of an entomological type—that is the finding of a psyllid gall on a fossil leaf of a *Metrosideros* tree in a Recent deposit at Red Hill (near Pearl Harbor, Oahu). To my knowledge, there never has been a fossil insect found on any Hawaiian or other mid-Pacific island. But there is the possibility that someday some may be found. There are certain deposits such as lignite in which some insects might be preserved, but, to my knowledge, no search for insect fossils has yet been made in such materials. Mid-Pacific islands do not provide favorable conditions for the fossilization of insects, and we may expect them to be very rare or absent. On the other hand, fossil land snails and marine fossils are abundant and plant fossils are common in some places. It is significant that no fossils older than Pleistocene have been found in Hawaii; most are Recent.

Marine fossils are found in emerged reefs in many places, and these are most abundant on Oahu. The fossil reefs on Lanai have already been discussed. These marine fossils are of Pleistocene or Recent age. In his paper on fossil marine Mollusca of Oahu, Ostergaard (1928) reports that only three species, two oysters and a *Strombus,* of the 82 fossils studied, appear to be extinct species, but that the *Strombus* might yet be found living. It is thought by some workers that, if carefully searched for, the oysters may also be found living. Eight species found as fossils in Hawaii are not now known to be living in Hawaii but are found living elsewhere in the Indo-Pacific. Three species are listed as fossils which are also found living in Hawaiian waters but are apparently on the verge of local extinction. About 70 species of marine fossils collected by Stearns at 16 sites on Oahu (Stearns and Vaksvik, 1935:166) and identified by W. C. Mansfield were considered no older than late Pleistocene.

Insofar as is known, all of the fossil plants found thus far appear to be Recent and identical with species now living in Hawaiian forests. A significant point, however, is that present-day upland forest types of plants are found as fossils at low elevations in dry areas where native forest plants have disappeared and where cultivated and immigrant plants now grow.

Fossil land shells all appear to have been found in geologically recent formations. Some of these fossils are identical with living species. Some species have been found first as fossils and later discovered in the living state. Others which are now known only as fossils may yet be found living. However, there is a wealth of Recent fossil species which are evidently truly extinct. In many regions now under cultivation or covered with adventitious vegetation and in dry areas far from the native forests—even on some small, offshore islets—are found rich fossil beds that show without question that these areas were at one time clothed with native plants, as are some of the undisturbed native forests today. Fossil land shells are good indicators of the character of the pre-existing forest cover in a given region, for it can be ascertained from study of them whether the forest was of the wet or dry type. Many of these species appear to have become fossil since man has so drastically upset the balance of native life in the lowlands. Dr. C. M. Cooke, Jr., tells me that there are fossil land shells by the thousands in eolian sand deposits on the island of Molokai. These fossils are so arranged in the sand that it can be ascertained where each tree stood on which the snails lived before they were buried by the drifting sand. Some of the fossil Hawaiian land snails appear to belong to extinct groups of species, but no fossil species has yet been found which belongs to other than a living genus.

Probably the most interesting fossil discovery in Hawaii is that of the bones of a goose taken from an ash a hundred feet below the surface during the excavation of a water tunnel near Kaumaikeohu, Kau, Hawaii, in 1926. Stearns (1930:60) records the following information. "They [the bones] were identified by Dr. A. Wetmore, of the United States National Museum, as those of a peculiar form of goose, representing an undescribed species, distinctly larger than that of the "nene" (*Branta sandwicensis*), the modern Hawaiian goose. The bones lay on top of an ash bed interstratified with basalt and according to W. O. Clark, who forwarded the bones to Dr. Wetmore and who examined the place where the bones were found, the skeleton of the goose was lying on the ash when the lava buried it." This goose has been described by Wetmore, from a few fragmentary bones, as *Geochen rhuax*, a new genus and species and considered most like an Australian form.

PRE-EXISTING HIGH ISLANDS IN THE MID-PACIFIC

Some authors are persistent in their arguments for mid-Pacific continental land masses or bridges to account for the distribution of Pacific plants and animals. Carl Skottsberg, a distinguished botanist, recently wrote (1940:707) that the composition of the Hawaiian flora "... can be understood only under the supposition that considerable changes have occurred in the distribution of land and sea, *making it possible for plants and animals to travel over land between regions now separated by deep water*." (The italics are mine.) My own research leads me to take issue with Skottsberg, and I have stated elsewhere (1942:283) that "At least for eastern Oceania the distribution of insects could have been accomplished with little change in the present proportion of land and sea." Such opposite conclusions are characteristic of the literature regarding the distribution of Pacific island life. They are the results of our incomplete knowledge of the history of the Pacific and its products.

Ernst Mayr (1940:200) has the following to say about land bridges in Polynesia:

> There was a period early in this century when most zoogeographers were busy manufacturing land bridges whenever they found it convenient to explain certain difficulties of faunal distribution. It is, of course, fascinating to be able to tell the uninitiated: "here are two islands with similarities in their faunas; consequently they must once have been connected! (Isn't science wonderful?)." These efforts culminated, so far as the Polynesian islands are concerned, in the work of F. Sarasin (Nova Caledonia, A. Zoologie, 4:160,1925), who constructed a whole network of land bridges and raised and lowered the sea level by two and three thousand fathoms in quick succession. But even much more conservative authors have always maintained the continental nature of the faunas of New Caledonia, the New Hebrides, Fiji, and other neighboring groups. I, myself, grew up in this belief and was rather surprised when my faunistic studies did not support the contention. They showed, rather, that even the just-mentioned islands are "oceanic."

I believe that those biologists who "create" continental land in the mid-Pacific to enable them to give an interpretation of the distribution of the groups of organisms which they are studying are overlooking the fundamental geologic nature of the mid-Pacific islands. They call for continental land where none is indicated by the geological record. They demand age beyond that indicated by the rocks. They create in their minds the physically and geologically impossible. Our imperfect knowledge of the diverse ways and means of dispersal of plants and animals is not fully recognized even by some of our best students.

An explanation will be offered here to account for the distribution of the mid-Pacific biota based upon what is believed to be foundations in keeping with the geological history of the Pacific Basin, and which at the same time will at least partially reconcile the differences between such opposite points of view as those of Skottsberg and myself. I have said that "Though the evidence for former extensive land masses is lacking, it is probable that high islands other than those represented on maps existed in past ages.... Such islands, when above water, may have been used by plants and animals as stepping stones." (1942:283.) Herein lies the crux of the situation, I believe.

From a synthesis and analysis of data gleaned from first-hand experience in the Hawaiian, Fijian, Samoan, Society, Tuamotuan, Mangarevan and Austral archipelagos as well as from such scattered islands as the Line Islands, Pitcairn, Rapa and Marotiri, Henderson and others, together with a review of the findings of other workers, the conclusion that many of the islands of the mid-Pacific appear to have passed through or are now passing through a definite cycle of geological metamorphosis that has been essentially similar for most of them is inescapable. This cycle has been outlined in the preceding pages, but it will not be out of place to restate it briefly and simply here. The islands have emerged from the sea, built up by volcanic outflow to various maximum sizes, shapes and elevations; volcanism has ceased; erosional activities have torn at the mountains until the older islands have been washed back into the sea where many of them have been capped with coralline materials and have become atolls, reefs or shoals. There are all stages and intergrades of this metamorphosis plainly visible today. The Tuamotu Archipelago and the Marshall and Gilbert and Ellice and Phoenix islands may be as much a part of this historical process as are the Hawaiian islands. The Samoan, Society, and Austral island chains are extraordinarily similar in basic formation to that of Hawaii as they exist today. According to this view, it is only a matter of time until all of these islands will assume the form of the leeward Hawaiian islands, the "dead" Tuamotus and similar coralline archipelagos.

It is not implied that all of the atolls, reefs and shoals in the mid-Pacific necessarily have the same history. There is no reason why some volcanoes could not

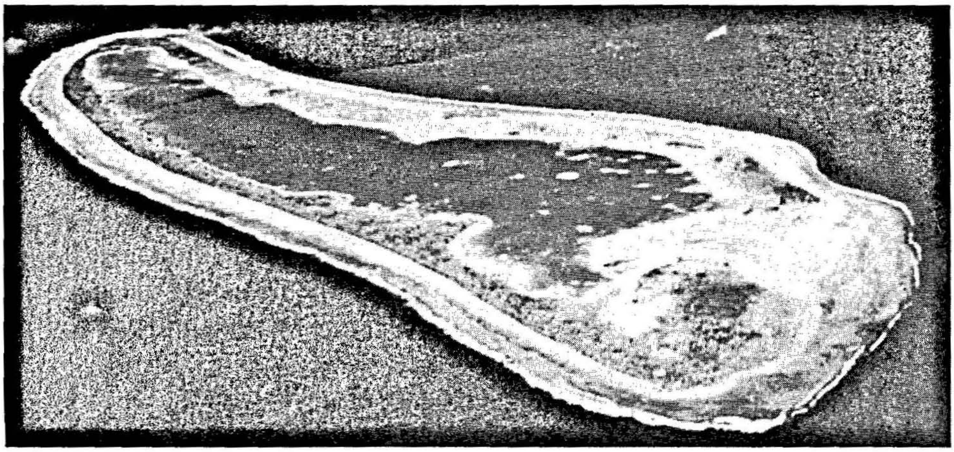

Figure 25.—A small atoll in the Phoenix Islands (Gardner Island).

build up to within the zone of reef-building plant and animal growth and then become inactive. Thus, some of the atolls might conceivably be built upon foundations which have never felt the air. Also, some of the atolls might be built upon volcanic masses that emerged to only a slight elevation above sea level, became extinct and are now capped with coralline growth because of their submergence by the rise of the sea following the retreat of glacial ice. We must also take into account the rise in sea level which has taken place because of the hundreds of cubic miles of water which have been displaced as the result of extensive volcanism, to say nothing of sedimentation and organic deposition. Moreover, there is the possibility of a volcano emerging from the sea, building up for a few hundred feet by erupting ash and cinders, then becoming dormant without capping itself with more resistant flow lava, thus enabling the sea quickly to plane it off below sea level by wave action against the unconsolidated material. Perhaps many atolls have been formed by such a process. We are told by geologists that there has been a submergence in Hawaii of about 1,000 feet; such submergence alone would provide a means of atoll formation from islands up to about 1,000 feet in elevation. In some areas, atoll bases may have been formed largely from the local subsidence of some high islands. But we do not yet know very much regarding atolls and coralline islands in spite of what some workers would like to have us believe! We need some careful work done on typical atolls with adequate borings made in the light of the experience gained at Funafuti and elsewhere (on grid patterns, not random holes). *One of the most pressing needs in contemporary studies of Oceania is deep, core borings on atolls!*

If this line of reasoning be followed, then it may be that during past ages Hawaii was decidedly less isolated than it is now. In other words, I believe that Hawaii is more isolated from other high islands today than ever before. The sea to the south and southwest of Hawaii is now studded with atolls, many of which may mark the graves of large, high islands which at one time were much the same as those of the main Hawaiian Islands or the Society Islands or the Marquesas, or Samoa and others. Perhaps parts of the Marshall, Gilbert, Ellice, Phoenix, Kingman-Christmas chain and Tuamotu islands were at one time or another majestic mountainous islands upon which flourished characteristic floras and faunas. Whereas the nearest high islands today are about 2,000 miles away, in past ages the isolation was possibly only about 500 miles (Johnston Island) —perhaps even less.

Such pre-existing high islands would provide stepping stones for the immigration of floristic and faunistic elements from the Asian, Malaysian, Papuan, Fijian and southeastern Polynesian sectors. It does not call for the jumping over of "thousands of miles" of open sea (as many workers believe is required), but rather for a series of smaller over-water steps.

It appears that not all of these routes were available at the same time. If they existed at different times, the influx of diverse groups of organisms was at different times, at different places, by different routes from different places.

This would account for the apparent differences in age of various sections of the biota. It now appears to me that the route through the Marshall and Gilbert sectors was cut off before that leading from southeastern Polynesia. I would guess that most of the extra-Hawaiian stepping-stone routes were cut off in Pliocene or by early Pleistocene times, that it now appears probable that some sources were blocked off even before the Pliocene, and that the amount of immigration since mid-Pleistocene has been greatly limited. However, there are elements in both the flora and the fauna that indicate that some colonizations have been made since all the high-island stepping-stone routes were obliterated —as they are today. Moreover, there is no reason to believe that natural immigration has ceased or that it was any less rapid 200 years ago than 10,000 years ago. Since the advent of white man, however, conditions have been greatly altered. Various distribution patterns in the Pacific may be the resultants of different stepping-stone access routes being open at different times. Thus, the influx to a given point may have been from different directions at different times.

Normal mid-Pacific atolls cannot serve as favorable stepping stones for high-island floras and faunas, and with few exceptions they support few or no endemic plants or terrestrial animals. The explanation for this is a simple one. The low coral atoll is subject to severe periodic fluctuations of inadequate precipitation; it is exposed to the full fury of storms, those in the hurricane belts are time and again swept bare of soil and vegetation by hurricane-driven waves, and tsunami ("tidal" waves) may play a definite role. I have seen the results of hurricanes in the Tuamotu Archipelago, and the devastation wrought is a sight to behold. Plants and animals are not normally left undisturbed on an atoll for a long enough time for variation, raciation or speciation to take place. Thus the flora and fauna of the atolls of a great archipelago like the Tuamotu are made up almost entirely of populations of widespread species. Most of the coral islands that do have endemic species are either slightly or distinctly elevated or are outside the hurricane belt. Henderson Island, at the southern end of the Tuamotu Archipelago, is an emerged atoll between 75 and 100 feet high, and it has endemic plants, land snails, insects and even an endemic genus (subgenus?) of birds (a rail)! When an atoll is emerged to an elevation above the point where periodically it can be swept bare of its terrestrial life, it enters into the phase where the development of endemic products is possible. Thus, most of the atolls which have been formed by the degradation of high islands have lost all or nearly all of their original flora and fauna by extermination. They develop the typical atoll association of plants and animals which varies according to the locality and climatic zone, either wet or dry or intermediate. Atolls mostly are ecological deserts unsuitable to most high-island plants and animals, and they cannot act as efficient stepping stones. A sufficient increase in elevation and the subsequent change in environment place atolls in the realm of high islands once again.

CHAPTER 2

DISPERSAL

> *As the ploughshare breaks up the green sward of arable land, and disturbs the closely interwoven roots of the existing assemblages of plants, so do tornados, whirlwinds, and storms furrow the surface of our globe in all directions, unsettling and scattering prosperous communities of living creatures, and rendering many of them for a time the helplessly drifting waifs of an ocean . . .*
>
> —*Müller* (1871:186)

GENERAL CONSIDERATIONS

A survey of the literature for the past 300 years or so will reveal a multitude of records concerning the many ways and means of occasional transport by which plants and animals are spread about the world. In spite of this great body of information, there are those who still fail to accept the evidence and who refuse to recognize that overseas dispersal to islands is fact and not theory.

Even the most ardent advocate of Pacific continents and land bridges would hardly be so bold as to suggest that each of the hundreds of mid-Pacific islands was at one time connected to some other area by dry land. Some islands have been strictly isolated from the time of their origin and have never known a subaerial connection with any other land. But all of the islands that can support a terrestrial biota have been populated by plants and animals. The elementary fact that these islands insulated by ocean barriers have been populated is proof enough that certain plants and animals can cross such barriers of open sea. Therefore, if some mid-Pacific islands have been so populated, then all the mid-Pacific islands including the Hawaiian Archipelago could have been populated by oversea transportation. To argue for land connections is to evade the question. ". . . if the micro-pulmonates can only travel on land, then well-nigh every island on the face of every ocean is an unsubmerged fragment of some previous continental land-bridge." (Addison Gulick, 1932:416.)

Spitsbergen was entirely covered with ice during the last glacial epoch, and its contemporary terrestrial biota has arrived from overseas since the retreat of the glacial ice has exposed soil. There has been no land connection between Spitsbergen and Europe since glaciation. Elton (1925) found that aphids and flies blow 800 miles from Europe to the islands, and he says that the present insect fauna has arrived principally through the air and on birds.

The uninhabited, isolated, elevated coral atoll, Henderson Island, is again brought to mind. This raised atoll, which is northeast of Pitcairn Island, is about

2.5 by 5 miles in extent and is elevated so that its top is between 75 and 100 feet above the sea. It is, as it exists today, certainly a young island whose subaerial age is to be counted in thousands of years rather than hundreds of thousands of years. The old lagoon depression and its included coral masses and irregularities can still be seen. It appears to have risen sterile from the sea, insofar as its terrestrial biota is concerned, yet it is now densely clothed with a tangled tropical jungle. More than 250 species of plants, mostly native, were found there in 1934 by Bishop Museum's Mangarevan Expedition. There are also endemic birds, including an endemic genus (subgenus?) of rail, endemic insects and endemic land snails. Thus, all of the major elements of the Polynesian terrestrial biota have succeeded in being transported across the sea, colonizing this tiny bit of isolated land, and have not only established themselves there but have evolved into new forms quite distinct from their forebears.

To my knowledge no one has stood on an island and watched hurricane winds blow insects or land snails from another island across the sea, or watched while seeds, insects or land snails were dislodged from birds or from materials drifting in on waves. However, there are those who saw very large sheets of iron roofing torn loose from a church on Tau, Samoa, by a hurricane and others who saw some of that iron crash onto the island of Olosenga six miles away across the sea! The iron could be seen, but not the seeds, small insects and land snails that might have been carried across the channel at the same time. I picked a living bark beetle out of the feathers of an owl knocked down in flight in the highlands of Fiji. Owls have been seen at sea 1,000 miles from the nearest land. Wheeler (1916:180) described a new species of ant from a colony taken from a log which had floated from Brazil to San Sebastian Island. A mallard duck shot in the Sahara had snail eggs on its feet.

These are just a few facts from the body of convincing evidence that shows without a doubt that overseas dispersal is an active reality.

My friend R. H. Van Zwaluwenburg spent about four months on the coral island of Canton (171.5°W 2.5°S) during two successive years and has, fortunately, recorded some of his observations made there. Because of the variation in annual rainfall, the island's vegetation cover ranges from desert-like to lush. During and following a period of dry years when the island was in "desert condition," only an occasional straggling, travel-worn *Hypolimnas bolina* butterfly was seen. After a period of rains which brought up a lush growth of plants from dormant seeds and roots, the butterfly became established from overseas immigrants. Single specimens of the monarch butterfly arrived, but this species had not succeeded in establishing itself up to 1941 (because of lack of a suitable host?). Also, after a period of rainfall which left some persistent ponds, two species of dragonflies became established from immigrant parents. No dragonflies were seen on the island during the previous year. A return to arid conditions would result in the local extermination of the butterfly and the dragonflies.

Van Zwaluwenburg (1942) says, "It seems probable that some or all of the above insects, as well as others similarly capable of traveling long distances, have been established on Canton at one time or another in the past. The fact that the present establishment of the three discussed is recent suggests that conditions of food and water favorable for their maintenance are only temporary; that establishment and local extinction succeed each other as favorable and unfavorable conditions alternate, and that the present colonies of these particular species will in turn die out when severe drought recurs."

The prevailing winds at Canton are easterly or southeasterly, and the normal current drift is westward. In 1940 few or no seeds were seen among the debris cast up on the beaches. Following a period of strong winds from the west (up to 55 knots), drift-borne seeds were common and conspicuous, and the seeds of about 20 species of plants were picked up. Some of the seeds found were of species which are not known to live on any island closer than several hundreds of miles from Canton.

The insects and seeds recorded here are all large, conspicuous, easily seen objects. How many minute seeds and insects might escape the notice of the observer?

> Seeds of many of the species listed had sprouted after stranding. Between 35 and 50 coconut sprouts were estimated to be still present in September along the entire 27-mile perimeter of the island, but these were only a small fraction of the total number of coconuts cast up. Some of the hazards attending the survival of the seedling plants from drift seeds are obvious: hermit crabs (*Coenobita olivieri* Owen) shred the husks of coconuts and eat out the contents of the sprouted nuts; flood tides drench many seedlings with sea water; in at least one case high water buried a sprouted palm deep in sand. So the complete failure of any of the above named plant species to become established on Canton in the past (all of the coconuts growing on the island are known to have been planted by man) is not surprising when, to the hazards already mentioned, are added the inevitable recurrent shortages of rain. (Van Zwaluwenburg, 1942:52.)

The great difficulty in the dispersal of animals from one locality to another on floating vegetation appears to be not so much dependent upon their being cast adrift and being transported, but rather in their landing in another locality and becoming established in a foreign and perhaps hostile environment. Sea beaches upon which flotsam is cast are not usually favorable environments for the establishment of most terrestrial organisms. Many kinds of insects which were purposely introduced and carefully cared for have failed to become established in Hawaii. The number of natural immigrants which have failed to establish themselves after surviving overseas journeys must be very great.

The crux of the problem is that insects, plants and terrestrial Mollusca do inhabit all habitable Pacific islands no matter how great the isolation, and, therefore, they possess advantages that fit them for selection by agents of overseas distribution and for survival. Many of the insect genera inhabiting mid-Pacific islands are flightless descendants of flightless ancestors, and because they inhabit islands separated by hundreds of miles of open sea, their distribution is obviously independent of their ability to walk. Such insects have crossed, and undoubtedly still are crossing, large bodies of open sea, not because they have wanderlust, but because of forces beyond their control—forces undoubtedly adverse to their general well-being. A bewildering fact is not that these islands have been colonized by overseas dispersal, but that so few animals have crossed the sea and have become established here.

As an example of comparatively recent interisland dispersal, the minute weevil *Microcryptorhynchus vagus* Zimmerman may be mentioned. There are more than 80 species of the genus described from southeastern Polynesia, but all except *M. vagus* are confined to single islands or parts of individual islands. However, *M. vagus* breaks the rule of absolute uni-insular endemicity, for I found it on four of the Society islands.

One may be asked, "If such distribution has accounted for the origins of these floras and faunas, why has it stopped? Why do we not find species blowing or drifting in now?" The answer to such questions is simple. What would be the chance of finding a few small seeds, molluscs or insects which might arrive in any one area from overseas? Almost nil, of course. If they became established, one might find a colony before long, but it is too much to expect actually to witness the arrival of such minute immigrants. In another section of this paper I have analyzed the Hawaiian insect fauna and found that over a period of several millions of years, only about 250 overseas stragglers succeeded in becoming established in the several thousand square miles of the Hawaiian Islands—perhaps only one successful colonization per 20,000 years! The very developments of the diverse parts of the biota reflect sporadic and interrupted immigration over long periods of time. Overseas dispersal has not stopped, but we are fortunate when we can record a few concrete facts. Our period of scientific research on such problems is but a passing moment, and we cannot expect to witness everything in a wink of time's eye.

MEANS OF DISPERSAL

There are three principal ways by which the terrestrial endemic biota of the Hawaiian Islands may have reached the archipelago. These are marine drift, wind and aid from other organisms.

The normal, contemporary ocean currents that sweep past the main Hawaiian islands are from the east, but the westernmost islands come within a zone that experiences at least a certain amount of drift from the west. During Pleistocene glaciation, the western current may have shifted farther to the south. Thus the archipelago may have been much more affected by currents from the west in the past than it is now. The problem of past climatic changes is worthy of careful study, and it has not received adequate attention in the Pacific. At the present time, logs from northwest America and fish net floats and other items from Japanese waters are commonly cast upon Hawaiian shores. There appears to be little information available concerning the routes of drift of these objects. It would be most worth while if a study of the material coming ashore at Midway Island, for example, could be made to determine how long the material had been in the water and by what route it had traveled. A study of the marine organisms adhering to floating objects would reveal much pertinent information.

However, the strong, eastward, counter currents set up by cyclonic disturbances should not be overlooked. Probably they are largely to be credited with the spread of the common strand plants that are as a group so similar from Micronesia and Melanesia eastward. Irregular currents may be more successful agents of dispersal than normal currents.

The literature is replete with examples of plants and animals being transported across wide stretches of sea. It is usually only the records of the larger animals that find their way into print, however, and crocodiles, monkeys and large and small reptiles are known to have made their ways, some on identified floating material, across ocean barriers. Wood-Jones (1910:290) records a tree which carried ashore at Cocos-Keeling a wheelbarrow load of soil in its buttressed base, and he considered that a small burrowing snake was carried to the island in such a manner. Large rafts or masses of debris making up "floating islands" are commonly washed out to sea from islands from Fiji westward. It has been shown that such masses may carry with them a varied assortment of plants and animals. Mr. C. E. Pemberton told me that while out of sight of land on a voyage between Macassar, Celebes and Sandakan, Borneo, many "floating islands" were seen. These mats of vegetation were lush and green, and palm trees 20 to 30 feet high stood erect on the floating masses. A survey of these rafts probably would reveal that numerous plants and animals were riding them. Although such rafts are probably broken up by rough water, it is possible that some of them, on rare occasions, could travel more or less intact for many hundreds of miles and deposit at least part of their living cargos on foreign shores. I have seen large trees washed from stream sides during a storm in Tahiti and have seen them floating out to sea with their large branches riding high out of the water. The large, heavy trunks, great root masses in which are entangled stones and soil, and the submerged limbs may act as keel, ballast and stabilizers and hold a part of such floating trees permanently out of the water. Some of the branches may be held 20 or more feet above the waves. At rare intervals, colonies of animals and seeds may be able to survive lengthy journeys in such perches. It is conceivable that over a period of several millions of years a few such floating trees have been beached in Hawaii and that from them there escaped ancestors of some of our insects, terrestrial molluscs and plants.

Visher (1925:122) said:

> The floods caused by the excessive rainfall associated with hurricanes influence the dispersal of land forms. There are numerous records of the fall of more than twenty inches in two days, and some records of more than sixty inches in three days. Under such conditions streams normally small may become great rivers and carry to sea vast quantities of driftwood. The river banks are eroded badly, and many trees are undercut and are carried out to sea. During the excessive rains, large masses of dirt and loose rock upon steep hillsides may slip, sometimes damming valleys. If the dam breaks, the sudden rush of water does its part to contribute natural rafts of driftwood with their load of land animals and seeds. Hence, the absence of long rivers flowing to the Pacific, with the exception of the Chinese rivers, should not lead to the assumption that natural rafts of considerable size and biological dispersing possibilities are lacking in the Pacific. Pilsbry has made this erroneous assumption. He states: "The argument

of the distribution of animals by natural rafts has never been more convincingly stated than by W. D. Matthew in his paper 'Climate and Evolution.' Much of his argument is not applicable to the Pacific islands. Here we have no large rivers to give forth natural rafts. If a single tree washed to sea it must be very exceptional."

Perkins (1913:lxvi), speaking of the dispersal of Hawaiian land snails, said, "We once found at the foot of the Waianae slopes a number of one of the terrestrial species of *Amastra,* quite outside of the forest, hiding in the hollows of a large log on the bank of a stream. This log had clearly been carried down in a flood, and probably for many miles before stranding, the stream arising in the Koolau range of mountains, the forest of which was miles distant."

However, because of the concomitant difficulties in transportation and establishment, it appears that marine drift is probably the least successful of the three methods of transport.

The bulk of the insect faunas of the mid-Pacific appear to me to be wind-borne. Adequate experiments have now been carried out to show that both winged and wingless insects are carried by air currents to great heights. The work of Glick (1939) has been previously reviewed and the interested reader is referred to his extensive discussion of the records obtained during a five-year period of trapping insects in the air by the use of airplanes. "Not only were thousands of insects taken at various altitudes up to 14,000 feet, but spiders and mites, wingless creatures, were not uncommonly captured. One spider was taken at 15,000 feet. Some opponents of dispersal by wind say that certain insects are weak fliers and are therefore not capable of traveling great distances on the wind. These weak fliers are just the insects which Glick found to be the most abundant in the air and which were carried to the greatest heights. Heavy-bodied, strong-flying insects were not taken high in the air. Not only were winged adult insects collected, but larvae, nymphs and wingless adult insects were captured as high as 14,000 feet. Glick says that these wingless forms are all at the complete mercy of the upper air currents." (Zimmerman, 1942:287.) An analysis of the endemic Hawaiian spider fauna shows that it is made up only of those groups that can be wind-borne; all other groups are absent.

It is not considered that normal trade winds are strong enough to blow even small insects for significant distances across open bodies of sea. The trade winds of the Hawaiian area blow from the east. In another section it is shown that relatively few insects have been derived from America. Therefore, the normal trade winds cannot be considered as primary agents for the dispersal of the predecessors of the Hawaiian insects. Also, the unbroken distance between America and Hawaii is great. However, it is largely abnormal rather than normal conditions that have accounted for the dispersal of the mid-Pacific biota. In reviewing the distribution of south Pacific insects (Zimmerman, 1942), it was noted that hurricanes have often swept from the west, crashed through insular forests stripping trees of their leaves and twigs, churned across the sea and passed over islands eastwardly of their origins. It is such abnormal, cyclonic winds which I believe have accounted for the dispersal of a large part of the insects of the mid-Pacific. Convection currents may carry insects high into the air to the anti-trade wind zone which blows strongly from the west, and upon attaining these high strata, insects might be transported for considerable distances.

The force of hurricanes is probably underestimated by those who have not actually experienced them or seen what they can do. "Men instinctively underestimate the lifting power of air. Many zoologists today find it as difficult to believe that winds and rising air currents can lift and carry moderately heavy organisms as persons once found it to believe that heavier-than-air machines could fly." (Darlington, 1938:280.) A wind of 75 miles per hour is said to have a force of more than 16 pounds per square foot. Cyclonic winds with speeds in excess of 150 miles per hour have been recorded on Pacific islands. The pressure of the wind increases as the square of its velocity. The force of such winds and the devastation wrought are astounding. Great blocks of coral reef as much as 30 feet high may be ripped up by the wind-driven waves and brought to rest on shore. Stone buildings are blown down, and the amount of plant material thrown into the air is great. Leaves and twigs hurled high into the air may well act as conveyances for flightless creatures which cling tightly to such material or which are living within it. It hardly seems necessary to point out the great increase in buoyant capacity with decrease in size of organisms. Thus, air currents which cause little concern to a man have a drastic effect upon small organisms whose surface is so greatly increased in proportion to their weight. Visher (1925: 120) said:

> Is it not highly probable that tropical cyclones have played a part in the dispersal of life from island to island in the Pacific? Along the Equator are many violent westerly winds, completely overcoming the prevailing easterlies; within the Tropics or just beyond the Tropics many storms move eastward. In moving eastward, the strong westerly wind on its equatorward side carries much with it, and sets up a strong drift as well.... The power of the wind to transport light objects through the air, as for example when birds and insects are carried out to sea in large numbers, is illustrated by hurricanes. Indeed the presence of butterflies and birds far out at sea has often been noted in connection with hurricanes.

On page 124 he says:

> It is conceded that the effects of a single hurricane are small, and the reason why hurricanes have been largely ignored by the students of plant and animal distribution is because hurricanes were believed to occur only at long intervals. But now that the records show more than two score annually, on the average, in the Pacific, hurricanes take on a different aspect and their significance is increased by the fuller appreciation of the diverse ways in which they affect the lands, streams and currents.

On occasion, sand from the Sahara Desert is blown as much as 400 miles to sea where ships have experienced sandstorms and have been littered with sand.

Notations are made of the birds, butterflies and large insects which can be readily seen, but the minute insects which cannot be seen except when close to the observer usually escape the records. Butterflies, dragonflies, Orthoptera, beetles, bugs, flies and other insects have been recorded at great distances from shore. Some insects have been taken at sea as much as 1,000 miles from their homes. Land snails from Cuba have been carried to Florida by hurricanes, and numerous colonies are now established on the mainland. A Pan-American Airways employee told me that after a westerly storm of several days' duration, a Chinese cuckoo came ashore at Wake Island. A pair of North American kingfishers flew ashore on the island of Hawaii a few years ago. *Proterhinus* (flightless) weevils were found by Perkins to have been blown far from their food plants, and he found (1913:lxvi) land snails which had been carried by the wind on leaves or small branches to a barren, treeless area on Molokai during a severe gale. Hardy and Milne (1937) flew kites carrying traps and attached nets to the masts of ships and found that the amount of "aerial plankton" drifting across the North Sea was considerable. They caught spiders, Hemiptera, Neuroptera, Trichoptera, Lepidoptera, Hymenoptera and Diptera at sea. "After reading about the recent developments of our knowledge of the upper air-strata, I am inclined more and more to regard the trans-oceanic distribution of insects as carried out mainly in the upper air." (Guppy, 1925:543.)

Overseas dispersal aided by birds is probably next in importance to occasional transport by wind, and in certain instances it may be more important. It appears that the role played by birds in the dispersal of the terrestrial floras and faunas of Pacific islands is underestimated. Numbers of sea birds such as shearwaters, terns and tropic birds nest in insular forests from sea level to over 6,000 feet. Some of these birds burrow in the soil or nest upon the ground in the midst of dense plant growth, while others build their nests in shrubs and trees. I have observed white-tailed tropic birds nesting in the high interior rain forests of Samoa. These birds build their nests in *Asplenium nidus* ("bird nest") ferns and on epiphyte-covered branches of trees. When they alight, they claw at and beat the surrounding foliage with their wings. By these clumsy actions they dislodge insects, land snails and parts of plants. The habits of such wide-ranging birds fit them admirably for having insects, land molluscs and seeds lodge on their bodies and thus be carried for long distances to other localities. Cyclonic winds will drive such birds out of their mountain haunts and they may not alight until another island many miles distant is reached. There are those who may belittle the importance of this possible means of dispersal, but we need only recall the record given previously of the finding of a living bark beetle on an owl (an owl was captured after it alighted on the "Duchess of Richmond," a thousand miles at sea in the Atlantic in 1938), that Perkins found a living achatinellid land snail on a Hawaiian bird, that a mallard duck shot in the Sahara had snail eggs on its feet and that experiments have shown that seeds are carried for long distances by many kinds of birds, to have the possibilities of dispersal aided by birds forcefully illustrated. No survey has been made of the foreign material adhering to birds in the Pacific. We do not know how much plant and animal life is carried by birds across the sea. It is highly probable that the several kinds of Boreal plants found on Hawaiian mountains, as well as certain land snails which are identical with, or closely similar to, certain northwestern American species, have been accidentally brought to Hawaii by birds. Ducks, geese, plover, sandpipers and about 40 other kinds of birds stray or regularly migrate to or through Hawaii from northwestern America. Some of these birds continue on to islands in the south seas, and pass back through Hawaii on their return to northern latitudes. In 1943 a flock of ducks landed at Palmyra Island, about a thousand miles south of Honolulu. Some of the ducks bore tags which had been placed on them in Utah. It is much more unlikely, however, that organisms coming from the north would become established here in Hawaii than would those from the south or west, because of the dissimilarity of the environments between high latitudes and tropical Hawaii. The comparative paucity of Boreal elements in the Hawaiian biota is easily understood, and the few exceptions only emphasize the general conclusion as to the tropical derivation of the biota. It may not be out of place to note here that a cuckoo migrates regularly over an east and west route in the south Pacific. I have seen the species as far east as Mangareva.

Some malacologists are reluctant to admit that land snails can be transported across ocean barriers. It has been said that the large snails such as the Hawaiian achatinellids and amastrids are particularly unsuited for such distribution. However, if we approach the problem differently, different conclusions may be reached. If, as I believe, the large Hawaiian snails have evolved from small or minute ancestors, then the argument based upon their large size loses its weight. However, if small snails can be distributed overseas, then what is to prevent eggs or tiny, immature specimens of large species from being similarly transported?

I agree with Mayr when he says (1940:201):

> The means of dispersal of most plants and animals are much more extensive than was formerly realized, and even rather irregular distributions can be explained without the help of land bridges. Dispersal across the sea is, of course, most obvious for birds, and ornithologists were among the first who accepted the ideas of the permanency of continents and oceans. Most entomologists are also beginning to realize that they can solve most of their distributional difficulties without land bridges. The conchologist, however, postulates even today continental connections between all or nearly all the islands where land shells exist. It seems to me that the wide acceptance of land bridges by conchologists is chiefly due to three reasons: (1) our almost complete ignorance of the means of dispersal of snails, (2) our lack of knowledge of the speed of speciation in snails, and (3) faulty classification, particularly generic classification. A. Gulick has already directed attention to the presence of snails on most oceanic islands. They were unquestionably carried there by some unknown means of transportation. Occasionally we must accept this even for larger snails. If one (or several) species of the large snail *Placostylus* are found in northern New Zealand, I would not, as Hedley did, create a continent embracing all the areas where the genus *Placostylus* is found (New Zealand, New Caledonia, New Hebrides, Solomon Islands, and eastern New Guinea), because the acceptance of such a land mass is contrary to all the other evidence. To me it seems incomparably simpler to assume a still unknown method of transportation than a land bridge that is unsupported by any other fact.

H. B. Baker, who has published the most modern monograph on Polynesian snails, states (1941:350) that "The most probable method, by which the accidental introduction of these land snails might be accomplished, would appear to be their rare transport by birds. As is known, certain of the latter, such as the golden plover, do annually migrate through Hawaii to islands in the south central Pacific and might occasionally transfer eggs, juveniles, or even adults." Baker (1941:355) also states that the long axis of the distribution of the Philonesiae snails from Hawaii to Rapa, which corresponds with the distribution of the recent Nearctic groups which have colonized Hawaii and Tahiti, "suggests that bird transport may also have been a factor in the dissemination of these Microcystinae."

> The transportation of snails by birds has not been well understood. There is a genus called *Succinea,* found not only on our islands, but also on many remote islands out in the ocean. *Succinea* has been found on the plumage of birds, and it can hardly be doubted that it thus reached various oceanic islands, but at very rare intervals. There is a remarkable genus of slugs called *Binneya,* discovered on the small Santa Barbara Island long years ago. Last year I found a couple of *Binneya* shells in a superficial deposit on San Nicolas Island. Far to the south, *Binneya* is also found on Guadalupe Island, but, as Pilsbry has shown, the species is distinct. It is difficult to understand how such an animal could cross the sea, but it is known that in the dry season it is covered with a mass of dried mucus which protects it from desiccation. It can be supposed that this sticky mucus, when fresh, might cause the slug to adhere to some bird, and thus obtain transportation. It is not surprising that actual proof of such transportation is rarely to be had; the event must be a very rare one, as otherwise the insular races, evolving under conditions of isolation, would be swamped by newcomers. (Cockerell, 1939:103.)

It should be emphasized here that conditions in the Hawaiian Islands have been changed drastically since the introduction of man, dogs, cats, swine, rats and the mongoose. The sea birds at one time nested on the main islands in myriads, as they do on certain other islands today. The sea birds no longer can use the main islands as they once did. Furthermore, these birds have had their numbers reduced to a small fraction of what they once were. We are apt to overlook these great changes which occurred before we began our studies. The change which has taken place in the development of the sea birds in Hawaii has been a profound one.

One of the most conspicuous features of the insect faunas of the eastern oceanic islands is the entire absence of some large groups, families and orders common to all continents. They have been eliminated by the selective agents of overseas dispersal. Scarab beetles are one of the most dominant groups of all the continents, yet there is not a single native species on the central Pacific islands east of Fiji. Most of them are subterranean in their larval stages, and most are strong fliers. The family is greatly developed in western Oceania. To my knowledge, the only native beetles with true subterranean larvae that occur on the islands of Oceania east of Samoa belong to the flightless genus *Rhyncogonus*—but the eggs of these weevils are deposited on leaves. The absence of endemic Chrysomelidae, or leaf beetles, from Oceania east of Samoa is difficult to explain; they are extensively developed in the western Pacific. With few exceptions, the entire endemic beetle fauna of southeastern Polynesia is composed of small, predominantly flightless species which breed in dead twigs, dead leaves or in or under dead bark, and these forms are more extensively developed than any of the other groups of terrestrial animals in that region.

We will do well to keep in mind Darwin's remark, "How ignorant we are with respect to the many curious means of occasional transport."

CHAPTER 3

ANALYSES AND SUMMARIES OF THE HAWAIIAN BIOTA

> *A classification which shall represent the process of ancestral evolution is, in fact, the end which the labors of the philosophical taxonomist must keep in mind.*
>
> —*Huxley*

The total number of insects recorded from the Hawaiian Islands exceeds 5,000 species, but many other species are known that await determination or description, and untold numbers of new species have yet to be collected from their mountain haunts. This assemblage is composed of two distinct elements—one native, the other foreign. Only the native insects will be included in this analysis, because it is limited to a discussion of the fauna of Hawaii before the advent of man so greatly disturbed the environment.

ENDEMIC AND INDIGENOUS, IMMIGRANT AND INTRODUCED

It is worth while, before proceeding, to define certain terms as they are used in this text to obviate the possibility of misunderstanding. In using the word *native,* reference is made to those insects which are either *indigenous* or *endemic. Indigenous* species are those which live naturally in Hawaii as well as in some other place or places, and whose distribution came about without the intervention of man. As an illustration we may use the ectoparasitic louse fly, *Olfersia spinifera* (Leach) (Hippoboscidae). This fly is a parasite on such sea birds as the frigate bird, which ranges far and wide among Pacific islands. These birds are found naturally in Hawaii, but also on many other islands. The fly has followed its hosts for untold thousands of years, and it is thus *indigenous* to Hawaii, but not *endemic* to Hawaii alone. Species *endemic* to Hawaii are those which are entirely restricted to Hawaii and are not naturally found elsewhere. As an example of an *endemic* insect we can list the ground beetle *Blackburnia insignis* Sharp (Carabidae) which has been found only in a restricted area in the Kaala section of the Waianae Mountains of Oahu and nowhere else in the world. Moreover, the genus to which it belongs is endemic, for it is found only on Oahu.

The foreign insects may also be placed in two categories. The first of these are the *immigrant* species, or those which have been unintentionally brought in by the intervention of man. Such insects are the granary weevils, which have come in cargos of rice, flour or other such materials, or the dozens of species of scale insects which rode into Hawaii on plants brought here for planting or on imported fruits and vegetables. The majority of our more than 1,300 foreign insects are immigrants. The second group of foreign insects are the *purposely introduced* species. The many species of parasitic or predaceous insects purposely introduced to aid in the biological control of insects and plants come under this heading. We are likely to use the term *introduced* loosely and to apply it to any foreign insect—I have unintentionally done so myself. But, according to some entomologists, it appears that, strictly speaking, the word *introduced* should be reserved for those species which have been purposely imported and not applied to accidental immigrants. However, I can see now no good reason why the qualified phrases *natural immigrant, purposely introduced* and *accidentally introduced* are not equally acceptable.

It is not always easy to tell to which of these four categories a particular species belongs. Fortunately, records of importation have been kept for most of the purposely introduced species. The common immigrant household pests such as cockroaches are also easily placed. Some species which we know are immigrants have been described from specimens collected in Hawaii and, because of our incomplete knowledge of other regions, these species have not yet been found in their native lands, and we do not know whence they came. Some species are considered as probably indigenous, but are not yet known from any other locality. However, some indigenous species known only from Hawaii when first described have since been found living natively elsewhere. The majority of the endemic species have definite characteristics which stamp them as endemic, and some of these features will be outlined in the following section.

THE INDICES OF ENDEMICITY

The natural evolutionary products of Hawaii for the most part have dominant characteristics of endemicity. A number of rules can be formulated to distinguish them, but, as with so many other natural phenomena, there are numerous exceptions to most of these rules. Some of the significant characters of endemic insects are as follows:

1. Most endemic species belong to Hawaiian species complexes. In other words, an endemic species usually is one that belongs to an association of Hawaiian species which are closely allied to one another or show obvious genetic community of origin. As examples of species complexes we may take extremes such as the genus of small moths, *Hyposmocoma,* with more than 200 described Hawaiian species, or the genus of small, flightless beetles, *Proterhinus,* with its 181 described Hawaiian forms. On the other hand, the singular, flightless stag beetle, *Apterocyclus honoluluensis* Waterhouse, is an endemic species belonging to a monotypic endemic genus. It is a polymorphic species, but evidently none but the single species restricted to the high mountains of the island of Kauai exists. This stag beetle, it is true, does not belong to a species complex, but it is distinctly isolated from any species known from the rest of the world. It appears to be a

relict form. The cosmopolitan butterfly genus *Vanessa* is represented in Hawaii by a single endemic species. This butterfly, as an adult, is not greatly different but yet is unlike any other member of the genus, but, according to Perkins, its larva is so distinct from other *Vanessa* larvae as to make it appear almost to belong to a different genus. It may be that compared to the *Hyposmocoma* and other lepidopterous complexes this single species of *Vanessa* is a newcomer to Hawaii. But its habits and make-up may be such that it would remain as a relatively stable species for a long period of time within the islands, yet develop certain unique characteristics as a Hawaiian species. It appears most probable that it has been derived from a comparatively recent (geologically speaking) natural immigrant, but it cannot now conclusively be shown that this is true.

Perkins had similar views in mind when he wrote (1913:cxlv),

> Many of the endemic genera, that contain a single, or a few species, are clearly offshoots from other of the larger endemic genera, or as one might say, they are species of these genera, which have diverged more widely in structure than the average.... While therefore the apodemic genera are usually very distinct or remote from one another, the endemic are often closely allied to one another, in such a way as to form aggregates of several allied genera, these aggregates being generally remote from one another and more nearly corresponding to the apodemic genera than do the individual genera composing them.

2. Most endemic insects are confined to native forest plants. Many of them are highly specialized in their host specificity. Some species are confined to a group of allied plant genera, others to a group of allied plant species, others to a single plant species, and others appear to be so specialized as to breed only on a particular variety of a plant species. Many species which are not herbivorous are also confined to certain species of plants. Some groups of Hawaiian insects are so host-specific that it is at times possible to determine a species by being given only its genus, the locality at which it was found and its hostplant. However, there are some exceptions to this rule. In *Nysius,* a genus of true bugs, certain endemic species may be found in great numbers on introduced or immigrant plants such as foreign *Portulaca* and amaranth. In fact, at least one of these species has the appearance of an immigrant, although it is a true endemic insect. If it were a plant it could well be called a "native weed." It is one of the few endemic insects that has been able to break out of its native realm and take to foreign plants outside the primitive forests.

3. Most endemic insects are confined to the mountain forests and are now reduced in numbers or are exterminated in the lowlands because of deforestation and pressure of immigrant enemies. Most of the endemic insects have been exterminated throughout the range of the voracious immigrant ant *Pheidole megacephala,* which is widespread from sea level to about 1,500 to 2,000 feet, more or less, according to locality and rainfall. However, some endemic insects, especially certain Heteroptera and Homoptera, have not been killed off by the ants and are even now widespread and thriving in the lowlands. Also, some species have quickly taken to immigrant or introduced lowland plants, especially when the foreign plants belong to the same or allied genera as their native hosts.

4. The majority of endemic species have a restricted geographical range. Most of the endemic species are found on single islands; many of them are restricted to certain mountain ranges, individual mountains or valleys or restricted ecological zones within single islands. However, some endemic species are found on most or all of the six main high islands, and some are found on two or three adjacent islands. The family Carabidae, or ground beetles, presents a good example of restricted specific distribution. Of the 222 certainly endemic species, only five are found on more than one island. Thus, almost 98 percent of the Hawaiian Carabidae are confined to single islands. Additional analysis would show that the species are further restricted to definite ranges within particular islands.

As an uncomplicated example to illustrate the foregoing discussion of endemicity, let us examine the beetle family Anobiidae. There are two groups of species—one foreign, the other native. There are three foreign species, each of these species is in a different genus, and each genus is in a different tribe. All three species are widespread immigrant pests of considerable economic importance to stored produce and other materials both in Hawaii and elsewhere. The native group includes 140 species and 19 "varieties" (some of these so-called varieties may be subspecies or species), and these 159 forms belong to three genera—an average of 53 forms per genus, all of which are endemic. The three genera belong to two tribes; two of the genera are endemic, and these belong to the same tribe. Almost all of the endemic species are now confined to the native mountain forests, and with the rare occasional overlap of hostplants on the part of a very few species, all are attached to native plants. About 80 percent of the species are confined to single islands, and some of these are further restricted to particular areas within single islands.

THE PERCENTAGE OF ENDEMICITY

The usual figures of endemicity are misleading. Authors tend to take the total number of species present in an area as a base and derive a percentage from that number. However, the proper procedure appears to be one based upon the native insects alone and excludes those brought in by the interference of man. Imported parasites and accidental immigrants brought in on plants, agricultural produce and other materials from diverse parts of the world should not be considered in the same light as those derived by natural means over millions of years. Should an island on which there are found species of endemic bats be considered to have less than 100 percent native mammalian endemicity because man has recently invaded the area and brought in horses, cows, sheep, goats, pigs, rats, mice, dogs and cats? Of course not. By the usual method of citing percentages of endemicity, each year would find a decrease in the percentage of native species because of the continual immigration and importation of foreign species. On this basis, then, the number of *native* Hawaiian insects is taken as 100 percent. The number of *indigenous* species has been found to be surprisingly small. The percentage of endemism among the native Hawaiian insects approximates 99 percent!

THE ORDERS OF INSECTS IN THE ENDEMIC FAUNA

The number of orders of insects in the world has not yet been definitely agreed upon by entomologists. In the 1933 edition of Comstock's *An Introduction to Entomology* there are 25 orders listed; Imms, in his 1934 edition of *A General Textbook of Entomology,* lists 23 orders, but Essig, in his recent *College Entomology* (1942), lists 33 orders. Essig's high number is reached by dividing the Thysanura into Thysanura and Aptera, by separating Grylloblattodea, Blattaria, Phasmida and Mantodea from the Orthoptera, splitting off the Diploglossata from the Dermaptera, the Zoraptera from the Corrodentia, separating Anoplura and Mallophaga and removing the Megaloptera and Rhaphidiodea from the Neuroptera. There appears good reason to divide some of the orders, but it does not seem that undue splitting of other orders is necessary. For example, should the obviously allied grasshoppers, cockroaches, mantids and phasmids each be given a high rank equivalent to that of such distinct groups as the beetles, wasps and flies at the other end of the series? It appears that a more logical system would place the five main divisions of the Orthoptera as suborders. However, this is not the place to enter into a critical discussion of such problems. For comparative purposes, I believe that the most recent list, but the least conservative one, of 33 orders will place the greatest emphasis on certain features which I wish to bring out in this book. Therefore, I shall adopt Essig's list of orders for this analysis of the Hawaiian Insecta.

The listing of the orders in which there are native representatives in the Hawaiian fauna is not so easy as it might appear. For example, there have been 32 species of Collembola recorded from Hawaii, but it cannot yet be shown that any of the species are native insects. Our knowledge of the order from the world as a whole is too poor to enable a conclusion to be reached. On the other hand, there are some species which might be native. As a whole, however, the Collembola appear to be immigrant insects, and for the purpose of this study, I shall place these dubious groups on the non-endemic list.

The orders of insects which appear to have native species in Hawaii are as follows:

1. Thysanura
2. Orthoptera
3. Corrodentia
4. Mallophaga
5. Odonata
6. Thysanoptera
7. Hemiptera
8. Neuroptera
9. Lepidoptera
10. Coleoptera
11. Hymenoptera
12. Diptera

THE ORDERS OF INSECTS UNREPRESENTED IN THE ENDEMIC FAUNA

There are 21 (63 percent) of the orders of insects unrepresented in the native fauna. Fifteen of these 21 orders are now represented in the islands by immigrant species, and the only orders not yet established are Grylloblattodea, Diploglossata, Plecoptera, Megaloptera, Rhaphidiodea and Mecoptera. It will be worth while to review the 21 orders of insects not found natively in Hawaii.

1. Protura. These peculiar, minute, soil- and humus-inhabiting organisms have been known only since 1907. Since that time species have been described from widely separated places about the world. Specimens have been found in the soil of sugarcane and other fields on Oahu, but these specimens were never identified. There appears good reason for believing the material to represent an immigrant species, however.
2. Diplura. There are four species belonging to four genera, two in the Campodeidae and two in the Japygidae recorded from Hawaii. One (*Japyx*) has evidently not been found elsewhere, and, although I am listing it as adventive, it may some day be found to be native. The Diplura are blind inhabitants of soil, humus and rotting logs and are comparatively poorly known, although they are world-wide in distribution.
3. Collembola. Collembolans make up a considerable part of the insect faunas of most continental regions, but they are a poorly known groups of organisms. There have been 32 species belonging to 24 genera included in the families Hypogastruridae, Onychiuridae, Isotomidae, Entomobryidae and Sminthuridae recorded from Hawaii. Of these, all but five species appear to be, without question, immigrants. The remaining five may also be immigrant species, and I am not including any of them as probable natives for this reason. None of them has all the characteristics of the endemic insects.
4. Grylloblattodea. Only a few of these wingless cricket-like insects are known, and these are restricted to certain snowy mountain areas in western North America and in Japan.
5. Blattaria. There are 18 immigrant cockroaches included in 15 genera in Hawaii. Although some other Pacific islands have native species, all the Hawaiian species are adventitious. Australia has a particularly rich and diversified cockroach fauna.
6. Phasmida. There are many native species of leaf and stick insects in the southwestern Pacific, but none has reached Hawaii.
7. Mantodea. Mantids are common in Australia, New Guinea and adjacent islands, but the only species we have in Hawaii are three immigrants. One is a native of Australia, one is recorded from Java, China and Japan, and the other is recorded from Java and the Philippines.
8. Dermaptera. There have been 12 earwigs belonging to 8 genera recorded from Hawaii. Most of these species are widespread insects, but a few have been described from Hawaii. However, there appears to be more reason for believing all the species to be adventive than to consider that any of them is a native insect.
9. Diploglossata. Only two species have been discovered in this order. Both of these insects are ectoparasitic on rats in Africa.
10. Plecoptera. Stoneflies (which are thought to be among the most primitive of living winged insects) are not represented on any Pacific oceanic islands. Their larvae are aquatic.

11. Isoptera. Although the south Pacific islands from Samoa and Fiji westward are richly endowed with native termites, no endemic species exists in Hawaii. Four immigrant species belonging to four genera have thus far become established in Hawaii.
12. Embioptera. A single immigrant species that is found widespread throughout many Pacific islands now also lives in Hawaii.
13. Zoraptera. One probably immigrant species represents this small but widespread order in Hawaii.
14. Anoplura. No native sucking lice are known in Hawaii. The lack of native land mammals (excluding bats) accounts for their absence. A few common immigrant species are now found on immigrant and introduced mammals.
15. Ephemeroptera. The may flies, whose larvae are aquatic, did not reach Hawaii naturally. The nearest islands in which members of this order have been found are the Samoan group where there is a single native species known. A foreign species has recently become established here, however.
16. Megaloptera. The sialids or dobson flies also have aquatic larvae. There are a number of species found in Australia and New Zealand (and also on the continents), but to my knowledge none has been found on oceanic islands.
17. Rhaphidiodea. This group is represented only in America and Eurasia with about 95 percent of the species confined to the Holarctic region. None is known from the Pacific.
18. Mecoptera. The scorpion flies are thought to be the oldest insects yet found in the fossil state (lower Permian) that belong to groups having complex metamorphosis. Most of them have terrestrial larvae. The order is worldwide in distribution with the greatest concentration of species in Asia and the Indo-Australian regions. None has been found on any mid-Pacific island.
19. Trichoptera. No caddice flies are native to Hawaii, but I recently found an immigrant species about some lily ponds in a Honolulu garden. Caddice flies are found natively in Samoa and are abundant from Fiji westward. Their larvae are aquatic.
20. Strepsiptera. Although a species and a variety of *Elenchus* have been described from Hawaii, in addition to a known immigrant species, I am inclined to consider all of the forms adventive. Little is known regarding these insect parasites in the Pacific, and only a few species have been discovered on islands.
21. Siphonaptera. There are seven kinds of fleas known in Hawaii, and all of them are adventive. One species was described as *Xenopsylla hawaiiensis* Jordan from an immigrant rat (the "native" Hawaiian rat presumably entered Hawaii by the canoe transport of the early Hawaiian immigrants, and I do not class it as endemic). *Xenopsylla hawaiiensis* now is considered to be a synonym of a southwestern Pacific species.

Thus, the 21 insect orders which are not represented in the endemic Hawaiian fauna may be placed in the following categories:

1. Four orders having exclusively aquatic larvae: Plecoptera, Ephemeroptera, Megaloptera, Trichoptera.

2. Three orders containing apterous, mostly delicate, minute, many blind, moisture-loving dwellers of damp soil or damp humus: Protura, Collembola, Diplura.

3. Three orders of external parasites principally restricted to mammals: Diploglossata, Anoplura, Siphonaptera.

4. One order of rather obscure insect parasites: Strepsiptera.

5. One order of aberrant orthopteroid insects containing a few species restricted to certain high mountain snow-field country in western North America and Japan: Grylloblattodea.

6. One order of terrestrial insects almost entirely confined to the Holarctic region and with no representatives in the Australia–Pacific area: Rhaphidiodea.

7. One widespread order of specialized forms, whose females are wingless; found under bark, under stones, in trash and humus: Embioptera; and one specialized, small order containing only about 20 known, delicate species which live in rotting wood: Zoraptera.

8. One small, ancient order of mostly terrestrial predaceous insects: Mecoptera.

9. One widespread order of specialized wood eaters: Isoptera.

10. Four orders of mostly ancient, widespread, apparently easily adapted, mostly orthopteroid insects: Blattaria, Phasmida, Mantodea, Dermaptera.

It will be noted that most of the ancient orders of insects are not represented by endemic species in Hawaii, and those that are present are poorly developed. The orders most extensively developed in the islands are geologically the youngest. None of the aquatic orders is present with the exception of the hardy, strong-flying Odonata, in spite of the favorable, abundantly watered environment. The soil dwellers are absent. For most of the missing orders there can be noted characteristics of their habits, life histories or distributions that are or appear to be the limiting factors which account for their being absent from Hawaii. However, it is more difficult to explain why such groups as the cockroaches, for example, are not represented by native species. (It is noteworthy that endemic cockroaches exist on islands as far east as the Marquesas in southeastern Polynesia.)

Because of the lack of adequate, monographic, revisional studies, and because of my unfamiliarity with all of the pertinent details of the many genera of Hawaiian insects, the following summaries have been difficult to prepare. Some of the statistics given and conclusions reached will be subject to modification as more detailed and specialized work is done on both the Hawaiian and extra-Hawaiian faunas. Some of the genera which are listed as endemic may someday be found to have representatives elsewhere. Some of the species which are listed as endemic may be found to be immigrant or indigenous. For some of the genera which have been described as endemic to Hawaii, authors have neglected to say anything regarding their systematic positions, relationships, affinities or probable faunistic derivations. Such inconsiderate negligence is to be deplored. Some authors have "allied" Hawaiian genera to genera known to them from other localities, but in so doing, they have made errors that may persist for years in literature. Some of these errors will be carried along here, because it is obviously impossible to detect all of them. However, these opportunities for error are in the minority, and the general conclusions should not be significantly influenced by them. This section is necessarily presented in an incomplete and tentative form; I am fully cognizant of its weak parts. I can only hope that the materials presented here will be food for thought and entice comment from scholarly specialists who may be able to aid us in our search for knowledge of Pacific insular life.

SUMMARIES OF THE ENDEMIC INSECTS

I. Summary of the Thysanura.—The only members of this primitive order which I consider possibly to be endemic are two species of *Machiloides* (Machilidae), but I am uncertain of their status. One of these species is known only from Kauai, but the other is widespread among the main islands. The group has received no attention since the original descriptive work by Silvestri in 1904. Both of the species have much in common with some of the Australian Machilidae, and it would not be surprising if these forms prove to be adventive.

II. Summary of the Orthoptera.—The 45 endemic forms are included in two families. The Tettigoniidae has two endemic genera: the monotypic *Conocephaloides* and *Banza* with 11 forms. The Gryllidae has 33 species included in four genera, three of which are endemic. *Paratrigonidium* (Indo-Pacific) has 16 species; *Prognathogryllus* (endemic) has 5 species; *Leptogryllus* (endemic) has 11 species; *Thaumatogryllus* (endemic) has 1 species. All of the endemic gryllid genera belong to a single assemblage and appear obviously to have sprung from a common ancestor. The affinities of the endemic Orthoptera are Indo-Pacific.

III. Summary of the Corrodentia.—It is difficult to summarize this order because of the chaos that exists regarding the status and relationships of genera and species. Enderlein has synonymized or reduced to varieties most of Perkins' species, but a careful, thorough revision is essential. For the purpose of this paper, I shall adopt the status of the species mainly as accepted by Perkins and Banks. (For references and details, see Volume 2 of this work.) The 24 species that appear to be native belong to the Psocidae and Elipsocidae. *Psocus* has 15 species (I have included the 14 species described in *Psocus* plus the single species described from a mutilated unique which Perkins placed in *Stenopsocus* but stated that it did not belong to that genus); *Kilauella* (endemic) has 8 species; *Palistreptus* (endemic) has 2 species. The other 16 species belonging to 13 genera all appear to be immigrants, although some of them are known only from Hawaii. Too little is known of the Corrodentia of the surrounding regions to enable a definite conclusion to be reached regarding the derivation of the Hawaiian fauna, but it appears to be southwestern Pacific in character.

IV. Summary of the Mallophaga.—Although there have been more than 50 species of Mallophaga recorded from Hawaii, few of them are endemic. Most of the species have been collected from domestic or introduced animals and sea birds. There never has been a careful search made for lice on the native birds, but a few species from some of them have been described. The Hawaiian lice are in great need of detailed study, for no definite conclusions can be reached with our present meager data. One would expect a wealth of interesting forms to be found on the highly modified endemic Drepaniidae which might lend themselves to aiding in solving the problem of the relationship and derivation of those birds. I consider it a great scientific loss that such a survey was not made years ago when so much bird collecting was being done. Dr. Perkins made a collection of lice from endemic birds, but it appears to have been lost without ever having been studied. An ardent student might yet be able to find lice on museum skins of some of the extinct or very rare species, and a permit to collect a few specimens of the more common of the protected living species could probably be obtained for such a worthy study.

Although 19 species and varieties have been described from Hawaii, the only species which I now consider as having a claim to being endemic are five species found on drepaniid birds. These five species are: *Philopterus macgregori* (Kellogg and Chapman), on *Chlorodrepanis virens; Degeeriella* (?) *diaprepes* (Kellogg and Chapman), on *Vestiaria coccinea; Myrsidea cyrtostigma* (Kellogg and Chapman), on *Chlorodrepanis virens, Himatione sanguinea* and *Vestiaria coccinea; Colpocephalum hilensis* (Kellogg and Chapman), on *Vestiaria coccinea;* and *Machaerilaemus hawaiiensis* (Kellogg and Chapman), on *Chlorodrepanis virens.*

There have been only three species out of the 62 kinds of endemic passerine birds from which lice have been described, and these three all belong to the Drepaniidae, which includes about 45 kinds of birds. No lice have been recorded from the endemic Sylviidae (warblers, 2 species), Turdidae (thrushes, 6 species), Corvidae (crows, 1 species), Muscicapidae (flycatchers, 3 species) or Meliphagidae (honey suckers, 5 species). No lice entirely confined to the endemic non-passerine birds (about 15 forms) have yet been found.

No conclusions can be drawn as to the relationships of the endemic Mallophaga at this time.

V. Summary of the Odonata.—There are 29 forms of endemic Hawaiian Odonata. These have come from three stocks. The first of these is the single species of Libellulidae, which has been separated as a "weak" Hawaiian genus from the Holarctic genus *Sympetrum* and is now called *Nesogonia blackburni* (McLachlan). The second stock is that represented by the giant endemic *Anax strenuus* Hagen, an apparent offshoot of the cosmopolitan species *Anax junius* (Drury) of the Aeshnidae. The remaining 27 forms constitute the endemic damselfly complex *Megalagrion* of the Coenagriidae. It is apparently only a matter of taxonomical convenience that the Hawaiian species are separated as a distinct genus from the Oriental–Pacific genus *Pseudagrion.* Thus, only three ancestral individuals have given rise to all of the Hawaiian Odonata. The extensively developed *Megalagrion* complex is of great interest, because some of the species have forsaken streams and ponds and habitually breed in little pockets of water at the bases of the leaves of certain kinds of forest plants; one is even more aberrant, for it is terrestrial and lives in damp trash under ferns far from water.

VI. Summary of the Thysanoptera.—There have been about 90 thrips recorded from Hawaii, but most of these are immigrants. Unfortunately, the Hawaiian Thysanoptera have not been carefully revised, and it is difficult for one unfamiliar with the group to draw many concrete conclusions. From present knowledge, it appears to me that there may be only about six or fewer genera which contain endemic species. There are 15 species of *Hoplothrips* (Tubulifera: Phlaeothripidae) which appear to be endemic. *Nesothrips* (Tubulifera: Phlaeothripidae), known from the Indo-Pacific, contains one possibly native form. *Dermothrips* (Phlaeothripidae) and *Conocephalothrips* (Urothripidae), both monotypic, may be native. *Haplothrips* (Phlaeothripidae) contains four species which may be endemic. There are seven species of *Isoneurothrips* (Terebrantia: Thripidae) which may be endemic. Although there are several species not yet recorded from outside Hawaii, and even some genera which have been described as new from Hawaii, there is no good evidence to indicate that some of these are not immigrants. As is true for the endemic thrips faunas of Fiji, Samoa and other Polynesian islands, there is a preponderance of Tubulifera, which are frequently met with beneath dead bark of shrubs and trees, and a dearth of flower-frequenting species. The endemic forms are evidently normal derivatives of Pacific faunas.

VII. Summary of the Hemiptera–Heteroptera.—There have been 223 kinds of Heteroptera listed from Hawaii, including 178 endemics. The greatest development and diversity of some genera occur in Hawaii, and a number of distinct genera and groups of allied genera are remarkable endemic products. Many new species are known and await description. Because there are so many endemic forms, I shall discuss each family separately.

1. Pentatomidae. The largest, most conspicuous and brightly colored of all endemic Heteroptera is a single species of *Coleotichus* which is widely distributed in the islands. The genus is Indo-Pacific in distribution. The genus *Oechalia* has 15 described species. Of these, only one species has been found outside of Hawaii, and it is widespread in many islands from Australia to eastern Polynesia but has not reached Hawaii. The 14 Hawaiian species are placed in the endemic subgenus *Hawaiicola.*
2. Coreidae. Two endemic species belonging to the endemic genus *Ithamar* compose the native Coreidae. *Ithamar* is an ally of *Daclera* and is of Indo-Pacific origin.
3. Lygaeidae.

   (a). The tribe Orsillini of the Lygaeinae with its 67 endemic species, 14 endemic subspecies and 3 endemic varieties is evidently the largest tribal unit of the Hawaiian Heteroptera. These forms are included in five genera and five subgenera: *Oceanides* (23 species), *Glyptonysius* (2 species), *Neseis* [with subgenera *Physonysius* (2 species), *Leionysius* (2 species), *Neseis* (1 species), *Trachynysius* (13 species, 12 subspecies, 2 varieties), *Icteronysius* (2 species)], *Nysius* (21 species, 2 subspecies, 1 variety) and *Nesomartis* (1 species). All of these genera and subgenera are endemic except the almost cosmopolitan genus *Nysius*. The species of *Nysius* are, however, all endemic and include the most divergent of all *Nysius* species. The tribe, as a whole, has its greatest known diversity in Hawaii. The entire Hawaiian group may have been derived from about seven, or fewer, immigrant ancestors from the south and western Pacific.

(b). The Metrargini of the Lygaeinae constitute an endemic tribe including the three endemic genera *Metrarga* (1 species, 2 varieties), *Nesoclimacias* (1 species, 2 varieties) and *Nesocryptias* (1 species). It appears that all of these forms could have been derived from a single immigrant ancestor from the same region as the Hawaiian Orsillini. It may be an aberrant local offshoot of some ancient Hawaiian orsilline type.

(c). The Cyminae include two allied, endemic monotypic genera, *Sephora* and *Nesocymus*. These are apparently derivatives from a common Indo-Pacific immigrant, and new species await description.

4. Enicocephalidae. One supposedly endemic species of *Nesenicocephalus* known only from a single specimen from Maui represents this family. The recently described genus is known only from the Philippines and Hawaii.
5. Reduviidae. One species of the endemic *Nesidiolestes* (Ploiariinae), allied to other genera which are widespread in the Indo-Pacific, is probably the only described endemic species of this family in Hawaii.
6. Nabidae. There are 25 endemic species described from Hawaii. These belong to the widespread genus *Nabis*. All of the endemic forms are so closely allied that perhaps a single immigrant from the south Pacific has accounted for the present endemic complex.
7. Anthocoridae. The six described endemic species are included in *Lasiochilus* (5 species) and *Lilia* (endemic, monotypic), and their relationships are Indo-Pacific.
8. Miridae. This family now comes next to the Lygaeidae in its development and diversification in the islands. It contains 27 endemic species, 1 variety and 9 endemic genera described, but a large number of undescribed forms are in our collections, and when they are described this family is expected to outnumber the Lygaeidae. Our representatives are all considered Pacific derivatives.

(a). The endemic Phylinae are included in the nearly cosmopolitan genus *Psallus*. There are four species and a variety described from Hawaii, but more native species await description.

(b). The Dicyphinae includes only two described endemic species of the widespread genus *Engytatus*, but many species remain to be described.

(c). The Bryocorinae is represented by four described species of the endemic genus *Sulamita* and by the monotypic, endemic *Kalania*. These genera are here placed in endemic tribes.

(d). The Heterotominae includes the endemic, monotypic *Nesidiorchestes* and *Sarona, Pseudoclerada* (endemic, 2 species, here considered a native tribe), *Orthotylus* (widespread, 7 Hawaiian species described, but many new ones at hand), *Kamehameha* (endemic, monotypic derivative (?) of *Orthotylus*), *Koanoa* (endemic, 2 species).

(e). The endemic, monotypic genera *Oronomiris* and *Nesiomiris* represent the Mirinae, but many new species are in collections and await description.

9. Saldidae. This family is represented in the islands by six described endemic species of *Saldula,* but new species await description. Evidently these species represent derivatives of a common Polynesian ancestral stock.
10. Gerridae. The pelagic water striders are represented by two species of *Halobates,* one of which appears to be endemic, the other indigenous.

These 10 families represent only about 20 percent of the families of Heteroptera (in deriving this and similar percentages, I have used the total number of families as given by Brues and Melander in 1932). Moreover, only the four families Pentatomidae, Lygaeidae, Anthocoridae and Miridae have more than a single genus containing native species represented in Hawaii. Four of the families are each represented by only a single native species. It will be noted that the aquatic forms are hardly represented, and that none of the families of fresh-water diving bugs is present. The entire bug fauna is strikingly insular.

VIII. Summary of the Hemiptera–Homoptera.—There have been over 500 species of Homoptera recorded from the Territory. However, more than 160 of these species are immigrants. The only families of the Homoptera that have proven endemic species in the Hawaiian Islands are the Pseudococcidae, Cicadellidae, Delphacidae, Cixiidae and Psyllidae, and I have listed 341 of these as native. These five families make up only about 8 percent of the families of Homoptera.

1. Cicadellidae. There are two species included in the endemic genus *Nesophryne,* which appears to resemble the Eurasian genus *Goniagnathus* and which is allied to our *Kirkaldiella* and *Nesophrosyne. Kirkaldiella* (endemic derivative of *Nesophrosyne*) has two species; *Nesophrosyne* (endemic; probably a derivative of the *Thamnotettix* complex) has 62 forms; *Balclutha* (*Nesosteles*) (well developed in the Pacific) has five native species and *Nesolina,* which may be a local endemic development, is monotypic. This group is Indo-Pacific in affinities.
2. Delphacidae. There are 139 endemic forms placed in the following genera: *Leialoha* (endemic, 12 species); *Nesothoë* (endemic, 22 species); *Nesodryas* (endemic, 2 species); *Aloha* (endemic, 9 species); *Nesorestias* (endemic, 2 species); *Nothorestias* (endemic, 2 species); *Dictyophorodelphax* (endemic, 4 species); *Nesosydne* (endemic, 82 species); *Kelisia* (5 endemic species). With the exception of the species of *Kelisia,* all of these genera belong to a group called Alohini by Kirkaldy. Two or three ancestral immigrants from the southwest Pacific could have given rise to the entire family in Hawaii. Some of the most remarkable endemic products are included in this family.
3. Cixiidae. There are 84 endemic forms in this family. Seventy-nine of these belong to *Oliarus* and five to *Iolania. Iolania* was described as an endemic genus, but it is now known from Fiji also. *Iolania* may be an offshoot of the widespread genus *Cixius.* Two Pacific ancestral stocks appear to be represented by this group.
4. Psyllidae. There have been 30 species and one variety of jumping plant lice described as endemic. These species are distributed as follows: *Swezey-*

ana (endemic, 2 species); *Paurotriozana* (endemic, 1 species); *Trioza* (9 species); *Kuwayama* (5 species, 1 variety); *Hevaheva* (endemic, 9 species); *Megatrioza* (1 species, but several other undescribed species are at hand); *Cerotrioza* (endemic, 2 species); *Crawforda* (endemic, 1 species). Most of these species are related to *Trioza* and might have sprung from a single immigrant ancestor. Perhaps two original southwestern Pacific immigrants representing the genera *Trioza* and *Cerotrioza* gave rise to the Hawaiian complex.

5. Pseudococcidae. We have now shown beyond a doubt that Hawaii has a peculiarly developed mealybug fauna of its own. The endemism as we interpret it is as follows: *Phyllococcus* (endemic, monotypic), relationships undetermined, an unusual form; *Clavicoccus* (endemic, 2 species), another striking group, evidently an old local development; *Pseudococcus* (9 species); *Trionymus* (1 species); *Nesococcus* (endemic, monotypic), another local offshoot, possibly of an old *Pseudococcus* form. Although we are unable to say at this time exactly where the closest affinities of the Hawaiian group lie, it is suggested that perhaps three or four immigrant Indo-Pacific stocks might have given rise to this faunal element.

IX. Summary of the Neuroptera.—There have been 60 species of Neuroptera recorded in Hawaii. Of these, 54 are endemic species; the remainder are either purposely or accidentally imported species. The endemic species are included in three families which represent only 15 percent of the known families of Neuroptera.

1. Myrmeleontidae. One species of *Eidoleon* is considered endemic. It is closely allied to a south Pacific species.
2. Chrysopidae. Twenty-six species belonging to the endemic genus *Anomalochrysa* have been described. The genus appears to have allies in Samoa, and seems to have developed in Hawaii from a single ancestral immigrant.
3. Hemerobiidae. The 28 endemic species are included in four genera as follows: *Nesobiella* (endemic (?), monotypic); *Nesomicromus* (endemic, 22 species); *Pseudopsectra* (endemic, 4 species); *Nesothauma* (endemic, monotypic). The five species last mentioned are flightless and have greatly reduced and modified fore wings, and the hind wings are atrophied and minute or absent. These are among the most aberrant of all Neuroptera, but are obvious local offshoots of *Nesomicromus*. Probably two immigrant Polynesian ancestors could have given rise to the endemic Hemerobiidae, or one if the *Nesobiella* proves to be non-endemic.

X. Summary of the Lepidoptera.—There have been approximately 1,000 species of Lepidoptera recorded from the islands. Hereinafter I have listed 850 species and 10 varieties of these as endemic forms. These are included in 21 families which amount to only 15 to 20 percent of the families of Lepidoptera. None of the primitive families is represented.

This review has revealed to me that chaos exists in the classification of the Lepidoptera. The Hawaiian group is in great confusion and is most difficult to work with in its present state. There are many erroneous generic and family assignments. Often none of the several authors who have worked upon a particular group agrees upon the position or relationships of the included insects. There appear to be numbers of misidentifications. Some of the published material is useless for the purpose of this paper because of errors and omissions. Unfortunately, I am unfamiliar with the order and cannot weigh evidence and correct errors which an authority on the order might do if he were particularly interested in this problem. Before any satisfactory analysis of the Hawaiian Lepidoptera can be attempted, careful revisions must be made of all of the groups of the order represented in Hawaii in the broad light of geographical distribution, derivation and evolution. Moreover, a more accurate and complete knowledge of the faunas of the south Pacific must be attained. I must admit that this section of the paper has many weak spots.

1. Gelechiidae. *Aristotelia* has 16 endemic species. This cosmopolitan genus is evidently poorly represented elsewhere in Polynesia, for there is only a single species recorded, and that is from Samoa. The affinities of the Hawaiian species have not been determined beyond their being considered Pacific. *Merimnetria* appears to be endemic and monotypic, and, although considered a Pacific derivative, it is of uncertain status.
2. Cryptophasidae. *Thyrocopa* (endemic, affinities unknown) has 34 endemic species. From this genus there appear to be five endemic generic segregates: *Hodegia* (monotypic), *Ptychothrix* (monotypic), *Diplosara* (monotypic; an aberrant form), *Psychra* (2 species) and *Catamempsis* (monotypic). These six groups evidently arose from a single immigrant. *Hodegia* is peculiar, because the female is flightless (the male is unknown), has greatly reduced wings and is a jumping insect found in bunch grass high up in the open country of Haleakala, Maui. These are considered south Pacific derivatives.
3. Cosmopterygidae. *Agonismus* (endemic; an ally of *Hyposmocoma*) has 3 species; *Aphthonetus* (endemic; allied to *Hyposmocoma*) has 33 species; *Rhinomactrum* (endemic; allied to *Aphthonetus*) has 2 species; *Neelysia* (endemic derivative of *Hyposmocoma*) has 25 species; *Dysphoria* (endemic ally of *Hyposmocoma*) is monotypic; *Bubaloceras* (endemic; allied to *Hyposmocoma*) has 2 species; *Hyposmocoma* (endemic; an ally (?) of the nearly cosmopolitan *Mompha*) contains more described species than any other Hawaiian genus, for it has 210 species and 6 varieties; *Euhyposmocoma* (endemic offshoot of *Hyposmocoma*) has 2 species; *Hyperdasysella* (= *Hyperdasys*) (endemic ally of *Hyposmocoma* ?) has 5 species; *Pthoraula* (endemic derivative of *Hyposmocoma*) is monotypic; *Euperissus* (endemic; supposedly allied to *Orthotaelia*) has 2 species; *Semnoprepia* (endemic; closely allied to *Euperissus*) has 7 species; *Petrochroa* (endemic; supposedly allied to *Coelopoeta*) has 6 species.

There appear to be only three ancestral stocks necessary for the origin of the endemic Cosmopterygidae. One has apparently given rise to

Hyposmocoma and 9 allied genera including 290 forms; one evidently produced *Euperissus* and *Semnoprepia* with 9 species; and the third gave rise to *Petrochroa* with 6 species. In addition to these, there are 2 endemic species incorrectly assigned to *Elachista* which are now of uncertain status, but which may also belong to the *Hyposmocoma* complex. These are all considered Pacific derivatives.

4. Tineidae. *Comodica* (Samoa, Australia, etc.) has 1 apparently (?) endemic species; *Ereunetis* (well developed in Samoa and elsewhere) has 5 apparently endemic species and several immigrants. *Paraphasis* (endemic; of uncertain status) is monotypic.
5. Yponomeutidae. *Mapsidius* (endemic; of undetermined affinities) has 4 species; *Acrolepia* (almost cosmopolitan) has 3 species of undetermined derivation.
6. Nepticulidae. *Opostega* (almost cosmopolitan) has 6 species of undetermined derivation.
7. Batrachedridae. *Batrachedra* has 9 species evidently of south Pacific derivation.
8. Caloptiliidae. *Parectopa* has 15 species evidently of western Pacific derivation.
9. Bedelliidae. There are 3 species of *Bedellia* which may be endemic and are probably of south Pacific derivation.
10. Orneodidae. *Orneodes* has 2 species possibly of western Pacific derivation.
11. Tortricidae. *Eccoptocera* (endemic; supposedly allied to *Holocola* of Australia, but status uncertain) is monotypic (immigrant ?); *Gypsonoma* has 1 species evidently with western Pacific affinities; *Adenoneura* (endemic; ally of *Eucosma* [*Thiodia*]) has 8 species of undetermined affinities; *Spheterista* (perhaps a derivative of *Capua*) has 4 species; *Bactra* (western Pacific affinities ?) has 3 species; *Pararrhaptica* (endemic; affinities uncertain) is monotypic; *Enarmonia* (widespread) has 4 species; *Eulia* (widespread) has 17 species; *Panaphelix* (endemic; ally of *Dipterina*) has 2 species; *Dipterina* has 1 species with south Pacific affinities; *Tortrix* (widespread) has 7 species; *Capua* has 13 species probably of south Pacific derivation; *Epagoge* has 5 species evidently of western Pacific affinities. Following Walsingham (1907), I list the Tortricidae as all belonging to the Indo-Pacific fauna.
12. Carposinidae. *Carposina* has 38 species and 2 varieties probably of south Pacific derivation.
13. Crambidae. *Prionopteryx* has 1 species possibly of south Pacific derivation; *Talis* has 6 species which appear to be allied to the Australian section of the genus.
14. Phycitidae. *Rhynchephestia* (endemic, of undetermined affinities) has 1 species; *Genophantis* (endemic; allied to *Crocydopora*) has 2 species with southwestern Pacific affinities; *Homoeosoma* has 3 species apparently allied to Australian species.

15. Pyraustidae. *Margaronia* (abundant on many Polynesian islands) has 2 species; *Omiodes* has 23 species with southwestern Pacific affinities; *Phlyctaenia* has 27 species with southwestern Pacific derivation; *Pyrausta* has 11 species with western Pacific affinities; *Tholeria* (*Mecyna*) has 2 species possibly (?) with North American affinities; *Loxostege* has 3 species with North American (?) affinities; *Promylaea* (endemic; closely allied to *Mestolobes*) has 2 species; *Mestolobes* (endemic, with south Pacific affinities, others known from the Marquesas) has 32 species; *Orthomecyna* (endemic; allied to *Mestolobes*) has 14 species; *Protaulacistis* (endemic; allied to *Mestolobes* and *Orthomecyna*) is monotypic; *Scoparia* has 64 species of south Pacific derivation; a number occur in the Marquesas.
16. Pterophoridae. *Platyptilia* (widespread) has 5 species which may be endemic and are Pacific in affinities.
17. Sphingidae. *Celerio* has 2 species and a variety which appear to have arisen from one ancestral stock—perhaps *Celerio galli* from North America. *Protoparce* has a variety (subspecies ?) of a common widespread species. The affinities of these large, strong-flying moths appear to be with North America. I have excluded the monotypic *Tinostoma*, which is said to be allied to the American *Pholus*. The only known example was collected about a half century ago in a dwelling on Kauai, and in spite of specialized searching no additional specimens have been found. I feel that it is possible that this species is an immigrant which might have been carried to the place of capture as a pupa in imported merchandise.
18. Geometridae. *Sisyrophyta* (endemic offshoot of *Scotorythra*) has 2 species; *Nesoclide* (endemic derivative of *Scotorythra*) is monotypic; *Scotorythra* (endemic; of south Pacific origin) has 36 species; *Tritocleis* (endemic offshoot of *Scotorythra*) is monotypic; *Eucymatoge* has 10 species of western Pacific or Asiatic derivation; *Hydriomena* has 4 species of western Pacific or Asiatic derivation; *Xanthorhoe* has 3 species of south Pacific derivation; *Prognostola* has 1 species with south Pacific affinities; *Dasyuris* has 1 species of south Pacific derivation.
19. Phalaenidae (Noctuidae, Agrotidae). *Eriopygodes* has 1 variable species with western (?) Pacific affinities; *Hyssia* has 3 species of south (?) Pacific derivation; *Acrapex* has 1 species with Oriental affinities; *Agrotis* has 29 species which appear to be of Asiatic derivation; *Autographa* (widespread) has 7 species with undetermined affinities; *Hypocala* has 1 species allied to south Pacific and Australian species; *Hypenodes* (endemic; with western Pacific affinities) has 7 species; *Prodenia* has 1 species of south Pacific origin; *Nesamiptis* (endemic; with North American affinities) has 6 species; *Cosmophila* has 3 species of western Pacific affinities; *Cirphis* has 3 species with North American (?) affinities which may be endemic; *Peridroma* has 6 species which appear to be Asiatic derivatives.

20. Nymphalidae. *Vanessa* has a single species which apparently is a North American derivative.
21. Lycaenidae. *Lycaena* has a single species which is apparently a western Pacific or Asiatic derivative. Its larva is unusual in that it lacks dorsal glands.

XI. Summary of the Coleoptera.—There have been more than 1,600 species of beetles listed from Hawaii. Of these, I have included 1,220 species and 70 varieties as endemic to the Territory. These species are included in 19 families which total only about 11 percent of the families of Coleoptera.

1. Carabidae. This family is one of the most extensively developed of any in the native fauna, for it contains 222 species. A revision of the group is in progress; many of the genera are being combined and others are being reduced to subgeneric rank.

   In the Bembidiini, *Bembidion* has 5 species, some of which may prove to be immigrants. From an early *Bembidion* ancestor have arisen *Nesocidium* (endemic) with 10 species, *Nesomicrops* (endemic) with 1 species, *Macranillus* (endemic) with 1 species, *Atelidium* (endemic) with 1 species and *Metrocidium* (endemic) with 1 species. The seemingly aberrant, endemic, monotypic genus *Gnatholymnaeum* appears to be closely allied to the North American *Amerizus,* according to E. B. Britton (personal communication). The endemic Bembidiini appear to have arisen from two or three Holarctic stocks, but it is not now known whether they came from America or Asia or two from Asia and the other from America.

   All the Nomiini at one time were considered to belong to the endemic genera *Mecyclothorax, Atelothorax, Thriscothorax* and *Metrothorax,* but we do not recognize these as distinct units now, and the entire group is merged with the Indo-Australian *Cyclothorax* under the name *Mecyclothorax.* All of the Hawaiian species are flightless, but some Australian *Cyclothorax* have well-developed wings. This genus is now known from Tahiti (4 species), New Caledonia (1 species), New Zealand (1 species), Australia (15 species), Java (3 species), St. Paul and Amsterdam (south Indian Ocean) (1 species) and Hawaii with 85 described species.

   The Anchomenini are the most extensively developed group. They are derivatives of *Colpodes,* a genus widespread and well developed in the Pacific. In an unpublished manuscript, many of the following genera are being synonymized, but Sharp's classification (1903) is used here. *Atrachycnemis* (endemic ally of *Blackburnia*) has 3 species; *Blackburnia* (endemic) has 2 species; *Deropristus* (endemic ally of *Blackburnia*) has 3 species; *Anchotefflus* (endemic ally of *Blackburnia*) has 2 species; *Pseudobroscus* (endemic ally of *Disenochus*) is monotypic; *Derobroscus* (endemic ally of *Pseudobroscus*) has 3 species; *Disenochus* (endemic) has 13 species; *Mauna* (endemic offshoot of *Disenochus*) is monotypic; *Brosconymus* (endemic derivative of *Disenochus*) is monotypic; *Apteromesus* (endemic ally of *Disenochus*) is monotypic; *Mysticomenus* (endemic offshoot of *Apteromesus*) has 2 species; *Colpodiscus* (endemic ally of *Disenochus*) has 2 species; *Anchonymus* (endemic ally of *Disenochus*) is monotypic; *Prodisenochus* (endemic ally of *Disenochus*) is monotypic; *Barypristus* (endemic ally of *Disenochus*) has 2 species; *Baryneus* (endemic offshoot of *Barypristus*) is monotypic; *Chalcomenus* (endemic ally of *Barypristus*) has 3 species; *Colpodes* (incorrectly assigned to *Platynus* in *Fauna Hawaiiensis*) has 2 species; *Metromenus* (endemic ally of the endemic *Colpodes* species) has 28 species; *Mecomenus* (endemic ally of *Metromenus*) has 2 species; *Colpocaccus* (endemic ally of *Metromenus*) has 6 species; *Atelothrus* (endemic ally of *Metromenus*) has 19 species and 1 variety; *Mecostomus* (monotypic, endemic ally of *Metromenus*); *Mesothriscus* (endemic ally of *Metromenus*) has 14 species and 2 varieties. One or two ancestral immigrants from the southwest Pacific are considered to have given rise to this entire closely knit complex.

It now appears to me that the entire endemic carabid fauna could have developed from only about four to six ancestral immigrant species.

2. Dytiscidae. One species of *Rhantus* and one of *Copelatus* appear to be endemic representatives of this family of water beetles. Both species are south Pacific derivatives.
3. Staphylinidae. *Thoracophorus* (endemic) has 2 species; *Lispinodes* (endemic) has 10 species; *Myllaena* (nearly cosmopolitan) has 11 species. The 28 species and 1 variety of Hawaiian *Oligota* (cosmopolitan) have been separated into 5 subgenera as follows: *Deroligota* (endemic) monotypic, *Holobus* has 1 species, *Gnatholigota* (endemic) has 5 species, *Nesoligota* (endemic) has 7 species, *Oligota* has 14 species and 1 variety; *Liophaena* (endemic; closely allied to *Oligota*) has 3 species. It is probable that all of these forms have sprung from a single immigrant. I am not convinced that the species placed in subgenera found elsewhere are typical of them, nor do I believe that they necessarily have anything more in common than generic relationship. The derivation of the Hawaiian complex is undetermined, but I consider an Indo-Pacific origin indicated. *Eudiestota* (endemic ally of *Diestota*) is monotypic; *Diestota* (widespread) has 29 species; *Eusipalia* (endemic ally of *Diestota*) is monotypic. It appears probable that the 31 species included in these last three genera have arisen from a common ancestral immigrant; the source is not known, but it is presumed to be Pacific. *Nesomedon* (endemic derivative (?) of *Medon*, cosmopolitan) has 3 species. *Xanthocorynus* (monotypic), *Holocorynus* (2 species) and *Leurocorynus* (monotypic) are three allied endemic genera all said to be allied to *Leptacinus* and *Pachycorynus* and are probably of south Pacific derivation.
4. Histeridae. The only endemic species in this family appear to be 32 species and 3 varieties of *Acritus*. The genus is nearly world-wide, but it is too poorly known to enable us to ascertain the affinities of the Hawaiian species at this time. From what I know of the histerid faunas

of south Pacific islands, I would suggest that it is probable that the Hawaiian forms are of south Pacific derivation.

5. Nitidulidae. The 133 endemic species and 10 endemic varieties of this family form a remarkable assemblage. There are two main stocks present. The first of these is a great complex of 11 endemic genera containing 129 species and 10 varieties. The other stock is represented by two genera including four species. I do not feel that this group as it now stands should be split up into so many loosely defined genera.

   The first of these groups is composed of *Goniothorax* (9 species), *Gonioryctus* (22 species, 1 variety), *Nesapertus* (2 species), *Eunitidula* (monotypic), *Orthostolus* (10 species), *Cyrtostolus* (monotypic), *Apetasimus* (monotypic), *Apetinus* (5 species), *Eupetinus* (24 species, 7 varieties), *Nesopeplus* (31 species) and *Nesopetinus* (23 species, 2 varieties). This entire complex of closely allied forms has evidently been derived from a common ancestral immigrant of *Brachypeplus,* a genus well developed in the southwest Pacific.

   The other section has two genera: *Notopeplus* (monotypic) and *Cillaeopeplus* (3 species). These genera were described as endemic. However, I have undescribed species of *Notopeplus* before me from the Marquesas. These genera also appear to be derivatives of *Brachypeplus.*

6. Cucujidae. The two genera containing endemic species are *Brontolaemus* (endemic) with 4 closely allied species and 3 varieties, and *Laemophloeus* (*Parandrita*) with 6 closely allied "species." The *Laemophloeus* forms may have to be placed in a new genus. This assemblage is here considered Indo-Pacific in origin.

7. Dermestidae. The endemic species are included in three allied genera: *Labrocerus* (endemic; 17 species), *Agrocerus* (endemic; 2 species) and *Eocerus* (endemic; monotypic). These genera and species appear to be derivatives of an ancestral immigrant *Trogoderma* which possibly came from the south Pacific.

8. Hydrophilidae. Two species of *Limnoxenus* with south Pacific affinities appear to be endemic.

9. Anobiidae. The 137 endemic species and 19 endemic varieties are included in three genera. *Mirosternus* has 70 species and 1 variety (originally described as endemic, but it is now also known from the Seychelles and Ceylon); some Central American species were formerly incorrectly assigned to it (see Scott, 1924:368); the genus *Dorcatomiella* of southern Polynesia appears to be a close ally. *Xyletobius* (endemic) has 53 species and 16 varieties. *Holcobius* (endemic ally of *Xyletobius*) has 14 species and 2 varieties. The Hawaiian Anobiidae are considered to be Indo-Pacific derivatives.

10. Ciidae. The cosmopolitan genus *Cis* is represented by 35 endemic species and 1 endemic variety. These forms perhaps are polyphyletic and may

have arisen from three independent immigrants. The derived genus *Apterocis* is an endemic, flightless complex of 13 species and 1 variety. A south Pacific origin for the entire group is probable.

11. Elateridae. *Eopenthes* is an endemic genus of 33 species and 1 named variety. It appears to be related to the Pacific *Melanoxanthus* complex which has *Pacificola* so well developed in the Marquesas. *Itodacnus,* an endemic ally of *Eopenthes,* has 9 species. *Dacnitus,* an endemic derivative of *Itodacnus,* is monotypic. *Anchastus* has 1 apparently endemic species whose affinities lie with the Fijian and western Pacific species.
12. Eucnemidae. *Dromaeolus* has 31 species and 1 variety endemic. The endemic, monotypic *Ceratotaxia* is probably a derivative of *Dromaeolus.* The members of this family could have developed from an ancestral immigrant from the south Pacific.
13. Alleculidae. There are 5 endemic species of *Pseudocistela* and 3 of *Labetis,* an allied, endemic genus. *Pseudocistela* is almost cosmopolitan, and our species may be allied to those of the southwest Pacific.
14. Cerambycidae. The 100 endemic Cerambycidae are among the most remarkable of all the endemic insects. They have been derived from three stocks. *Parandra* has a single species which closely resembles the Fijian species. *Megopis* (*Aegosoma*) has one endemic species derived from the western Pacific. The remainder of the endemic Cerambycidae are grouped in and around *Plagithmysus,* and have evidently all arisen from an ancient immigrant ancestor allied to or belonging to the widespread *Neoclytus* (Dr. W. H. Anderson and Dr. Fritz Van Emden inform me that the larvae are hardly distinguishable from *Neoclytus*). Whence this ancestral stock came is not known. It is one of those early Hawaiian stocks whose affinities are now most difficult to trace, but it appears that these beetles are of North American origin.

    Plagithmysus has 55 species and 2 varieties, *Neoclytarlus* has 26 species and 1 variety, *Callithmysus* has 2 species and 1 variety, *Paraclytarlus* has 5 species, *Nesithmysus* has 4 species and *Aeschrithmysus* has 2 species. All of these genera are endemic, are closely allied to one another and all appear to have sprung from a single introduction.
15. Anthribidae. Two species of endemic *Araecerus* of south Pacific derivation represent the Anthribidae.
16. Aglycyderidae (Proterhinidae). The genus *Proterhinus* contains 164 endemic species and 17 varieties (or subspecies ?). The genus was long considered to be restricted to Hawaii, but new species have since been described from Samoa and the Phoenix and Marquesas Islands. I have collected new species in the Society and Austral Islands and have a new species from Fiji. The Samoan species also occurs in Fiji and is fully winged, whereas all the Hawaiian species are flightless. The other

known species of the family are found as follows: two in New Zealand, one in New Caledonia and one in the Canary Islands.

17. Curculionidae. *Rhyncogonus* was described first from Hawaii where there are 34 described species. The genus is now known from the Cook, Austral, Society, Tuamotu and Marquesas archipelagos as well as from Christmas, Fanning and Wake atolls. The genus is more highly developed in southeastern Polynesia than in Hawaii, and it belongs to a tribe (Celeuthetini) which is greatly developed in the western Pacific.

    There have been 22 endemic species assigned to the supposedly cosmopolitan genus *Acalles*. They will probably prove to be western Pacific or Asiatic derivatives through a common ancestral immigrant. *Chaenosternum* is a monotypic, local endemic derivative of some endemic *Acalles*.

    Dryophthorus is nearly cosmopolitan, but the 17 endemic Hawaiian species are more than are found in any one other locality. The Hawaiian species appear to have affinities with the species of Samoa and Fiji. *Stenotrupis* has two endemic species which are south Pacific derivatives. *Orothreptes* has not been recorded outside of Hawaii, but I know it from the Marquesas. Its single species may be indigenous instead of endemic. *Nesotocus* is evidently a relict endemic genus of four closely allied species, and there appears to be nothing like it elsewhere. I have suggested that it appears that it may be of western Pacific origin. *Oodemas* with its 58 species and three varieties is the largest genus of the Hawaiian Cossoninae. This genus, together with its close ally *Anotheorus* (three species), is endemic, and I know of no genus or group of genera from any region from which it might have come. It is an anomaly. *Heteramphus* has 12 species and *Dysomma* is monotypic; both genera are peculiar endemics. These two genera, which are allied, are in the same category as *Oodemas* and *Nesotocus*, for they are apparently without living ancestors. However, I have certain undescribed weevils from the south Pacific which may shed some light on the possible affinities of the group. *Deinocossonus* is endemic and monotypic, but it or allied genera may possibly yet be found in the south Pacific.

    These weevil genera belong to only three (Otiorhynchinae, Cryptorhynchinae and Cossoninae) of the more than 70 subfamilies of Curculionidae! The Curculionidae appears to be the largest family of organisms, and although approximately 40,000 species have been described, the group is poorly known.

18. Scolytidae. Although there have been a number of minute Scolytidae described from the islands in such genera as *Hypothenemus,* it appears to me that these have little claim of endemicity. For the present, then, I shall include in this list only the members of the genus *Xyleborus* which are considered to be endemic. The genus *Xyleborus* is widespread, but the Hawaiian group of about 22 species and one variety may possibly have been derived from the south Pacific.

19. Lucanidae. On the island of Kauai there exists the aberrant, endemic genus of flightless stag beetles, *Apterocyclus.* It is polymorphic, and what were at one time considered to be seven species are now thought to represent one species and two varieties. The genus is evidently an aberrant derivative of Oriental *Dorcus,* and it is the only Hawaiian representative of that great series of beetles known as the Lamellicornia, which is so greatly developed on all the continents and most continental islands.

XII. Summary of the Hymenoptera.—There have been nearly 1,000 species of Hymenoptera recorded from the Territory, but many of these are immigrants or purposely introduced species. Herein I have listed 618 as native insects.

1. Ichneumonidae. *Agrypon* (*Atrometus*) has 11 species evidently derived from the western Pacific (these may belong to a new genus); *Echthromorpha* has 1 species of south Pacific affinity; *Enicospilus* is the most highly developed of the local Ichneumonidae, for it contains 17 species of south Pacific derivation in addition to the endemic subgenus *Glyptogastra,* which contains 2 species; *Eremotyloides* is an endemic derivative of *Enicospilus* containing 3 species; *Banchogastra* (endemic ally of *Enicospilus*) has 2 species; *Pleuropeurophion* (endemic segregate of *Enicospilus*) has 2 species; *Pycnophion* (endemic ally of *Enicospilus*) has 3 species; *Abanchogastra* (endemic ally of *Enicospilus*) has 2 species. Excepting *Agrypon* and *Echtromorpha,* all of these endemic species belong to the one tribe, Ophionini.

   (Braconidae. All of the Braconidae with the possible exception of the possibly endemic genus, or species of, *Ecphylopsis,* of undetermined affinity and which contains a single species, are evidently foreign insects. The status of this insect is so uncertain that I have omitted it from the tabular summary.)
2. Encyrtidae. *Anagyrus* (widespread) has about 7 native species described, and others known but undescribed; *Coelopencyrtus* (endemic; affinities undetermined) has 4 species; *Hypergonatopus* (endemic; ally of *Echthrogonatopus,* and evidently of south Pacific derivation) has 7 species; *Xanthoencyrtus* (subgenus *Mirastymachus*) widespread, has 6 species endemic. I consider all of these Pacific derivatives.
3. Eupelmidae. *Eupelmus* (widespread) contains 54 described native species and a number of undescribed species. *Lepideupelmus* (endemic derivative of *Eupelmus*) has 3 species. These have Pacific affinities.
4. Miscogasteridae. All of the native species belong to the Lelapinae. *Toxeuma* (widespread) has 6 species; *Neolelaps* (endemic) is a monotypic offshoot of *Toxeuma,* if distinct; *Calolelaps* (endemic; ally of *Neolelaps*) has 2 species; *Stictolelaps* (endemic; ally of *Neolelaps*) has 3 species; *Mesolelaps* (endemic; ally of *Neolelaps*) is monotypic. These species are of unknown derivation but they differ from the American Lelapinae and are here considered Pacific derivatives.

5. Spalangiidae. One species of *Spalangia* with south Pacific affinities may be endemic.
6. Aphelinidae. *Ophelinus* has 2 species with southwestern affinities.
7. Eulophidae. It is difficult to ascertain which, if any, of the species are positively endemic, but the following may be native: *Eulophus* (widespread) has 1 species; *Hemiptarsenus* (widespread) has 1 species; *Necremnus* has 1 species of undetermined derivation; *Sympiesis* (widespread) has 1 species. Perkins (1913:cvii) said that in some of these genera several new species were known, but they remain undescribed.
8. Mymaridae. Evidently the only endemic species belong to *Polynema* (widespread), which contains 16 Hawaiian species.
9. Diapriidae. *Phaenopria* has 7 species; *Zacranium* (endemic derivation of *Phaenopria*) is monotypic; *Platymischoides* (endemic, flightless derivative of *Phaenopria*) is monotypic. These are Pacific derivatives.
10. Scelionidae. *Prosanteris* contains 6 endemic species of undetermined affinity. The other genera of Scelionidae evidently all contain foreign species, but *Microphanurus* contains 5 species, some of which may be native, others are known from Fiji.
11. Cynipidae. All of the native species belong to the parasitic Eucoilinae, and although they were split up into several genera, they appear to belong to *Eucoila* with 9 species and *Cothonaspis* with 16 species and 2 varieties. It is possible that these two groups have really descended from one ancestral stock, for there appear to be intermediate species here. A south Pacific derivation of the group is probable.
12. Bethylidae. *Sclerodermus* has a complex of 16 species; *Sierola* is the greatest Hawaiian hymenopterous complex with 181 species and 1 variety described. These species have apparently been derived from south Pacific ancestral immigrants.
13. Dryinidae. *Pseudogonatopus* has 2 species which are south Pacific derivatives.
14. Formicidae. All of the endemic ants are of south or western Pacific derivation. *Cerapachys* has 1 species; *Ponera* has 1 species (the others listed in literature have now been found elsewhere). *Pseudocryptopone* has 2 species; *Epitritus* has 1 species. The following genera are represented only by subspecific forms of Pacific species: *Leptogenys* (1 subspecies), *Cardiocondyla* (1 variety), *Strumigenys* (1 variety), *Camponotus* (1 subspecies), and *Paratrechina* (1 subspecies). Some or all of these forms may prove not to be prehistoric Hawaiian endemics. Five of the 15 forms listed as endemics by Wheeler (1934:4) have now been found elsewhere.
15. Vespidae. The Eumeninae are represented by the greatest single complex of the nearly cosmopolitan genus *Odynerus*. There are 104 species and 1 variety endemic. In the closely allied endemic genus *Nesodynerus*

there are 9 species. *Chelodynerus* (monotypic) is an endemic derivation of *Odynerus* as is *Pseudopterocheilus* which contains 3 species. The affinities of the entire group are evidently Oriental, and they appear to represent two ancestral stocks.

16. Sphecidae. The genera *Nesomimesa* and *Deinomimesa,* both endemic and each containing 5 species, appear to have sprung from a single ancestral immigrant *Mimesa.* It has not been ascertained what region is the source of the Hawaiian species. I tentatively refer them to the western sector.
17. Crabronidae. The 22 endemic Crabronidae are placed in five endemic genera as follows: *Xenocrabro* (11 species), *Nesocrabro* (5 species, 1 variety), *Melanocrabro* (2 species), *Hylocrabro* (1 species, 1 variety), and *Oreocrabro* (1 species). All of these species appear to have arisen from a single immigrant ancestor, probably of Asiatic origin.
18. Hylaeidae (Prosopidae). The widespread genus *Hylaeus* (*Prosopis*) is represented by 52 species and 3 varieties placed in the subgenus *Nesoprosopis* erected for them. All of these forms appear to have arisen from a single Asiatic immigrant. Some of the species have independently developed into semi-parasitic forms within the islands.

There are no members of the primitive Hymenoptera of the suborder Chalastogastra (sawflies, etc.). Only one genus out of the great superfamily of parasites, the Ichneumonoidea, is extensively developed in the islands. Excepting the Eupelmidae, the Chalcidoidea is surprisingly weak in endemic forms and many of the species here listed as probably endemic may prove to be immigrants. The Cynipoidea have a fairly well-diversified group of species representing only the parasitic Eucoilinae; the gall-formers are unknown here. The ants are poorly represented. The Bethyloidea are represented by the great complex of *Sierola* and a few Dryinidae. The Vespoidea have the extensive development of the *Odynerus* group. The Sphecoidea are represented by the *Mimesa* derivatives and the crabronid complex of genera. The Apoidea has a single extensively developed genus of Hylaeidae. The Chrysidoidea, Scolioidea and Psammocharoidea are unrepresented. The 17 families that are represented in the islands make up only about 16 percent of the families of Hymenoptera. It is significant and noteworthy that the parasitica are conspicuously disharmonic.

XIII. Summary of the Diptera.—There have been nearly 400 named species of Diptera recorded from Hawaii. I have included 246 of these as endemic. The 13 families represented by endemic species make up only about 10 percent of the families of Diptera.

1. Tipulidae. *Limonia* (subgenus *Dicranomyia*) has 12 species, one of which is extraordinary because it is a leaf miner. *Gonomyia* (subgenus *Lipophleps*) has 1 species. The crane fly fauna is typically oceanic. Only the Limoniinae are represented. The large crane flies are absent.
2. Chironomidae. *Chironomus* (well represented in the western Pacific and elsewhere) has 3 endemic species. *Tanytarsus* has 3 endemic species evi-

dently of south Pacific derivation. Two Samoan species are marine. *Telmatogeton* has 5 endemic species of Pacific derivation. *Dasyhelea* has 1 species evidently allied to south Pacific forms. *Clunio* has 3 endemic marine species of Pacific origin. All of these species, except *Clunio,* are fresh-water aquatics. The extra-Hawaiian species of *Telmatogeton* are marine in habit, and two of these non-endemics are also found in Hawaii.

3. Mycetophilidae. *Platyura* is represented by 3 species, evidently western Pacific derivatives.
4. Sciaridae. *Sciara* (subgenus *Neosciara*) has 1 species of south Pacific origin.
5. Dolichopodidae. In numbers of described species, this family leads all others in the native fly fauna. *Chrysotus* has 5 species evidently of western Pacific origin; *Asyndetus* (Pacific) has 1 beach crab-hole species; *Campsicnemus* has 49 species derived from the south or western Pacific; *Emperoptera* (endemic, flightless derivatives of some species of native *Campsicnemus*) has 2 species; *Chrysosoma* has 2 species with western Pacific affinities; *Syntormon* has 1 species with western Pacific affinities; *Eurynogaster* (endemic; probably western Pacific in affinity) has 15 species; *Hydrophorus* (widespread) has 2 species which may prove to be immigrants; *Sigmatineurum* (a Pacific derivative) is monotypic and endemic.
6. Pipunculidae. This family is represented by 12 species of *Pipunculus* leafhopper parasites apparently of south Pacific derivation.
7. Calliphoridae. *Dyscritomyia* is an endemic genus of 5 species. *Prosthetochaeta,* closely allied to, if not the same as, *Dyscritomyia,* is endemic and contains 4 species. These flies are the most conspicuous of all of the endemic Diptera. The species whose habits are known have been reared from land shells. The derivation of the group appears not to have been ascertained. They may be allies of *Lucilia,* according to a personal communication from Fritz Van Emden. I tentatively treat them as Pacific derivatives.
8. Anthomyiidae. *Lispe* has 2 species of south Pacific derivation; *Lispa* has one species with south Pacific affinities; *Lispocephala* has 38 described species, but Perkins (1913:clxxxvii) thinks there are more likely to be nearer 100 species. The Hawaiian species are of south or western Pacific derivation, and the genus appears to be better developed in Hawaii than in any other region.
9. Sapromyzidae. *Homoneura* has 1 species which may be an immigrant. It has western Pacific affinities.
10. Trypetidae. *Tephritis* (subgenus *Trypanoidea*) has 5 described species and some known undescribed species of undetermined origin.
11. Ephydridae. *Procanace* has 1 species, *Scatella* 6, and *Paralimna* 1 species which may be endemic. These are considered Pacific derivatives. A number of new Hawaiian species await description in this family.

12. Drosophilidae. *Tantalia* is an endemic, monotypic ally of *Drosophila*. *Titanochaeta* is a monotypic, endemic genus of spider egg parasites. *Idiomyia* is an unusual endemic derivative of *Drosophila;* it contains 7 species, among which are the largest of the Hawaiian Drosophilidae. *Drosophila* (widespread) has 47 species and 1 variety (?) endemic, but it has been estimated that there are at least 250 species in the islands. Some of the most remarkable of all *Drosophila* are found in Hawaii, but no study has yet been made of their faunistic affinities. I tentatively place the entire group as Pacific derivatives.
13. Asteiidae. *Asteia* has 2 apparently endemic species with south Pacific affinities. *Bryania* is a monotypic genus now known only from Nihoa. It is an offshoot of *Asteia*.

TABULAR SUMMARY OF THE ENDEMIC HAWAIIAN INSECTS

This summary is a preliminary and tentative attempt to present a very large body of facts in concise form. I am aware that it has many weak points, and that it undoubtedly includes numerous errors. It is too early in our study of the complex Hawaiian fauna to present a more complete and accurate summary, but I believe that this account, weak though it is in many places, is worthy of inclusion here. It may stimulate further research and lead to a more rapid elucidation of the status of some groups than if it were omitted.

The various Pacific, Oriental and Asiatic faunal sectors have been combined for convenience and I have referred to these faunal sources together as "Pacific," to differentiate them from the American. It is sometimes difficult or impossible to assign a descendant line to one sector and exclude another in the Pacific, although some sources are well defined. Details of derivation have been given in the foregoing analysis.

I have combined the subspecific categories under "species" in the table. For convenience, I have totaled the details under each order, and the subtotals are enclosed in parentheses.

The genera have been used as indicators of the sources of the fauna, instead of the species, because I believe that they are more accurate subjects for the purpose. A single introduction may have given rise to over 100 species in one genus, but in another group a lesser number of species may be represented by many genera from many separate introductions.

These totals are not complete and accurate; some of them are only approximations. The totals in columns 6 and 7 refer to the number of genera whose affinities are now known or surmised. Forty-three genera are omitted from these totals because of lack of information. Although these data are admitted to be incomplete and subject to revision, it would take a large shift to alter significantly the conclusions as presented.

SUMMARY OF ENDEMIC HAWAIIAN INSECTS

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
THYSANURA	Machilidae	(1)	(0)	(2)	(1)	
ORTHOPTERA	Tettigoniidae	2	2	12	2	
	Gryllidae	4	3	33	4	
	Subtotal (2)	(6)	(5)	(45)	(6)	
CORRODENTIA	Elipsocidae	2	2	10	2	
	Psocidae	1	0	14	1	
	Subtotal (2)	(3)	(2)	(24)	(3)	
MALLOPHAGA	Menoponidae	1	0	3		
	Philopteridae	2	0	2(?)		
	Subtotal (2)	(3)	(0)	(5?)		
ODONATA	Libellulidae	1	1	1	1	
	Aeshnidae	1	0	1		1
	Coenagriidae	1	1	27	1	
	Subtotal (3)	(3)	(2)	(29)	(2)	(1)
THYSANOPTERA	Thripidae	1	0	7(?)	1	
	Phlaeothripidae	4	1	21(?)	3	
	Urothripidae	1	1	1	1	
	Subtotal (3)	(6)	(2)	(29?)	(5)	
HETEROPTERA	Pentatomidae	2	0	15	2	
	Coreidae	1	1	2	1	
	Lygaeidae	11	10	95	11	
	Enicocephalidae	1	0	1	1	
	Reduviidae	1	1	1	1	
	Nabidae	1	0	25	1	
	Anthocoridae	2	1	6	2	
	Miridae	12	9	28	12	
	Saldidae	1	0	4	1	
	Gerridae	1	0	1	1	
	Subtotal (10)	(33)	(22)	(178)	(33)	
HOMOPTERA	Cicadellidae	5	4	73	5	
	Delphacidae	10	8	139	10	
	Cixiidae	2	0	84	2	
	Psyllidae	8	5	31	8	
	Pseudococcidae	6	3	14	6	
	Subtotal (5)	(31)	(20)	(342)	(31)	
NEUROPTERA	Myrmeleontidae	1	0	1	1	
	Chrysopidae	1	1	26	1	
	Hemerobiidae	4	4	27	4	
	Subtotal (3)	(6)	(5)	(54)	(6)	

SUMMARY OF ENDEMIC HAWAIIAN INSECTS—*Continued*

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
LEPIDOPTERA	Gelechiidae	2	1	17	2	
	Cryptophasidae	6	6	40	6	
	Cosmopterygidae	14	13	307	14	
	Tineidae	3	1	7	2	
	Yponomeutidae	2	1	7		
	Nepticulidae	1	0	6		
	Batrachedridae	1	0	9	1	
	Caloptiliidae	1	0	15	1	
	Bedelliidae	1	0	3	1	
	Orneodidae	1	0	2	1	
	Tortricidae	14	4	70	14	
	Carposinidae	1	0	40	1	
	Crambidae	2	0	7	2	
	Phycitidae	3	2	6	2	
	Pyraustidae	11	5	185	8	2(?)
	Pterophoridae	1	0	5	1	
	Sphingidae	3	1	5		3
	Geometridae	9	4	59	9	
	Phalaenidae	12	2	68	9	2
	Nymphalidae	1	0	1		1
	Lycaenidae	1	0	1	1	
	Subtotal (21)	(90)	(40)	(860)	(75)	(8?)
COLEOPTERA	Carabidae	29	26	222	27	2(?)
	Dytiscidae	2	0	2	2	
	Staphylinidae	12	8	93	12	
	Histeridae	1	0	35	1	
	Nitidulidae	13	12	143	13	
	Cucujidae	2	1	13	2	
	Dermestidae	3	3	20	3	
	Hydrophilidae	1	0	2	1	
	Anobiidae	3	2	156	3	
	Ciidae	2	1	50	2	
	Elateridae	4	3	45	4	
	Eucnemidae	2	1	33	2	
	Alleculidae	2	1	8	2	
	Cerambycidae	8	6	100	2	6
	Anthribidae	1	0	2	1	
	Aglycyderidae	1	0	181	1	
	Curculionidae	14	7	159	12	
	Scolytidae	1	0	23	1	
	Lucanidae	1	0	3	1	
	Subtotal (19)	(102)	(71)	(1,290)	(92)	(8?)

SUMMARY OF ENDEMIC HAWAIIAN INSECTS—*Continued*

ORDER	FAMILY	GENERA CONTAINING ENDEMIC SPECIES	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC SPECIES	GENERIC AFFINITIES	
					Pacific	American
HYMENOPTERA	Ichneumonidae	8	5	40	8	
	Encyrtidae	4	2	24	1	
	Eupelmidae	2	1	57	1	
	Miscogasteridae	5	4	13	5	
	Spalangiidae	1	0	2	1	
	Aphelinidae	1	0	2	1	
	Eulophidae	4	0	4		
	Mymaridae	1	0	16		
	Diapriidae	3	2	9	3	
	Scelionidae	2	0	11	1	
	Cynipidae	2	0	27	2	
	Bethylidae	2	0	197	2	
	Dryinidae	2	0	2	2	
	Formicidae	9	0	10	9	
	Vespidae	4	3	117	4	
	Sphecidae	2	2	10	2	
	Crabronidae	5	5	22	5	
	Hylaeidae	1	0	55	1	
	Subtotal (18)	(58)	(24)	(618)	(48)	
DIPTERA	Tipulidae	2	0	13	2	
	Chironomidae	5	0	15	5	
	Mycetophilidae	1	0	3	1	
	Sciaridae	1	0	1	1	
	Dolichopodidae	9	3	78	8	
	Pipunculidae	1	0	12	1	
	Calliphoridae	2	2	9	2	
	Anthomyiidae	3	0	41	3	
	Sapromyzidae	1	0	1	1	
	Trypetidae	1	0	5		
	Ephydridae	3	0	8	3	
	Drosophilidae	4	3	57	4	
	Asteiidae	2	1	3	1	
	Subtotal (13)	(35)	(9)	(246)	(32)	
Grand Total 13 orders	103 families	377 genera containing endemic species	202 endemic genera	3,722 endemic species	334 (95%) with Pacific affinities	17(?)(5%) with American affinities

LIST OF GENERA CONTAINING TEN OR MORE ENDEMIC SPECIES

10–25 SPECIES

ORTHOPTERA
Paratrigonidium 16
Banza 11
Leptogryllus 11

CORRODENTIA
Psocus 14

THYSANOPTERA
Hoplothrips 15

HETEROPTERA
Oechalia 15
Oceanides 23
Nysius 24

HOMOPTERA
Leialoha 12
Nesothoë 22

NEUROPTERA
Nesomicromus 22

LEPIDOPTERA
Aristotelia 16
Neelysia 25
Parectopa 15
Eulia 17
Capua 13
Omiodes 23
Pyrausta 11
Orthomecyna 14
Eucymatoge 10

COLEOPTERA
Nesocidium 10
Disenochus 13
Atelothrus 20
Mesothriscus 16
Lispinodes 10
Myllaena 11
Gonioryctus 23
Orthostolus 10
Nesopetinus 25
Labrocerus 17
Holcobius 16
Apterocis 14
Acalles 22
Dryophthorus 17
Heteramphus 12
Xyleborus 23

HYMENOPTERA
Agrypon 11
Enicospilus 17
Polynema 16
Cothonaspis 18
Sclerodermus 16
Xenocrabro 11

DIPTERA
Limonia 12
Eurynogaster 15
Pipunculus 12

Total: 47 genera,
716 species

26–50 SPECIES

ODONATA
Megalagrion 27

HETEROPTERA
Neseis 34
Nabis 25

NEUROPTERA
Anomalochrysa 26

LEPIDOPTERA
Thyrocopa 34
Aphthonetus 33
Carposina 40
Phlyctaenia 27
Mestolobes 32
Scotorythra 36
Agrotis 29

COLEOPTERA
Metromenus 28
Oligota 29
Diestota 29
Acritus 35
Eupetinus 31
Nesopeplus 31
Cis 36
Eopenthes 34
Dromaeolus 32
Neoclytarlus 27
Rhyncogonus 34

DIPTERA
Campsicnemus 49
Lispocephala 38
Drosophila 48

Total: 24 genera,
824 species

51–100 SPECIES

HOMOPTERA
Nesophrosyne 62
Nesosydne 82
Oliarus 79

LEPIDOPTERA
Scoparia 64

COLEOPTERA
Mecyclothorax 85
Mirosternus 71
Xyletobius 69
Plagithmysus 57
Oodemas 61

HYMENOPTERA
Eupelmus 54
Hylaeus 55

Total: 10 genera,
739 species

OVER 100 SPECIES

LEPIDOPTERA
Hyposmocoma 216

COLEOPTERA
Proterhinus 181

HYMENOPTERA
Sierola 182
Odynerus 105

Total: 4 genera,
684 species

THE NUMBER OF ENDEMIC SPECIES PER GENUS

The average number of species per genus for the entire endemic insect fauna is 9.8 (for convenience, I have combined the subspecies and varieties with the species for use in this section). This number is too low, because some of the genera known to have only a single representative in Hawaii may be found to be immigrant, the numbers of species in other genera will be expanded as opportunity arises to describe the new species now at hand and to collect others, and a number of closely allied genera will be combined. In the positively endemic groups, however, the number of forms ranges from 1 to 216 per genus.

The accompanying table includes the genera which contain 10 or more forms.

It is noteworthy that 79.3 percent (2,963) of the endemic species of Hawaiian insects are contained in only 85 genera which include 10 or more species, and 20.7 percent (759) of the endemic species are included in 292 genera, each of which has less than 10 species per genus. The first group contains only positively endemic species, and these average 34 per genus. The second group includes, in addition to unquestioned endemic species, all those species of dubious endemicity and most of the genera which may be merged in the future. The second group has an average of 2.6 species per genus. The first group contains 22.6 percent of the genera containing endemic insects, and the second group contains 77.4 percent. The first group with its large number of species contained in so few genera is a strong index of insularity. Fifty-three percent of the 377 genera which contain the endemic species are endemic.

AN ESTIMATE OF THE NUMBER OF ANCESTRAL SPECIES NECESSARY FOR THE ORIGIN OF THE HAWAIIAN INSECTA

It has long been recognized that the Hawaiian biota has originated from a comparatively small number of immigrants. It is not an easy task to ascertain how many ancestral species gave rise to the Hawaiian insects, but an attempt has been made here which has resulted in some most significant data. There is no doubt that some of these figures will be modified by future research, but it is believed that such revision will not significantly alter the results obtained.

It is estimated that the total number of ancestral species which gave rise to the 3,722 known endemic insects was between about 233 and 254. There is reason to believe that future modification of these last numbers may be downward rather than upward. The significant conclusion reached here is the fact that perhaps only 233 to 254 fertilized female insect immigrants could have given rise to the entire endemic insect fauna! (It will be of interest to note here that only 14 original colonizations have given rise to the entire Hawaiian land-bird fauna.) Of all the data that indicate extreme insularity for the Hawaiian Insecta, these seem to be the most striking. How few have been the successful immigrants over the several millions of years available for dispersal and colonization!

The foregoing figures have been derived from the study of each genus containing Hawaiian insects, but only a summary by order will be given here. In the following list, the first figures refer to the number of ancestral species, and those in parentheses refer to the present number of derived species.

Thysanura	1 (2)
Orthoptera	3 or 4 (45)
Corrodentia	2 (24)
Mallophaga	3 to 5 (5)
Odonata	3 (29)
Thysanoptera	6 (29)
Heteroptera	22 to 28 (178)
Homoptera	12 to 19 (342)
Neuroptera	4 (54)
Lepidoptera	72 to 73 (860)
Coleoptera	39 to 41 (1,290)
Hymenoptera	35 to 47 (618)
Diptera	31 (246)
Total	233 to 254 (3,722)

According to these conclusions, the average number of species derived from each ancestral immigrant has been 14 or 15. These figures are, of course, too low, because the islands have not been completely explored, and the numbers of species in many genera are known to be, or will be found to be, much greater than are now known. The Coleoptera has the greatest average number of derived species, for there are now 31 to 33 species represented for each hypothetical ancestor. The following table shows the approximate average number of derivatives for all of the orders:

Thysanura	2
Orthoptera	11 to 15
Corrodentia	12
Mallophaga	1 to 2
Odonata	9
Thysanoptera	4
Heteroptera	6 to 7
Homoptera	17 to 28
Neuroptera	13
Lepidoptera	11
Coleoptera	31 to 33
Hymenoptera	13 to 17
Diptera	7

THE HAWAIIAN INSECT FAUNA IS OCEANIC

There is only one possible conclusion to be reached from the study of the foregoing material in regard to the status of the archipelago, and that is that these islands are truly oceanic. There is no evidence whatsoever to indicate that there was any Hawaiian continental land mass or that these islands were ever connected by dry land to any continent. The very character of the fauna expresses the essence of oceanic isolation. How could this impoverished, disharmonic fauna be considered other than extreme in its insularity?

DERIVATION OF THE HAWAIIAN INSECT FAUNA

Although it is admitted that our knowledge is at present incomplete and that numerous errors and irregularities exist in the foregoing analyses, the data displayed by the tabular summary are most significant. There can be no doubt as to the faunistic affinities of the Hawaiian Insecta: they are more than 90 percent Pacific. These conclusions are based upon averages. To attempt to base broad conclusions regarding the derivation and distribution of the biota upon aberrant minorities, instead of the average of the sum of the biota, is to me as

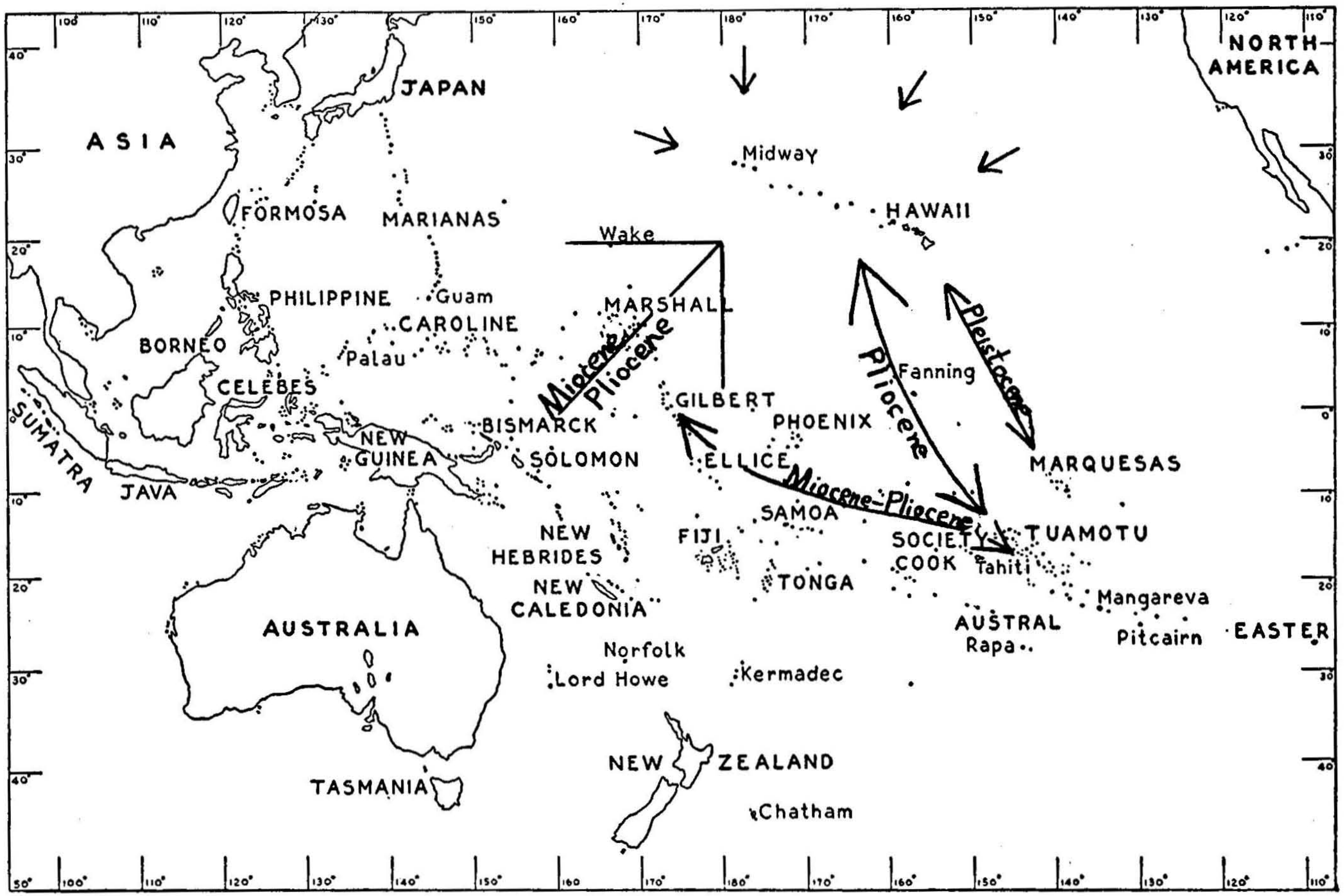

Figure 26.—Hypothetical lines and suggested ages of the principal inmigration routes of the endemic terrestrial biota of Hawaii. The Boreal elements are Tertiary to Recent. The eastern Austral routes have continued a limited exchange to the Recent epoch. The southwest sector has long been comparatively inactive.

fallacious as using the extremes of temperature and rainfall, instead of the means, to indicate the temperature or rainfall of a given region. The reason for the weak American representation is the fundamental fact that there has always been an extreme and unbroken water gap of more than 2,000 miles between continental America and Hawaii; whereas, to the south and west there are strings of islands some of which have acted as stepping stones (placed at intervals of at most a few hundred miles instead of thousands of miles) between the Indo-Polynesian regions and Hawaii. Few, indeed, are the insects which have succeeded in crossing the barrier from America. It is noteworthy that most of the American elements are large, strong-flying insects. It should not be overlooked, however, that the continental outlying Aleutian Islands are only about 1,400 miles from the end of the decadent leeward islands (at Kure Island). Also, in future studies we should pay more attention to the past climate of the Aleutians and its bearing upon the flora and fauna.

It is worth while to note here that the endemic Hawaiian plants, in development, endemism and derivation, parallel the insects very closely, for they are considered 92 percent Indo-Pacific derivatives and about 8 percent American and Boreal (see St. John, 1946:378). [But see new data, pages 106–119.] On the other hand, Mayr (1943) has concluded that the birds are predominantly American and Holarctic with only two or three Polynesian lines represented out of 14. The native land snails are about 70 percent Pacific and 30 percent "Holarctic." The Holarctic snail element contains a few recent forms from North America, and one group of over 140 forms in the Cochlicopinae (Leptachatinae) which may be Asiatic in origin, but their source is undetermined.

Insofar as the insects are concerned, it is impossible to divorce Hawaii from the Polynesian Subregion, using that term in its broadest sense. However, there are so many peculiar internal developments that the separation of the Hawaiian Islands into a distinct subdivision is justified. Hawaii has a unique geographical position, and therefore it has a unique flora and fauna for Polynesia. It has received immigrants not only through ancient stepping-stone routes, but also a "rain" of waifs and strays from many points of the compass over a long period of time. It is not as typically Polynesian as Samoa, for example, because it has a large number of non-Polynesian elements overlaying (or underlaying?) its Polynesian base. These elements give it a characteristic facies, and we might refer to the area as the Hawaiian Province of the Polynesian Subregion.

THE NATIVE LAND MOLLUSCA

The endemic Hawaiian land-snail fauna is considered by some workers to be perhaps the most remarkable of all land-snail faunas. The number of endemic genera is proportionately large, and it includes many unusual and isolated types. Because there is no general summary available to use for comparative purposes, I have included a tentative analysis of the group here.

I am indebted to Dr. C. M. Cooke, Jr., and to his protégé Mr. Y. Kondo for aid in drawing up these notes and supplying much unpublished information from the great and unequaled Polynesian collections at Bishop Museum.

Family HYDROCINIDAE

Three species of *Georissa* (considered a subgenus of *Hydrocena* by Thiele) have been described from Kauai, but, according to Dr. Cooke, they all appear to belong to forms of a single species. These are operculate snails and are probably oviparous. The genus is widespread in tropical and subtropical Europe, Asia and the Pacific. The Hawaiian forms are less than 1 mm. in length and are considered most closely allied to the Tahitian species. The Hawaiian representatives were collected from a clump of moss on a single occasion.

Family HELICINIDAE

These operculate land snails have representatives in many parts of the world, but are evidently absent from Europe, Africa and New Zealand, and are principally a tropical and subtropical group. Most of the Hawaiian species are terrestrial, but a few frequent low shrubs. These are small snails which range from about 3 to 6 mm. in diameter; they are probably oviparous.

Orobophana is distributed from Tonga to the Marquesas in southeastern Polynesia. Seven species and 14 varieties have been described from Hawaii. It is possible that these forms are Hawaiian segregates from *Pleuropoma* instead of representing a distinct stock descendant from the extra-Hawaiian *Orobophana.*

Pleuropoma is distributed from India and Burma to eastern Polynesia. There are 9 species and 29 varieties described from Hawaii.

The 59 Hawaiian members of this family appear to have developed from one, or possibly two, original immigrant stocks.

The two foregoing families are operculates, whereas the following families are all non-operculates and are true pulmonate terrestrial Mollusca.

Family PUPILLIDAE

This family is world-wide in distribution and contains small to minute snails. There is a greater development of species in Hawaii than on any other group of Pacific islands. The Hawaiian species range in length from about 0.75 to 2.5 mm. Most of the Hawaiian pupillids are egg layers, but some are ovoviviparous.

Nesopupa is distributed from Polynesia through the Orient to Africa and St. Helena. In Hawaii there are 20 species, 12 subspecies and 1 variety. Some of these are found on the ground, on rocks and on damp cliffs; one group lives under lichens on tree trunks, and some species are arboreal.

Lyropupa is a peculiar endemic genus which possibly has developed locally as an offshoot of *Nesopupa.* There are 24 species and 12 subspecies, all of which are ground forms.

Pronesopupa contains 10 species and 2 subspecies which evidently have had a local origin from the Hawaiian *Nesopupa.* These species are arboreal.

Pupoidopsis (a close ally of the cosmopolitan *Pupoides*) has a single ground-dwelling representative in Hawaii which appears to be indigenous. The same species is found on some other eastern Polynesian islands. It appears to be a comparatively recent natural immigrant from America.

Punctum (?) (no anatomical work has been done on our species, and it is not certain that the Hawaiian species belongs to *Punctum*; but the true *Punctum* is widespread) has one ground species (plus other undescribed forms) in Hawaii. The source is undetermined, but it may be North America.

Columella is a Holarctic genus which is also found in the Canary Islands. In Hawaii there are three arboreal species which appear to be American derivatives.

It is possible that four ancestral species gave rise to the 86 Hawaiian forms.

Family COCHLICOPIDAE

The amastrid snails are in a rather confused taxonomic state at present. I follow Watson (1920:24) in placing them as allies of *Cochlicopa*. Cooke and Kondo tell me that there are differences which appear to indicate that *Leptachatina* and its derivatives represent a different line from *Amastra* and its associates. Hence, the two groups are treated here as subfamilies. Pilsbry (1911) and Watson (1920) have found that no apparent differences exist between *Cochlicopa* and *Leptachatina,* but it appears permissible to retain the name *Leptachatina* until further anatomical studies are made.

This group includes the largest of the Hawaiian land molluscs. The species range in size from *Leptachatina,* 6 mm. long, to giant *Carelia,* 85 mm. long. With few exceptions, the species of all genera except *Laminella* are found on the ground; *Laminella* is arboreal.

Subfamily COCHLICOPINAE

The species are all oviparous and all live on the ground.

Leptachatina contains 125 species and 13 varieties and has been found on all of the islands, including fossils on Niihau and Kahoolawe.

Armsia is a local monotypic offshoot of *Leptachatina,* and is found only on Oahu.

Pauahia, a local derivative of *Leptachatina* confined to Oahu, contains 3 species.

One immigrant Holarctic *Cochlicopa* stock could have given rise to these 142 forms.

Subfamily AMASTRINAE

All of the species are ovoviviparous.

Amastra contains 157 species and 68 subspecies contained in several subgenera; with few exceptions, these are all found on the ground.

Laminella has 13 species and 12 subspecies which are arboreal.

Pterodiscus contains 7 species and 2 subspecies all of which are remarkably flattened forms. All of these are ground snails.

Planamastra is an allied group of flattened forms containing 5 species and 1 subspecies.

Carelia is probably the most remarkable of the group, for it includes the giants of the Hawaiian land shells (some are more than 3 inches long). The genus is restricted to Kauai and its neighboring island of Niihau (fossil only on Niihau). More than one-half of the species are now extinct. Twenty species and 9 subspecies have been described.

It appears that the 294 described forms of this subfamily have been developed from a single basic stock. In spite of the great divergence in the form of the shells, the anatomy shows that all of the genera are closely interrelated.

Family TORNATELLINIDAE

Subfamily TORNATELLININAE

This subfamily is restricted largely to eastern Polynesia, where it has its greatest development and diversity. The classification, however, is in taxonomic chaos. Species have been described from various localities from New Caledonia through Malaya to the Indian Ocean and from Japan, but it has not yet been ascertained whether all of these species belong to the family. A number of extra-Polynesian forms may be found to be synonyms and may be widespread Pacific species; their status remains dubious. The origin of the subfamily is undetermined. The species range in size from about 2 to 10 mm. in length and include both oviparous and ovoviviparous forms.

Auriculella is an endemic genus whose affinities are undetermined. It contains 30 species and 2 subspecies. These forms are arboreal.

Gulickia is an endemic genus containing a single arboreal species which is restricted to West Maui. Dr. Cooke believes that when the soft anatomy is studied the species might be found to be an *Auriculella.*

Elasmias is widespread in the Pacific and it contains three Hawaiian species which are arboreal.

Lamellidea is also widespread in the Pacific and contains 10 species and 3 subspecies, some of which are found on the ground, whereas others are arboreal.

Tornatellides has 46 species and 4 subspecies described from Hawaii, but Dr. Cooke believes that there may be over 100 in his collections. The genus is widespread in the Pacific and contains arboreal and ground species.

Tornatellaria is an endemic genus whose affinities are undetermined, but it appears to be closest to *Tornatellides* and may have developed from that genus. It contains 16 species and 2 subspecies, all found on the ground.

It may be that these 117 forms have been derived from four or fewer ancestral forms.

Subfamily ACHATINELLINAE

This is an endemic subfamily which forms one of the most characteristic elements of the distinctive Hawaiian biota. All of the species are arboreal, and their large size (1 to 2.5 cm.), beautiful colors, striking color patterns and seemingly unending array of varieties have made them the objects of the most intensive collecting and study of any of the Hawaiian molluscs. In appearance they are much like the species of *Partula.* They vie with the drepaniid birds for first place as the most discussed group of the Hawaiian biota, and it was through his study of these shells that Gulick was inspired to write various articles on evolution, including his book *Evolution, Racial and Habitudinal.*

In spite of all the attention given the group, the origin of the Achatinellinae has long remained obscure. However, its development appears not unlike that of the Amastrinae, and it is now believed by some workers that the group represents only an aberrant local offshoot of the family Tornatellinidae. All the species are ovoviviparous.

No Achatinellinae, living or fossil, are known from the old island of Kauai. Yet, malacologists consider the group one of the oldest of the Hawaiian Mollusca. The Molokai–Maui island complex is suggested as the hypothetical place of origin of the group. From there, the ancestral stock of *Achatinella* (a typical *Partulina* ?) colonized Oahu, where it remained completely isolated for a great length of time. The topographic features of Oahu have been fitted admirably for the breaking up, through geographical isolation, of the mutable *Achatinella* into an astounding number of forms. In comparatively recent geological time, however, *Partulina* has succeeded in recolonizing Oahu—a secondary invasion—but it has not had time to set up a secondary complex. It is interesting that the two other offshoots of *Partulina, Perdicella* and *Newcombia,* are found on both Molokai and Maui.

No two authorities seem to be in entire agreement as to what constitutes a genus, species, subspecies, variety or color form in this group. It is truly a complex of complexes. I have followed Caum's list (1928) but have altered it in some places.

Achatinella contains 42 species, 75 subspecies, 4 named varieties and a seemingly unending array of unnamed varieties. The numbers given are tentative and will be subject to change. Welch (1938) added 21 new subspecies to 1 species, and described, but did not name, many new varieties. Gulick, who split the various forms of *Achatinella* finely, said (1905:39), "*Achatinella* is one of ten genera of the Achatinellidae, of which there are between 200 and 300 species and over a thousand varieties, on this island only 40 miles long." This remarkable genus is confined to the island of Oahu.

Partulina is obviously a close ally of *Achatinella,* and it is probably the most primitive genus of the Achatinellidae. Sykes (1900) considered it a subgenus of *Achatinella,* and perhaps its affinities would be better indicated if it were reassigned to that category. Representatives of the genus are found on Molokai, Lanai, Maui and Hawaii with only a couple of species on Oahu. In all, there are 44 species, 28 subspecies and 1 named variety.

Perdicella is an offshoot of *Partulina.* It contains 8 species and 1 named variety and is confined to Molokai and Maui.

Newcombia is another offshoot of *Partulina.* It includes 9 species and 3 subspecies and is confined to Molokai and Maui.

It appears certain that this subfamily had its origin and development in the Hawaiian area and all of the 215 forms listed here may have been derived from a common tornatellinid ancestor.

Family ENDODONTIDAE

This family is world-wide in distribution and many species are found in Polynesia. In Hawaii the genus *Endodonta* has 25 species and 1 subspecies described, but Dr. Cooke believes that the description of material which has come into Bishop Museum in the last 25 years or more will raise the total to more than 100 species. Many of the undescribed species are known only from Recent fossil material collected in the lowlands, where the species have evidently been exterminated.

The Hawaiian species are Pacific derivatives and evidently have arisen from a single ancestral stock with great divergence and development since the original colonization. Some of the species are found on the ground and others live on tree trunks. They range in size from 2 to over 12 mm. and are oviparous. They occur on all the islands.

Family HELICARIONIDAE

This family is world-wide in distribution and is abundantly represented in the Pacific. Some of the Hawaiian species are found on the ground and many are arboreal. The species range in size from about 5 to 13 mm. and are ovoviviparous.

Subfamily EUCONULINAE

This subfamily is represented in Hawaii by 6 species and 2 subspecies of the endemic subgenus *Nesoconulus* of the principally Holarctic genus *Euconulus*. It is noteworthy that the shells of the Hawaiian subgenus and those of a species of the subgenus *Euconulops* from the highlands of Tahiti are larger than those of the continental members of the genus (H. B. Baker, 1938–1941). The eight Hawaiian forms are divided into three taxonomical sections, but may all have arisen from a common Holarctic (Nearctic ?) ancestral stock.

Subfamily MICROCYSTINAE

This is one of the characteristic groups of land snails of Polynesia. The subfamily is "Mainly developed on the islands in the Pacific Ocean but with some species (especially the smaller ones) reaching the East Indies and the mainland of Asia." (H. B. Baker, 1938:10.) According to Baker (1938:11), the subfamily is "closely related to the Euconulinae, which include the most primitive members of the Helicarionidae."

Philonesia is the largest genus of the family found in eastern Oceania, and Baker (1940:106, etc.) has divided it into 13 subgenera, 4 of which are found in Hawaii. The subgenus *Kipua* is confined to Kauai and has 2 species. The subgenus *Waihoua* contains 1 species found on the island of Hawaii. *Philonesia, sensu stricto,* is, according to Baker's classification, confined to the Hawaiian and Marquesas Islands; in Hawaii there are 24 species and 4 subspecies. The subgenus *Aa* is confined to Hawaii and includes 13 species and 1 subspecies.

Kaala contains a single species and is confined to the higher slopes of Mount Kaala on Oahu. It has characters of both *Philonesia* and *Hiona*.

Hiona is allied to *Philonesia,* is confined to eastern Polynesia and contains 6 subgenera, according to Baker's classification. Two of the subgenera are confined to Hawaii, one is common to Hawaii and the Marquesas and the other three are restricted to southeastern Polynesia. The subgenus *Neutra* has one species on Oahu and one on Uapou in the Marquesas, and each has been placed in a different section of the subgenus by Baker. The subgenus *Hionarion* contains two Kauai species only. *Hiona, sensu stricto,* is confined to the Hawaiian Islands and includes 10 species and 3 subspecies found from Kauai to Hawaii.

There are 62 forms contained in the subfamily Microcystinae, and these may have developed from as few as two ancestral stocks.

Family ZONITIDAE

This family is closely allied to the Helicarionidae. Unlike most of the other groups of Hawaiian land snails, all of the Hawaiian representatives of the family are Nearctic or Holarctic derivatives. None of the genera is well developed in the islands, and all of them appear to have become established in the islands in Recent geological time. *Trochomorpha,* so characteristically developed in the south Pacific, has not reached Hawaii. All of the Hawaiian species are terrestrial in habit, and they range in size from approximately 3 to 10 mm. They are ovoviviparous.

The Vitrininae are represented by a single species of the Nearctic *Vitrina,* found at high altitudes on the island of Hawaii. It may prove not to be specifically different from a northwestern American species. Could it have been carried here by the plover?

The Gastrodontinae are represented by the subgenus *Pseudohyalina* of *Striatura. Pseudohyalina* is confined to North America and Hawaii. There are three species in the Territory: one is found on Kauai, and is thought to be the same as a western North American species, and there are two other endemic species.

The Holarctic Zonitinae are represented by three endemic species of the Holarctic and Hawaiian subgenus *Nesovitrea* of *Retinella,* and by three Kauai species belonging to the endemic genus *Godwinia,* which is evidently allied to the American *Patulopsis.*

These 10 species appear to have arisen from four or five comparatively recent immigrants. Because of their habits and habitats, the species which are, or which may prove to be, the same as North American species are considered here to be indigenous rather than artificially imported.

Family SUCCINEIDAE

This family is world-wide in distribution. In Hawaii, the cosmopolitan genus *Succinea* is represented by 44 described species, and the greatest development and diversification of the genus is found in these islands. Many species inhabit other Polynesian high islands. The genus includes both arboreal and ground species; they are oviparous and range in size from 10 to almost 25 mm. Evidently the Hawaiian complex has developed from one ancestral form, but it is not known whence it came. Species of this genus are found on all the main islands.

TABULAR SUMMARY OF THE NATIVE TERRESTRIAL MOLLUSCA

GROUP	GENERA CONTAINING ENDEMICS	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC FORMS	NUMBER OF INDIGENOUS FORMS	AFFINITIES			
					Pacific		Holarctic	
					Genera	Forms	Genera	Forms
HYDROCINIDAE	1		1		1	1		
HELICINIDAE	2		59		2	59		
PUPILLIDAE	6	2	85	1	3	81	3(?)	5
COCHLICOPINAE	3	3	142				3	142
AMASTRINAE	5	5	294		5	294		
TORNATELLININAE	6	3	117		6	117		
ACHATINELLINAE	4	4	215		4	215		
ENDODONTIDAE	1		26		1	26		
EUCONULINAE	1		8				1	8
MICROCYSTINAE	3	1	62		3	62		
ZONITIDAE	4	1	8	2(?)			4	10
SUCCINEIDAE	1		44		1	44		
Total: 10	37	19	1,061	3(?)	26	899	11(?)	161

Fifty-one percent of the genera which contain native land snails are endemic. The average number of native species per genus is 28.8. It is estimated that about 22 or 24 ancestral colonizations gave rise to the 1,064 derived native species. Hence, each postulated ancestor gave rise to an average of from 44 to 48 species. The ancestral amastrid has given rise to the greatest number of derived forms, for there are now 5 genera and 294 known species and lesser forms known in that group.

THE NATIVE LAND AND SHORE BIRDS

The endemic land birds have been so carefully collected that it is extremely unlikely that any living form remains undiscovered. A number of species apparently became extinct in rather recent times without having been collected by scientists, and a deplorable percentage of the described forms is now extinct. So much literature has been assembled on these animals that a detailed summary of them group by group is not needed here. The table on page 105 presents information for comparative purposes.

Sixty-two percent of the genera which contain endemic birds are themselves endemic. The average number of endemic forms per genus is 2.9. Fifteen ancestral immigrants are believed to have given rise to the 70 endemic species and lesser forms. The average number of known forms derived from each of these 15 ancestors has been calculated at 4.6. The ancestral drepaniid gave rise to 42 known forms and is the only line to have speciated extensively in the islands.

The Meliphagidae with its two derived genera and five species is the next important local complex. The Drepaniidae is believed to have been the earliest of this group of organisms successfully to have colonized Hawaii. If the endemic rails are not Pacific derivatives, then 17 percent of the genera and 14 percent of the species are Pacific and 83 percent of the genera and 85 percent of the species are Holarctic. If the rails are Pacific derivatives, then 25 percent of the genera and 18 percent of the species have Pacific affinities and 75 percent of the genera and 81 percent of the species are Holarctic derivatives. (Species and subdivisions of species have been combined under "species" in the foregoing percentages.) There appears to be no doubt that the goose, the hawk, the waterhen, the coot, the stilt and the thrushes are American derivatives. The ducks, the owl and the crow may be either American or Asiatic. The balance of opinion as to the origin of the drepaniids seems to lean more toward America than toward the Palearctic, but much study remains to be done on the group. The sea birds are tropical derivatives and are mostly widespread Polynesian or wider-ranging forms.

TABULAR ANALYSIS OF THE ENDEMIC HAWAIIAN LAND AND SHORE BIRDS

FAMILY	GENERA CONTAINING ENDEMICS	NUMBER OF ENDEMIC GENERA	NUMBER OF ENDEMIC FORMS	NUMBER OF ANCESTRAL STOCKS	AFFINITIES			
					Pacific		Holarctic	
					Genera	Forms	Genera	Forms
ANATIDAE	2	0	3	2			2	3
ACCIPITRIDAE	1	0	1	1			1	1
RALLIDAE	4	1	5	4	2(?)	3(?)	2	2
RECURVIROSTRIDAE	1	0	1	1			1	1
STRIGIDAE	1	0	1	1			1	1
CORVIDAE	1	0	1	1			1	1
TURDIDAE	1	1	6	1			1	6
SYLVIIDAE	1	1	2	1	1	2		
MUSCICAPIDAE	1	1	3	1	1	3		
DREPANIIDAE	9	9	42	1			9	42
MELIPHAGIDAE	2	2	5	1	2	5		
Totals	24	15	70	15	4(6?)	10(13?)	18	57

THE FLORA OF HAWAII

The native plants of Hawaii form an assemblage which has been referred to as one of the most distinctive floras in the world. There are many unusual types represented, such as the shrubby violets, the arborescent lobelias and the peculiar composites. Some of these are old types which correspond to those discussed under the foregoing sections on animals, which appear to be without known living relatives or whose relationships are masked. From these types, there is a gradation down to native forms which are conspecific with species occurring outside Hawaii. These facts duplicate those which have been discussed already for insects, land molluscs and birds.

A section attempting to analyze the flora in accordance with the plan adopted for the insects was started, but I found the problem too involved for anyone other than a skilled botanist with a wide knowledge of Polynesian plants. Therefore, my preliminary manuscript was set aside for about six years, and there was the possibility that this work would be issued without an analysis of the flora. Fortunately, however, F. R. Fosberg, an old friend and a companion of the Mangarevan Expedition, came to Hawaii on a visit when this volume was in press. Dr. Fosberg did not have an opportunity to read the foregoing pages, which were in page proof before his manuscript was received. We were both so busy with other tasks that only a limited amount of time was available for conferences to outline this section. However, in spite of the heavy pressure of other duties and the limited time available, and in spite of the fact that Dr. Fosberg did not have access to his own library or to his invaluable personal notes and manuscripts, he has produced a commendable digest. I am proud and happy to include "Derivation of the Flora of the Hawaiian Islands" as a section of this text, and my indebtedness to Dr. Fosberg is great. We both want to emphasize that this digest, like the foregoing ones, is incomplete and premature, and, perhaps, in part inaccurate, but we believe that such presentations are justified now because they will stimulate further thought and study.

DERIVATION OF THE FLORA OF THE HAWAIIAN ISLANDS

By

F. R. FOSBERG

Speculation as to the affinities and derivation of the Hawaiian flora has not been lacking in the past. Unfortunately there have been more guesses than careful investigation.

The flora is a small one, typically that of an oceanic island. The total known flora of seed plants is, according to the census which follows, 1,729 species and varieties scattered through 216 genera; that of ferns, 168 species and varieties in 37 genera.

Because of its isolation and high endemism, this flora has always attracted attention, and many competent botanists have worked and written on it. It early had one of the finest general descriptive floras (Hillebrand, 1888) ever written on a tropical region. Yet, according to modern standards we know remarkably little about this flora. Many of the most difficult genera have not been monographed. Some monographs which have been written are so poor that they must be redone. The reputation for polymorphism enjoyed by Hawaiian plants has led taxonomists to avoid undertaking major problems on them.

Especially little has been written specifically on the relationships of Hawaiian genera and species to their relatives elsewhere. Even in the most modern and extensive revisions and monographs one frequently finds no indication that the plants have or do not have relatives elsewhere. It seems that much of the work has been done on the assumption that all Hawaiian plants are isolated endemics.

This has made it very difficult to compile any list of the affinities of Hawaiian groups. It has also made the quality of the compilation very uneven. Wherever possible the compiler has relied on his own knowledge or opinions. Unfortunately, there are many groups with which he has had only superficial contact outside of their Hawaiian representation. In the cases of these, an attempt has been made to find where a competent student has expressed an opinion, or to persuade one to express himself. In many instances the last opinion to be expressed was that of Hillebrand 60 years ago. The writings of Dr. Carl Skottsberg have been freely drawn upon. Most of the recent monographs and revisions have given surprisingly little assistance.

It must be emphasized that the present state of our knowledge permits only the most tentative conclusions as to the relationships and origin of most Hawaiian plants, and that even the numbers of species and varieties are by no means definitely known. Current explorations still yield numerous new ones.

Merely writing down some of these approximations may give them more weight than they deserve. However, it has been considered worth while to compile this summary to bring together the best current information.

The tabular arrangement selected, though more complex than that for animal groups, is, if anything, too simple. It seems that the history of plant distribution in the Pacific may have been more complex than that of animals. Plants have apparently come to Hawaii *from all directions, more or less indiscriminately,* with a preponderance, of course, from the island-rich areas to the southwest. It would be misleading to divide the affinities into Pacific and American, since the Austral group is so strong.

In the tables, where doubt as to two alternatives is expressed by question marks, the least likely of the two has been enclosed in parentheses and the other has been counted in the totaling. In the interest of simplification, question marks have been used only in the most doubtful cases.

The term *Indo-Pacific* is applied to groups following the common distributional pattern of a concentration of species in Indonesia or southeastern Asia and attenuating out into the Pacific, or to groups showing a portion of this distribution: generally, those plants having their affinities to the west and southwest of Hawaii.

Austral is applied to those whose affinities are in the south Pacific, from Australia to Patagonia, but not usually to any extent west of Australia, and not restricted to America. This includes the "Antarctic" element of previous compilers.

American is of obvious circumscription, except that certain plants of far northern connection may be referred to the Boreal category. The Galapagos and Juan Fernandez Islands are regarded as American.

Boreal refers to northern North America and extra-tropical Eurasia. This is not entirely satisfactory, as certain East Asiatic groups should perhaps have a category of their own.

Pantropic includes groups which have such a wide tropical or cosmopolitan distribution that it is difficult or impossible to suggest from which area the original immigrant may have come. A great many of these are groups that are strand or widespread lowland plants.

The *Obscure* category includes such plants as are so isolated as to have no apparent living relatives. There may be some that are placed here only from lack of adequate study. This is certainly true in such ill-classified groups as certain large grass genera, etc. In general, however, these may well be the oldest members of the flora, isolated for so long either that all their relatives have succumbed to competition or to other causes of extinction, or that they have had time to change so completely that evidence of their kinship has been lost.

The philosophy adopted in this tabulation is that actual percentages of the flora are of little significance in speculation on its origin. An attempt has been made to determine by affinities the probable number of original immigrants that established themselves and were the ancestors of the present flora. Countless others may have come, flourished, then become extinct leaving no trace. The indications of the affinities in the tables are on the basis only of these lines of descent. Therefore, the percentages derived from the six general categories of sources do not indicate percentage of the flora but of the original immigrants.

Separate tables have been made for seed plants and Pteridophytes, as their propagules are so different in nature that different principles may well govern their dispersal and distribution. One would naturally expect a much more continuous rain of microscopic fern spores on an isolated island than of heavy seeds or fruits.

Where genera that are widely accepted are here considered as synonyms (or as subgenera) of others, they are placed beneath the accepted genera in parentheses and in italics. Where several genera are considered to represent the progeny of one introduction, the derived ones are placed in parentheses, but not italicized, under that genus believed closest to the original immigrant. Where there are divergent ideas on the number of species and varieties in a group and the compiler has no definite opinion, the least probable number has been added in parentheses, and this number is not incorporated in the totals. Question marks in the first five data columns indicate strong doubt as to numbers. In the columns under "Affinities" they indicate doubt as to direction of affinity. When alone they are counted as one; when in parentheses they are not counted as they are the less likely alternatives.

Introduced species, either recent or aboriginal, have been excluded where the compiler is satisfied that they are introduced.

SUMMARY OF THE HAWAIIAN SEED PLANTS

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Pandanaceae	Freycinetia	w	1	1		1	1					
	Pandanus	w	1		1	1	1					
Potamogetonaceae	Potamogeton	w	2		2	2			1		1	
	Ruppia	w	1		1	1					1	
Naiadaceae	Naias	w	1		1	1					1	
Hydrocharitaceae	Halophila	w	1		1	1	1					
Gramineae	Agrostis	w	3	2	1	2		2				
	Andropogon	w	1		1	1	1					
	Calamagrostis	w	2	2		2		2				
	Cenchrus	w	3	3		1	1					
	Deschampsia	w	3	3		1				?		
	Digitaria	w	1		1	1	1					
	Dissochondrus	e	1	1		1			1			
	Eragrostis	w	12	12		2		2				
	Festuca	w	1	1		1				?		
	Garnotia	w	1	1		1	1					
	Heteropogon	w	1		1	1					1	
	Isachne	w	2	1	1	2	2					

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
	Ischaemum	w	1		1	1		1				
	Lepturus	w	1		1	1	1					
	Microlaena	w	1		1	1	1					
	Oplismenus	w	1		1	1			1			
	Panicum	w	23	23		3			1			2
	Paspalum	w	2		2	2	1				1	
	Poa	w	(3)–4	(3)–4		1			?			
	Sporobolus	w	1		1	1					1	
	Trisetum	w	2	2		1				1		
Cyperaceae	Carex	w	9	6	3	6	1	1	2?	1	1	
	Cladium (*Baumea*) (*Vincentia*)	w	3	2	1	3		2	1			
	Cyperus	w	23	16	7	8	3		1		4	
	Eleocharis	w	1		1	1		(?)	?			
	Fimbristylis	w	2	1	1	2	1					1
	Gahnia	w	6	6		2	2					
	Oreobolus	w	1	1		1		1				
	Rhynchospora	w	3	1	2	2	2					
	Scirpus	w	(4)–5	1?	4	(4)–5			4		1	
	Scleria	w	1	1?		1			1			
	Uncinia	w	1		1			1				
Palmae	Pritchardia	w	2–(38)	2–(38)		1	1					
Flagellariaceae	Joinvillea	w	1	1			1					
Juncaceae	Luzula	w	3	3		1					1	
Liliaceae	Astelia	w	12	12		1		1				
	Dianella	w	3	3		1	1					
	Dracaena (*Pleomele*)	w	2–(4)	2–(4)		1	1					
	Smilax	w	2	2		1	1					
Iridaceae	Sisyrinchium	w	1	1		1			1			
Orchidaceae	Anoectochilus	w	2	2		1	1					
	Habenaria	w	1	1		1	1					
	Liparis	w	1	1		1	1					
Piperaceae	Peperomia	w	50	48	2	3	1		1			1
Ulmaceae	Trema	w	1		1	1	1					
Moraceae	Pseudomorus	w	1	1?		1		1				

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Urticaceae	Boehmeria	w	1	1		1	1					
	Hesperocnide	w	1	1		1			1			
	Neraudia	e	9	9		1						1
	Pilea	w	1		1	1	(?)		(?)		?	
	Pipturus	w	13	13		1	1					
	Touchardia	e	5?	5?		1	1?					
	Urera	w	3	3		2			2			
Santalaceae	Exocarpus	w	3–(5)	3–(5)		1		1				
	Santalum	w	6	6		2		1				1
Loranthaceae	Korthalsella	w	8	6	2	2	1	1				
Polygonaceae	Polygonum	w	1		1	1					1	
	Rumex	w	2	2		1						1
Chenopodiaceae	Chenopodium	w	1	1		1			1			
Amaranthaceae	Achyranthes	w	2	2		1	1					
	Aerva	w	1	1		1	?					
	Amaranthus	w	1	1		1	1					
	Charpentiera	w	3	3		1		1				
	Nototrichium	e	5	5		1		1				
Nyctaginaceae	Boerhavia	w	3		3	3	3					
	Pisonia (*Ceodes*) (*Rockia*) (*Heimerliodendron*)	w	3	3		2	1	1				
Phytolaccaceae	Phytolacca	w	1	1		1			1			
Aizoaceae	Sesuvium	w	1		1	1					1	
Portulacaceae	Portulaca	w	6	4	2	3		1	1		1	
Caryophyllaceae	Sagina	w	1	1		1				?		
	Schiedea (*Alsinodendron*)	e	45	45		1						1
	Silene	w	5	5		1						1
Ranunculaceae	Ranunculus	w	2	2		1		?				
Menispermaceae	Cocculus	w	1		1?	1		1				
Lauraceae	Cassytha	w	1		1	1					1	
	Cryptocarya	w	2	2		1	1					
Papaveraceae	Argemone	w	1	1		1			1			
Capparidaceae	Capparis	w	1		1	1	1					
	Cleome	w	1	1		1			1			

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Cruciferae	Cardamine	w	1	1		1					1	
	Lepidium	w	(3)–4	(3)–4		2	1					1
Droseraceae	Drosera	w	1		1	1				1		
Saxifragaceae	Broussaisia	e	2	2		1	1					
Pittosporaceae	Pittosporum	w	50	50		1	1					
Rosaceae	Acaena	w	2	2		1		1				
	Fragaria	w	1		1	1			1			
	Osteomeles	w	1		1	1	1					
	Rubus	w	2	2		1			1			
Leguminosae	Acacia	w	3	3		1	1					
	Caesalpinia	w	2		2	2					2	
	Canavalia	w	2	2		1	1					
	Cassia	w	1	1		1	1					
	Entada	w	1?		1	1					1	
	Erythrina	w	1	1		1	1					
	Mezoneurum	w	1	1		1	1					
	Mucuna	w	2		2	2					2	
	Sophora	w	1	1		1		1				
	Sesbania	w	1	1		1		?				
	Strongylodon	w	1		1?	1	1					
	Tephrosia	w	1?		1	1	1					
	Vicia	w	1	1		1			?			
	Vigna	w	3	2	1	2					1	1
Geraniaceae	Geranium	w	6	6		1						1
Zygophyllaceae	Tribulus	w	1		1	1					1	
Rutaceae	Fagara	w	14	14		1	1					
	Pelea	w	94	94		1	1					
	(Platydesma)	e										
Euphorbiaceae	Antidesma	w	6	6		1	1					
	Claoxylon	w	8	8		1	1					
	Drypetes	w	1	1		1	1					
	Euphorbia	w	60	60		1	1					
	Phyllanthus	w	2	2		1	1					
Aquifoliaceae	Ilex	w	1		1	1		1				
Celastraceae	Perrottetia	w	1	1		1	?					
Anacardiaceae	Rhus	w	1	1		1	1					

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Sapindaceae	Alectryon	w	1	1		1	1					
	Dodonaea	w	18	18?		1					1	
	Sapindus	w	2	2		2	1		1?			
Rhamnaceae	Alphitonia	w	1	1		1	1					
	Colubrina	w	2	1	1	2	1?				1	
	Gouania	w	3	3		1	1					
Tiliaceae	Elaeocarpus	w	1	1		1	1					
Malvaceae	Abutilon (*Abortopetalum*)	w	3	2	1	2			1			1
	Gossypium	w	1	1		1			?			
	Hibiscadelphus	e	4	4		1						1
	Hibiscus	w	10	9	1?	4	2?	1			1	
	Kokia	e	4	4		1						1
	Sida	w	2		2	2	1				1	
Sterculiaceae	Waltheria	w	1	1		1			?			
Theaceae	Eurya	w	2	2		1	1					
Violaceae	Isodendrion	e	4	4		1			?			
	Viola	w	7	7		1						1
Thymeleaceae	Wikstroemia	w	14	14		1	1					
Flacourtiaceae	Xylosma	w	2	2		1	1					
Cucurbitaceae	Sicyos	w	8	8		1						1
Myrtaceae	Eugenia	w	4	4		2	2					
	Metrosideros	w	18?	18?		1		1				
Begoniaceae	Hillebrandia	e	1	1		1						1
Halorrhagaceae	Gunnera	w	7	7		1			1			
Araliaceae	Cheirodendron	w	5?	5?		1		1				
	Reynoldsia	w	1	1		1		1				
	Tetraplasandra (*Pterotropia*)	e	10?	10?		1						1
Umbelliferae	Daucus	w	1		1	1			1			
	Hydrocotyle	w	1		1	1					1	
	Peucedanum	w	3	3		1						1
	Sanicula	w	4.	4		1						1
	Spermolepis	w	1	1		1			1			
Ericaceae	Vaccinium	w	8	8		1		1				
Epacridaceae	Styphelia	w	2	1	1	1		1				

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Primulaceae	Lysimachia	w	13	12	1	2	1	1?				
Myrsinaceae	Embelia	w	2	2		1	1					
	Myrsine	w	25	25		1?					1	
Sapotaceae	Nesoluma	w	1		1	1		1				
	Pouteria	w	6?	6?		1	1					
	(*Planchonella*)											
Ebenaceae	Diospyros	w	7	7		1	1					
	(*Maba*)											
Plumbaginaceae	Plumbago	w	1		1	1	1					
Loganiaceae	Labordia	e	75	75		2	2					
Gentianaceae	Centaurium	w	1		1	1			1			
Oleaceae	Osmanthus	w	1	1		1	1					
Apocynaceae	Alyxia	w	1	1		1	1					
	Ochrosia	w	1	1		1	1					
	Pteralyxia	e	2	2		1						1
	Rauvolfia	w	7	7		1						1
Convolvulaceae	Breweria	w	2	2		1						1
	Cressa	w	1		1	1			1			
	Cuscuta	w	2	2		1			1			
	Ipomoea	w	9	4	5	7	5				2	
	Jacquemontia	w	1	1		1			1			
Hydrophyllaceae	Nama	w	2	2		1			1			
Boraginaceae	Heliotropium	w	2	1	1	2		(?)	2			
Verbenaceae	Vitex	w	1		1	1	1					
Labiatae	Lepechinia	w	1		1	1			1			
	Phyllostegia	w	108	108		1		1				
	(Stenogyne)	e										
	(Haplostachys)	e										
	Plectranthus	w	1		1	1	1					
Solanaceae	Lycium	w	1		1	1			1			
	Nothocestrum	e	6	6		1			1			
	Solanum	w	7	7		1						1
Scrophulariaceae	Bacopa	w	1		1	1					1	
Myoporaceae	Myoporum	w	1	1		1	1					

SUMMARY OF THE HAWAIIAN SEED PLANTS—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Gesneriaceae	Cyrtandra	w	110	110		1?	1					
Plantaginaceae	Plantago	w	19	19		2?		2				
Rubiaceae	Bobea	e	4?	4?		1	1					
	Canthium	w	1		1	1	1					
	Coprosma	w	27	27		3?		3				
	Gardenia	w	2	2		2	2					
	Hedyotis	w	76	76		1	1					
	(Gouldia)	e										
	Morinda	w	3	3		1	1					
	Nertera	w	1		1	1		1				
	Psychotria	w	11	10	1	2	1		1			
	(*Straussia*)											
Campanulaceae	Brighamia	e	2	2		1						1
	Clermontia	e	42	42		1		1				
	Cyanea	e	100	100		1						1
	(Rollandia)	e										
	(Delissea)	e										
	Lobelia	w	23	23		1	?					
	(Trematolobelia)	e										
Goodeniaceae	Scaevola	w	12	11	1	1	1					
Compositae	Adenostemma	w	1		1	1	1					
	Argyroxiphium	e	61	61		1						1
	(*Wilkesia*)											
	(Dubautia)	e										
	(*Railliardia*)											
	Artemisia	w	5	5		1				1		
	Aster	w	1	1		1			1			
	Bidens	w	60	60		1		1				
	Gnaphalium	w	1	1		1					1	
	Hesperomannia	e	7	7		1			1			
	Lagenophora	w	3	3		1		1				
	Lipochaeta	e?	55	55		1	1					
	Remya	e	2	2		1			?			
	Tetramolopium	w	20	20		1	1					
Totals 83	216	28e 188w	1,729	1,633	96	272	109	45	50	7	35	28

The table of seed plants yields the following information:

- 83 families
- 216 genera
  - 28; 13 percent endemic
  - 188; 87 percent non-endemic
- 1,729 species and varieties
  - 94.4 percent endemic
  - 5.6 percent non-endemic
- 272 original immigrants
  - 40.1 percent Indo-Pacific
  - 16.5 percent Austral
  - 18.3 percent American
  - 2.6 percent Boreal
  - 12.5 percent Pantropic and Cosmopolitan
  - 10.3 percent Obscure

Significantly absent are gymnosperms, *Ficus*, Cunoniaceae, mangroves, *Piper*, Bignoniaceae, Araceae, and the several large predominantly American tropical families. Significantly few are Orchidaceae, palms, Loranthaceae, Lauraceae, Scrophulariaceae. Significantly numerous are grasses and Compositae.

Not evident from the table is the interesting fact that of the American element a far greater part of the species are only slightly distinct from their American relatives (probably indicating geologically recent arrival) than is true for the other elements.

For the Pteridophyte table much of the basic information was kindly supplied by W. H. Wagner, Jr. However, the generic concepts, arrangement of the table and interpretations are those of the compiler.

The Pteridophyte table shows that there are:

- 10 families
- 37 genera
  - 3; 8.1 percent endemic
  - 34; 91.9 percent non-endemic
- 168 species and varieties
  - 119; 64.9 percent endemic
  - 49; 35.1 percent non-endemic
- 135 original immigrants
  - 48.1 percent Indo-Pacific
  - 3.7 percent Austral
  - 11.9 percent American
  - 4.4 percent Boreal
  - 20.8 percent Pantropic and Cosmopolitan
  - 11.1 percent Obscure

Most notably absent are *Cyathea* (sensu lata) and *Blechnum*. (*Sadleria*, however, is of blechnoid affinity.)

SUMMARY OF THE HAWAIIAN PTERIDOPHYTES

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
Psilotaceae	Psilotum	w	2	1	1	1					1	
Lycopodiaceae	Lycopodium	w	13	9	4	9	4		1		4	
Selaginellaceae	Selaginella	w	3	3		3				1	1	1
Ophioglossaceae	Ophioglossum	w	4	1	3	3	1				2	
	Botrychium	w	1	1		1	1					
Marattiaceae	Marattia	w	1	1		1	?		(?)			
Schizaeaceae	Schizaea	w	1	1		1		1				
Gleicheniaceae	Gleichenia (sensu lata)	w	4	2	2	3	2		1			
Hymenophyllaceae	Hymenophyllum (sensu lata)	w	3	3		3	1				2	
	Trichomanes (sensu lata)	w	6	5	1	6	3	2			1	
Polypodiaceae	Adiantum	w	2(?)		2(?)	2(?)	1(?)				1	
	Asplenium (sensu lata)	w	21	12	9	21	13		2	2	2	2
	Athyrium (*Diplazium*)	w	9	7	2	9	6		2			1
	Cibotium	w	5	5		1	?		(?)			
	Coniogramme	w	1	1		1	1					
	Cystopteris	w	1	1		1					1	
	Diellia	e	8	8		1						1
	Doodia	w	2		2	2		2				
	Doryopteris	w	2	2		1					1	
	Dryopteris (*Lastrea*) (*Ctenitis*) (*Cyclosorus*)	w	25	20	5	25	14		5		2	4
	Elaphoglossum	w	9	9		9	5				2	2
	Histiopteris	w	1		1	1					1	
	Hypolepis	w	1		1	1	1					
	Lindsaea	w	1		1	1	1					
	Microlepia	w	2		2	2	2					
	Nephrolepis	w	4		4	4					4	
	Pellaea	w	1		1	1			1			

SUMMARY OF THE HAWAIIAN PTERIDOPHYTES—*Continued*

FAMILY	GENUS	GENERA ENDEMIC (e); NON-ENDEMIC (w)	NO. SPECIES PLUS VARIETIES	NO. ENDEMIC	NO. NON-ENDEMIC	NO. ORIGINAL IMMIGRANTS	AFFINITIES					
							Indo-Pacific	Austral	American	Boreal	Pantropic	Obscure
	Polypodium	w	16	13	3	7	3		1	2		1
	(*Pleopeltis*)											
	(*Microsorium*)											
	(*Grammitis*)											
	(*Xiphopteris*)											
	(*Amphoradenium*)											
	Polystichum	w	4	2	2	4	1		1	1		1
	(*Rumohra*)											
	(*Cyrtomium*)											
	(*Phanerophlebia*)											
	Pteridium	w	1	1		1			1			
	Pteris	w	4	3	1	3	1				2	
	Sadleria	e	(4)-5	(4)-5		1						1
	Schizostege	e	1	1		1						1
	Sphenomeris	w	1		1	1	1					
	Tectaria	w	1	1		1					1	
	Vittaria	w	1		1	1	1					
Marsileaceae	Marsilea	w	1	1		1			1			
Totals 10	37	3e 34w	168	119	49	135	65	5	16	6	28	15

The low percentage of Austral affinities is interesting in view of Dr. Copeland's (1939) derivation of almost all ferns from Antarctica, and in view of the much higher percentage in seed plants. Interesting, also, is the relatively low endemism and, particularly, the low ratio (1.24) of present species and varieties to original introductions.

Tables for the lower cryptogams were not prepared because of the lack of critical knowledge of these groups on the part of the compiler, and also because of the rudimentary state of available information on Hawaiian members of many groups.

These statistics from the two tables clearly support the commonly held idea that the flora is basically an attenuated Indo-Malayan one, but not nearly so predominantly so as previously thought. The American element, on the present basis, is stronger than the most commonly accepted recent view has held.

The picture, on the basis of the small number of original immigrants, the diversity of their origin and the important groups not represented, seems to be that of a flora that has always been insular. It is exactly the type that might be expected to be descended from a random aggregation of chance waifs carried overseas by a combination of factors such as storms, currents and birds. Of seed plants, an average of one successful arrival and establishment every 20,000 to 30,000 years would account for the flora. This is granting an estimate of 5 to 10 million years of above-water history for the entire Hawaiian chain, starting with the islands at the extreme northwest, such as Kure, Midway and Lisianski.

The preponderance of Indo-Pacific affinities seems satisfactorily explained by the number of islands in that direction as compared with the lack of islands to the east and north. The Austral element, too, is more or less in proportion on this basis.

If we resort to land bridges or continents to account for the presence of the Hawaiian flora, then we may well have to build them in all directions.

CHAPTER 4

DEVELOPMENT OF THE ENDEMIC FAUNA

> *Although I appreciate and admire the vast amount of experimental zoology that has been done within recent time, yet, when it is all considered, it does not give direct or indirect evidence enough to base a belief in evolution upon. This belief is based upon nature's own experiments, upon our studies of development, comparative morphology and anatomy of living and fossil animals, upon the geographic distribution in past and present time, and the time sequence as shown by fossils. Most of this information is the direct result of systematic zoology. . . . Yet we are constantly being told that systematic work is only worthy of inferior intellects, and that great intellects turn their attention to . . . other superior subjects.*
>
> —*Muir* (1924:480)

It has been shown that upon these oceanic islands of Hawaii there has been developed an array of endemic organisms characterized by certain features which mark the Hawaiian biota as one of the most distinct in the world. The extreme isolation of the archipelago has resulted in great restriction upon the types of organisms which have succeeded in reaching it and becoming established. We have estimated the number of ancestral immigrants and have found that only a relatively few individuals have given rise to the extensively developed groups of genera and species now existing here. It now follows that some discussion of evolution and the nature of the development of the biota should be included.

The contemporary endemic floras and faunas of the Hawaiian Islands are largely those which have developed upon lands which, for the most part, we can examine today. A fundamental problem is, therefore, an analysis of these floras and these faunas upon *this* land. It is not so much a question of the foreign ancestors of the contemporary biota as it is a study of the biota as it exists today. The rate of erosion is such that these main islands could not have stood here as they are longer than from a period late in the Tertiary. An attempt to place the main islands farther back in the geological time scale would be unsupported by geological facts. We are dealing with many specific complexes of plants and animals which owe their very existence to the developments which have taken place on visible insular landscapes or on those which can be reconstructed by the interpretation of erosional and topographic features. If it is admitted that geographical isolation is a factor in evolution, and that geographical and topographical barriers are of fundamental importance, then it must be admitted that such evolution as has taken place on a given island has come about through the interplay of influences which may have been brought about on the land upon which the organisms exist today. Moreover, the lesser phylogenetic categories, as well as some of the higher categories, resulting from such evolution must be admitted to be younger than some of the topography. We speak of "explosive" speciation resulting in the large complexes of species so common in the islands. I believe that these outbursts of species development have resulted in part from the late Pliocene and particularly the great Pleistocene erosion which has left such a spectacular and rugged topography in its wake. *New land open to colonization is conducive to speciation.*

INTER-INSULAR SEGREGATES AND EVOLUTION

One of the most commonly discussed features of the Hawaiian biota is the extreme isolation of certain of its components. There are a number of genera whose relationships appear to be so cryptic that no one has yet been able to discover anything closely allied to them outside of Hawaii. Various explanations are given to account for these phenomena, including the commonly expressed theory calling for a great, ancient, foundered continent, land area or bridge.

Various factors or combinations of factors have influenced the biota to produce these special results, and no one explanation can account for all of them. From my studies of island life, I have been led to conclusions which, it appears to me, may shed some light upon the intricate and perplexing problem. At the beginning, each of these islands was barren of life—each a sterile mound of steaming lava surrounded by ocean (fig. 7); so we must look elsewhere for the source of the original immigrant stocks. But where should we turn to discover the ancestral affinities of these many groups of organisms which are peculiar isolates, whose relationships are most cryptic and whose allies are masked or have been lost from the residuum of the evolution of Pacific biotas?

To account for some of the aberrant Hawaiian segregates, the following explanation is proposed. All of the Pacific island insect faunas which I have studied have their own characteristic developments. Thus, in the large weevil genus *Microcryptorhynchus* (more than 100 species described and many undescribed), which is distributed through most of the south Pacific from Australia eastward to the Marquesas and to western Micronesia in the north Pacific, most islands or island groups have characteristic divergent species or groups of species. For example, the only known species with well-developed sclerotic spines or tubercles at the bases of the elytra are found on Guam; the only smooth, shiny, black species are found on Rapa. Such great structural deviations are found among species of the Society and Austral Islands that a person unfamiliar with the group would be likely to place various species in different new genera, and some are so distinct that they might be placed in different tribes or even different subfamilies! As a matter of fact, some of these allied species will run to different subfamilies in existing keys in use in other parts of the world. These various species have developed and diverged in their isolation upon their respective islands. If one of these highly divergent species should happen to be carried by some agent of dispersal to another island and be successful in establishing itself, the new population set up might, given ample time and complete isolation, develop an entirely new group of divergent species, many of which might be utterly different from the basic stock that gave rise to the species on the ancestral island. If one of the more divergent species of the second population series is in turn isolated on another island, the process will repeat itself and the intensity of divergence will be increased. Now, if enough time has elapsed, the original island sources will have passed through a period of intense erosion and may perhaps be reduced to atolls, their characteristic faunas will have been exterminated and out on the newer island will be left peculiar segregates without obvious ancestral relationships. This theory may be elucidated by the diagram included as figure 27.

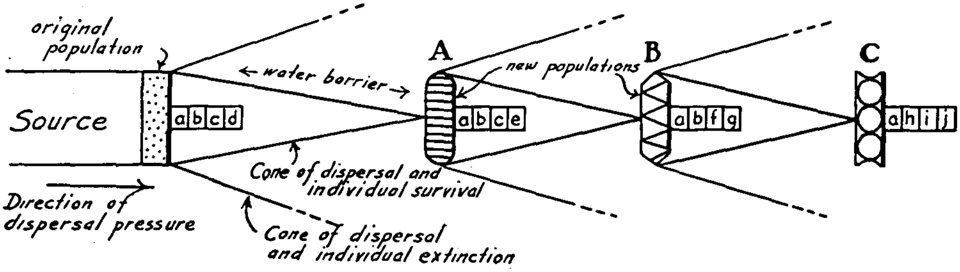

Figure 27.—A diagram to illustrate the theory of inter-insular segregate evolution as explained in the accompanying text.

A, B and C each indicate an archipelago. The lower-case letters in the squares indicate hypothetical characters of an organism, and the changes in letters indicate evolution and the divergent immigrant stocks which have populated A, B and C. According to Darlington's formula (1938:274), if the distance between Source and A, and between A and B are the same, and the chance of survival of an individual from Source to A is 1 out of each 1,000 dispersed, then the chance of an individual from Source reaching B is only 1 in 1,000,000 (compare fig. 28).

The diversity of the fauna, as based upon *suprageneric categories,* will be inversely proportional to the distance between Source and A, B or C. The greater the distance between any of these points, the more disharmonic will be the out-

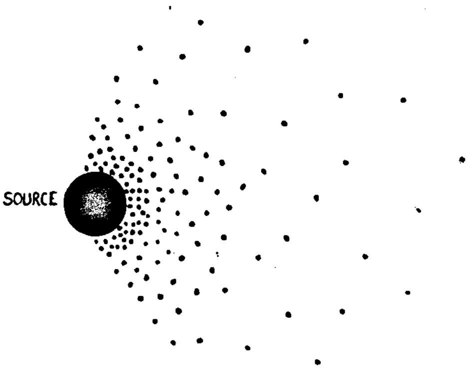

Figure 28.—A diagram to illustrate dispersal intensity. The opportunity of an island lying to the right of Source to be colonized by overseas dispersal is inversely proportional to the distance between it and Source.

lying biotas. The greater the age and isolation of C, the greater will be the percentage of endemism and the greater will be the peculiar forms of life. If A and B archipelagos are eroded away, and their terrestrial biotas thus exterminated, it may be difficult or impossible to reconcile various elements of C with Source. Thus, Hawaii appears to be in the position of C, with A and B now represented by coralline archipelagos. Time and extreme isolation are essential for the development of a biota such as that of Hawaii. One of the reasons why the Hawaiian biota is so unique and has so many endemic forms is because of its great isolation which was especially emphasized when some of the ancient routes of immigration were eliminated by the formation of atolls.

One of the most significant points to keep in mind here is the lifting out of a population (and quite possibly an aberrant population) a single fertilized individual from which may spring a new and isolated population series and eventually an array of forms. The impregnated female carries only the genotypes of herself and her mate, not the genetic make-up of an inbreeding species population. She does not represent an average of her population. The implications and potentialities of such action are great.

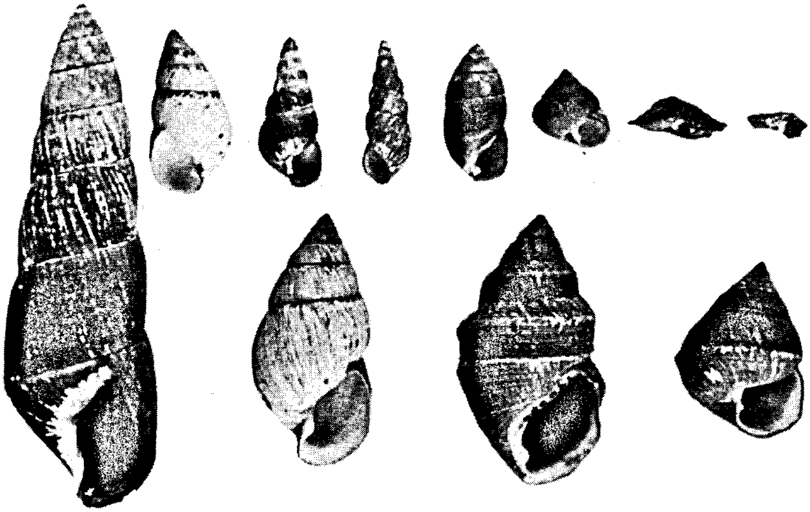

Figure 29.—Radiation within a single group of Hawaiian land snails. This plate shows the comparative sizes and shapes of 11 groups of Amastrinae. The snails in the top row, left to right, are: *Laminella gravida* (Ferrusac), *Amastra* (*Paramastra*) *turritella* (Ferrusac), *Amastra* (*Metamastra*) *textilis* (Ferrusac), *Amastra* (*Cyclamastra*) *sphaerica* (Pease), *Pterodiscus wesleyi* (Sykes), *Planamastra diginophora* (Ancey). Bottom row, left to right: *Carelia turricula* (Mighels), *Amastra* (*Amastra*) *violacea* (Newcomb), *Amastra* (*Armiella*) *knudseni* (Baldwin), *Amastra* (*Kauaia*) *kauaiensis* (Newcomb). All figures are natural size. According to the thesis developed here, it is believed that any one of these snails might set up an entirely new evolutionary line, if through the natural processes of the development of oceanic faunas it were introduced into a new area and succeeded in establishing a new population. If, for example, the extremes of *Carelia* and *Planamastra* were removed to new archipelagos of high islands with unfilled, favorable ecological niches and given time, is it not easily understood how they might set up such distinctive lines of radiating types that they would ultimately end in complexes equivalent to what we find today in the drepaniid birds and similar well-known developments? (I am indebted to Dr. Cooke for helping me to arrange this plate.)

We should not lose sight of the fact that every individual of a population differs in a number of ways (gene differences). Any change in the gene complex of an organism is reflected upon the other genes of that organism, and once a change is made it is believed that other changes may follow in a more or less geometric increase with consequent accelerating action on further change and ultimately on species formation. If this action be accompanied by conditions conducive to isolation and survival, then rapid and diversified speciation may follow. Islands are ideal places for such processes. We may have introductions, reverse introductions back to the original source and reintroduction upon reintroduction after time-lapses sufficient to change the original populations as well as the new (fig. 45). This may be repeated over and over again with consequent formation of large species complexes. This method is not restricted to inter-island segregation, but it may apply to mountains and ranges, to ridges and valleys, to dry and wet areas, to highlands and lowlands, to hostplants, and, in the case of sedentary land snails, perhaps even to different rock piles or to isolated trees.

A fundamental, inescapable fact is that we are dealing here with *small* populations—often unusually small populations. It is these small populations which restrict gene flow and encourage random divergence where nonadaptive characters can flourish, and these populations exist in an environment favorable to the survival of changed or changing forms. The loss of the power of flight in one of these populations, even if drastic and rapid, need not be detrimental to the changed population, for if that population is situated in a favorable niche, it may continue to thrive because in this particular instance the power of flight would not be vital to existence.

The isolated products of such inter-insular segregate evolution may lead some workers to the conclusion that a given present-day biota is of great age, whereas actually the contemporary biota may be in comparative youth and its distinctiveness is but a reflection of its mode of origin and development. Thus, to me the Hawaiian biota, although it is truly an old insular one, appears not to belong to geological antiquity.

This biota of Hawaii is "older than the rocks"—in a way. One of the most significant features of the development of our flora and fauna appears to have been overlooked in previous discussions. Those who have argued for great age for the main Hawaiian Islands (an age far beyond what geological facts allow for them), to account for the ultimate development of the biota, have advanced the opinion that this biota has developed entirely upon these present main islands or upon a hypothetical continental mass of which they are the remnants. This opinion is, in my considered judgment, a fundamental error. The biota as we know it today is in part the ultimate product of a progressional development which has moved and evolved along great insular archipelagos over periods of time much longer than the ages required for the development of the main Hawaiian Islands and their contemporary biota. Various genera and stem forms of groups of species may have evolved in islands—now atolls such as some of the leeward Hawaiian chain, the great Micronesian archipelagos, the Line Islands—which form the approaches to Hawaii. However, some of the genera and the bulk of the species known today have originated on our present main islands. This is obvious from their developments, distribution and interrelationships. Some have come directly from North America or elsewhere. The crux of this argument is that in contemporary Hawaii there are preserved remnants of a biota which has in part developed by unique methods and in which are preserved forms which are the end products of species chains that carry back, through archipelagos now worn away, to geological ages indeterminant.

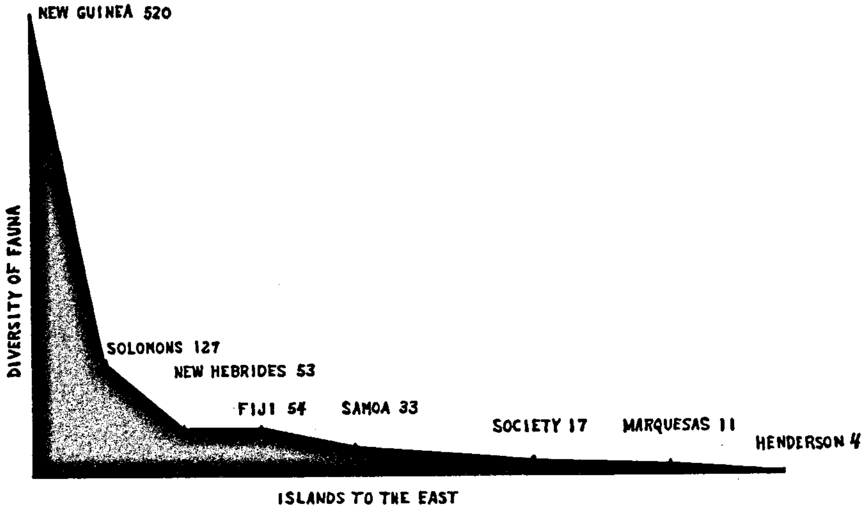

Figure 30.—A typical curve of progressive insular biotal deficiency in the Pacific. This chart shows the number of native land birds in several south Pacific archipelagos from New Guinea eastward. These data (from Mayr, 1940) are nearly complete. Similar curves can be drawn for most groups of organisms in the area.

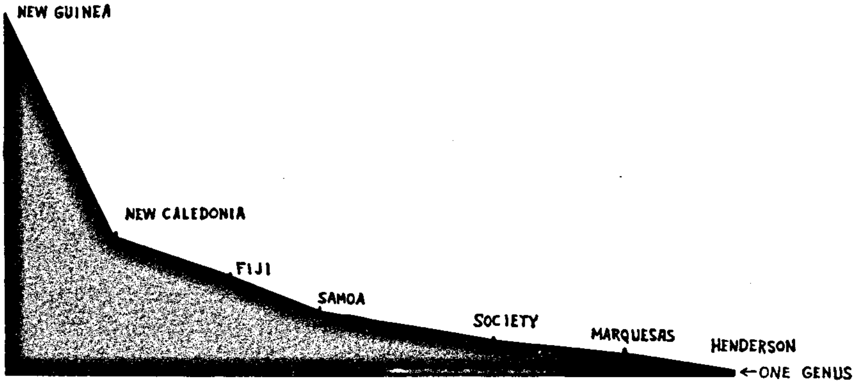

Figure 31.—A curve of progressive insular biotal deficiency derived from a group of insects for comparison with the preceding curve of bird distribution. This curve has been derived from an analysis of the genera of the weevil subfamily Cryptorhynchinae. The data from Samoa westward are incomplete and unsatisfactory, and the curve will rise much more abruptly on the west when our collections from the area are reported upon.

I believe that the great atoll chains of the Pacific may hold some of the now hidden clues to the stories of the magnificent biological development of Polynesia. Many of the peculiar endemic groups of the Hawaiian and southeastern Polynesian islands owe their existence, if not their very origin, to ancient high islands of the one-time splendid archipelagos now marked by clusters of coral reefs. Surviving lines of middle Tertiary and of perhaps even older continental faunas may have had their germ plasm filtered down through succeeding changing generations which have passed successfully through island maturity and degradation to atoll formation and have carried over to new high islands in different archipelagos. Thus, some supposedly old types such as certain land molluscs could have maintained themselves (but evolving) in insular isolation through long periods of time while their continental progenitors became extinct or restricted under continental conditions. Thus, for groups like the Aglycyderidae (Proterhinidae) with representatives on certain Atlantic and Pacific islands only, and for such isolated snails as the Tornatellinidae, we find a possible explanation for most peculiar types of distribution and development. Atolls have been overlooked, generally, because most of them are so alike floristically, faunistically and in outward physiographical appearance, because they are more or less biological deserts terrestrially and because they contain few or no endemics to excite the biologist looking for *new species.*

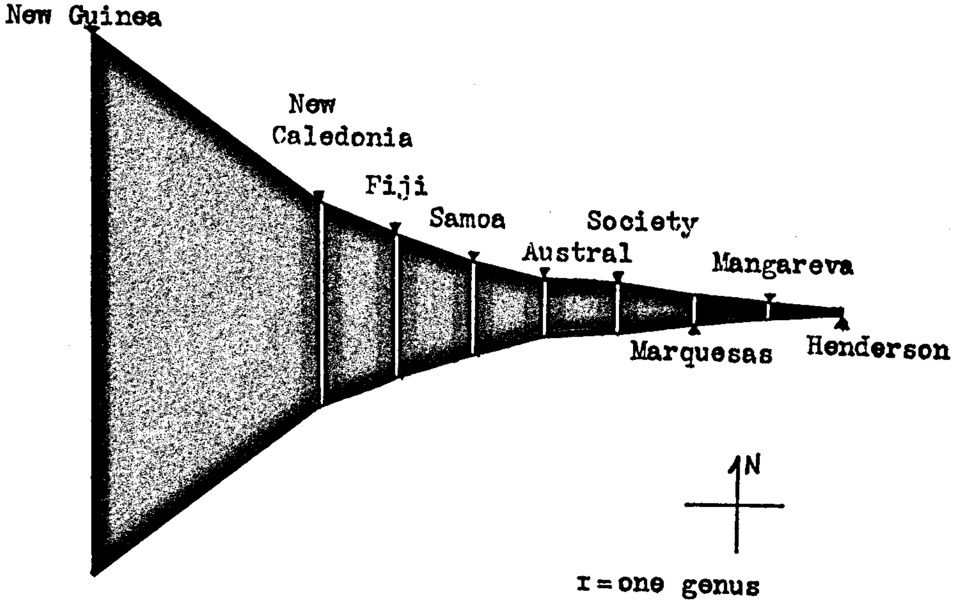

Figure 32.—A diagram based upon the same data as the preceding curve. If one turns the chart on its side so that the point is downward, it will appear as a great funnel fitted with graded filters, and one can visualize the ocean barriers between the islands acting as finer and finer sieves which progressively exclude more and more genera as one progresses from west to east. This chart is based upon several hundred species included in more than 100 genera.

GEOGRAPHICAL METAMORPHOSIS AND EVOLUTION

By their very nature, mid-Pacific high islands have comparatively fast-changing topographies. Speed of erosion is great, and the results achieved are remarkable. The comparative influence of topographic change upon the biota is not specifically known, but from the resulting patterns of evolution in the biota, it appears that the effect is great. Within confined land areas, the principle outlined in the discussion of inter-insular segregates and evolution may be applied to a lesser degree. When it is discovered that on one side of a river there are certain organisms which are different from allied forms on the other side of the river, it appears obvious that the river may have had some influence on the distribution and evolution of the respective forms. The same applies to mountain ranges, ridges and valleys. Moreover, if such barriers have acted upon or resulted in the differentiation that is observed, then the evolutionary products must be younger than the topographical features which exerted the pressure.

There is an old statement which is brought up whenever we speak of Hawaii in terms of geological youth. It is: "If you say that these islands are of late Tertiary age, then the fauna is older than the rocks!" To a degree, that is correct, for, if looked upon in a particular way, part of the fauna is older than these rocks. Is not the fauna of certain glaciated areas, in the sense of the land being capable of supporting a flora and fauna, essentially older than the newly uncovered land left after the retreat of the glaciers? Of course it is; and now in such areas there are groups of organisms which are known to be of pre-Glacial age—some of them are archaic—and which have maintained their lines elsewhere during glaciation. But, we can compare only some of the higher categories here in Hawaii. Because, if it is admitted that isolation is a major factor in evolution, then the species, and even some of the higher categories, must be acknowledged as being developed upon this land, and it must be admitted that such forms are younger than the rocks. To account for some of the supra-specific developments in Hawaii, reference can again be made to the chart and discussion of inter-insular segregates in the foregoing section (fig. 27). By such selection, isolation, development and extinction, it is considered that higher categories such as those represented in the Hawaiian biota may be accounted for. However, this theory is not proposed as a "cure-all," because there are many other factors at work now and others which may be recognized at some future time which must also be taken into consideration. But it is believed that this interpretation, or modifications of it, will be useful in aiding in the analysis of some of the peculiar developments of Hawaii.

It is considered probable that some of our unusual endemic genera were well differentiated in the Hawaiian area before the present main islands rose from the sea. An early development in the leeward Hawaiian islands when they were high and forested, and the subsequent passage of certain elements from those early faunas and floras to the new eastern islands as the western islands eroded down, are considered most possible.

Far to the south of Tahiti lies the unique, greatly eroded, isolated island of Rapa, and almost 50 miles to the east of it is situated a group of about ten almost unknown rocks called Marotiri or Bass Rocks. Most of these rocks are awash, but four of them rise precipitously to elevations estimated to be between 200 and 300 feet (quite similar in appearance to illustrations in figures 23 and 24). These rocks appear to be all that is left of an ancient island, probably similar to Rapa, which has been almost completely eroded away. All the exposed rocks serve as nesting places for myriads of sea birds, and the deposits of excrement and bird remains are thick. However, we found there a dozen species of plants, some of them distinct new species, and on some of those plants were found new species of insects and spiders. The insects belong to genera which are characteristic of the well-watered forests of high islands. I consider these species to be the last survivors of a fauna which had its beginning upon the slopes of a high, densely forested island, and believe these few forms, now eking out a most precarious existence and at the point of extermination, to be among the only species which were adaptable and fortunate enough to continue their populations through the very drastic changes brought about by the tremendous erosion, degradation and

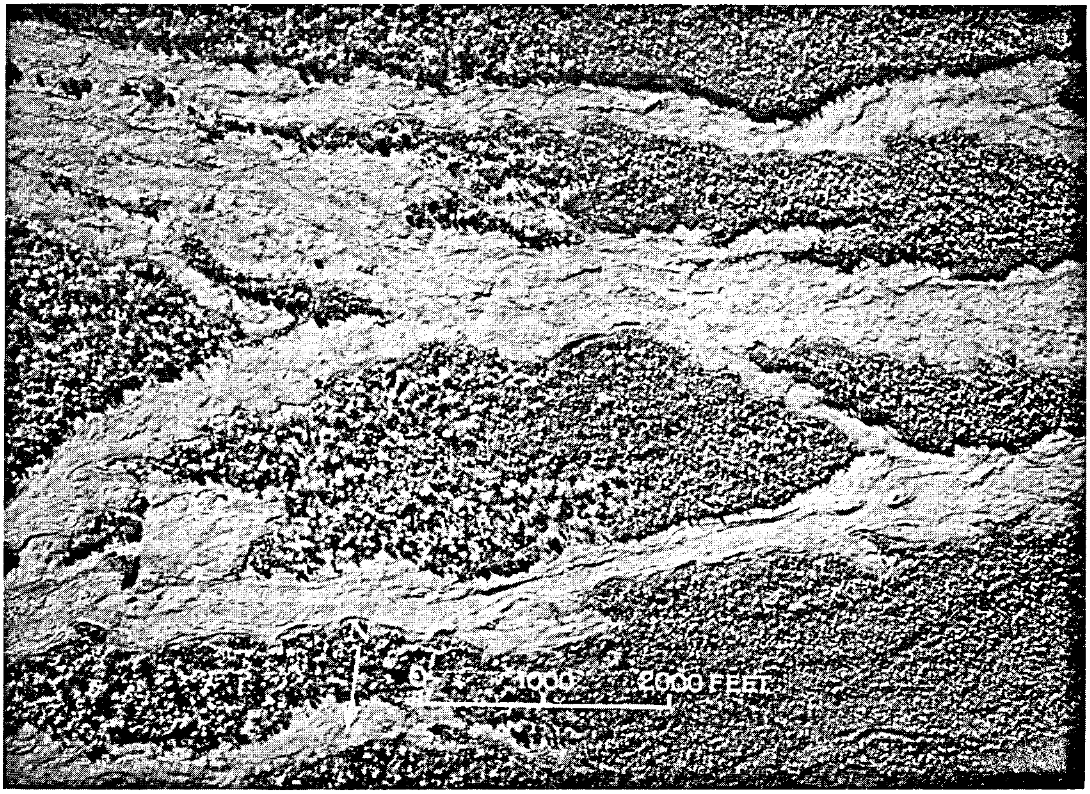

Figure 33.—A vertical air view of aa lava flows of 1916 and 1926, at an altitude of 4,000 feet on the southwest slope of Mauna Loa, to show appearance in a forest with an annual rainfall of about 50 inches. The gray color is caused by a complete cover of lichens. Note the "kipukas," or islands of forest cut off and surrounded by the lava flows. Compare the following figure. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

partial submergence of their environment. At least some of these Marotiri species stand by themselves in their genera. The dispersal of one of such peculiar species to a new and favorable locality may result in the development of a distinctive set of species which might in time be called a section of a genus or, in more time, a higher category. Marotiri cannot last much longer, for it has almost entirely returned to the sea, and soon all of its original terrestrial biota will be lost forever. Could not part of the unique biota that is found on Rapa today have had its origin on ancient Marotiri?

In these islands of Hawaii, built by successive lava flows and pyroclastic ejectamenta, the upbuilding process may in itself have exerted an influence upon evolution by isolation and extermination. A visit to the island of Hawaii, for example, where volcanic activity is at present continuing, will reveal "islands" of climax forest ranging from a few acres to many square miles in extent surrounded by great areas of barren lava flow "deserts" (figs. 33, 34). These "islands" are termed "kipuka" (key-poo-kah) by the Hawaiians. Within the kipukas are found plants

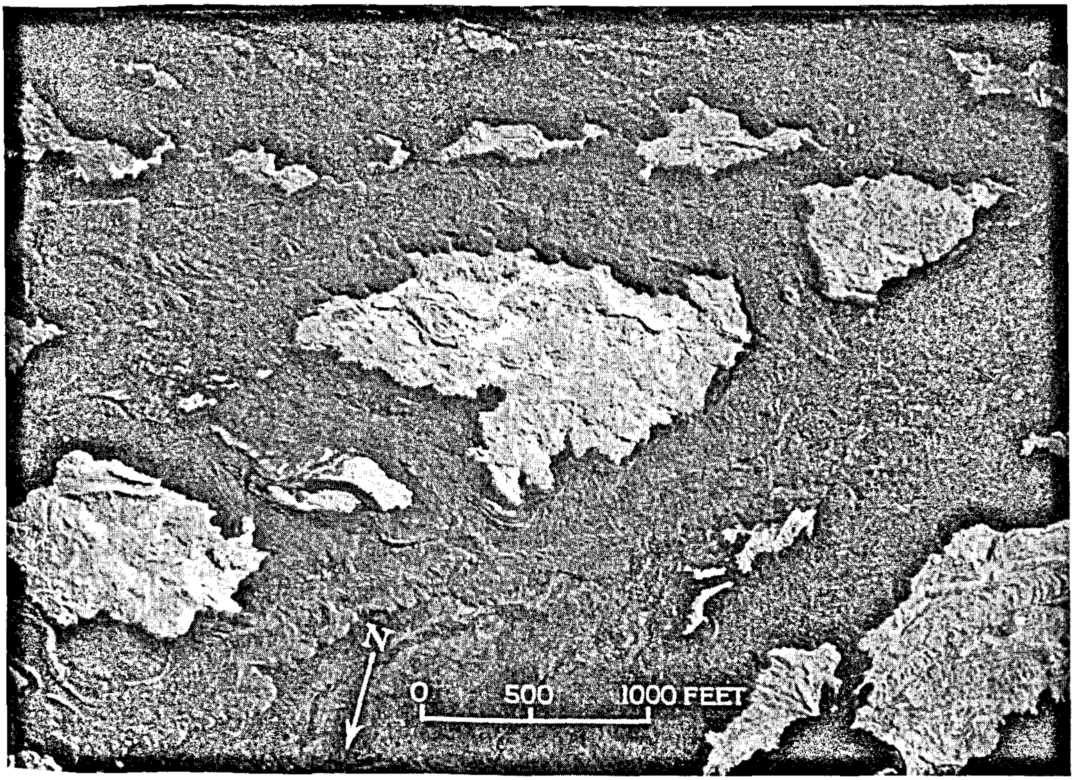

Figure 34.—A vertical air view of bare black aa lava flows of 1916 and 1926 at an altitude of 6,500 feet, six miles northeast of those shown in the previous figure and above the forest, where the rainfall is about 30 inches annually. Compare the previous figure, and note the contrast in the vegetation of the lava flows because of the differences in rainfall. (After Stearns and Macdonald, 1946. U.S.A.A.F. photograph. Cut loaned by U. S. Geological Survey, Honolulu.)

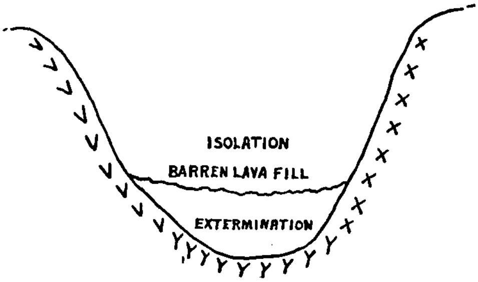

Figure 35.—Diagram showing how isolation may be achieved by recurrent volcanism filling the floor of an old valley with lava. The **V**, **Y** and **X** marks along the valley margins represent a population which is distributed in a linear manner along the mountain range and differs in some characters from right to left. It is presumed that the ancestral population spread into the area from the right.

and animals which have been cut off from the surrounding areas by the fiery rivers of lava which have killed and buried all living things in the area over which they have passed. The flows break up populations into series of small populations, sometimes over wide areas, and the long, bare, inhospitable flows form, for a time, barriers to population movement. Within one of these kipukas Rock found some trees which have been found only in a 56-acre "oasis." In this same kipuka the only known surviving individual of the remarkable tree *Hibiscadelphus giffardianus* was found. This endemic genus is evidently an offshoot of endemic species of *Hibiscus,* and three species from Hawaii and one from Maui have been discovered. Rock considered that the plant association found in the kipuka represented the type of forest which extended over a considerable area before most of it was wiped out by lava flows. Future lava flows may result in the extermination of

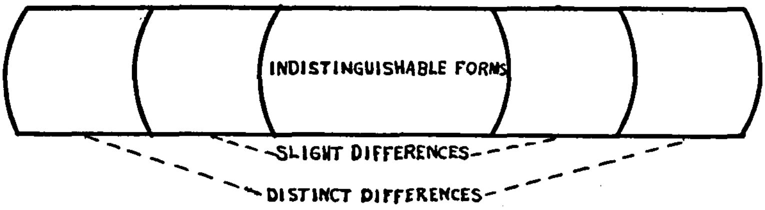

Figure 36.—A diagram of a "species chain." The vertical lines might represent ridges separating valleys including the major populations.

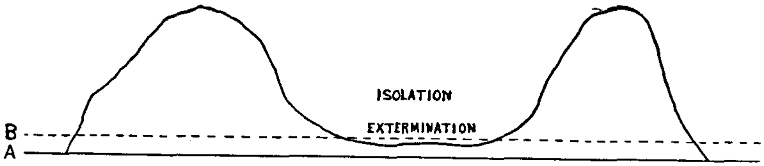

Figure 37.—Diagram showing how isolation of faunas of two mountain ranges may be achieved by a rise in the level of the sea. **A**, old level; **B**, new level.

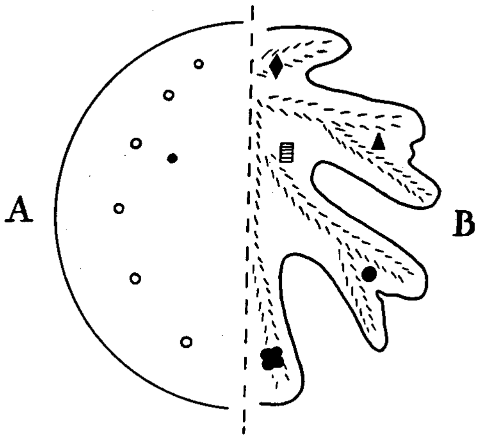

Figure 38.—A diagram illustrating changes brought about on an island through age, erosion and the subsequent isolation of changing populations on the dissected and rugged topography of the areas longest exposed to erosion. **A**, indicates a relatively new island area with little erosion and a species widespread over it. **B**, represents the area after a lapse of time sufficient to develop a rugged topography of deep valleys and high, steep ridges with derived, changed populations representing new evolved entities inhabiting isolated areas and/or different ecological situations made available by erosion, but not available on the new area at **A**.

some contemporary species. Giffard (1925:146), speaking of the *Oliarus* leafhoppers, said, "The maculate Kilauea examples of *inconstans,* with one exception, were taken by the author from mixed scrubby vegetation in an old crack or fissure in the arid desert hardly a stone's throw from the edge of the Halemaumau active crater. (This deep fissure was later filled up by the 1922 lava flow.)" The breadth of the lava flows varies considerably, but some of them are one to several miles across, as much as 10- to 30-feet thick and many miles long. Some few kinds of plants are quick to become established on new flows in areas of abundant rainfall, but it takes years for the forest to come back on the flows and develop a climax association once again. The rate of reforestation is, of course, dependent upon the locality, elevation and rainfall (figs. 33, 34).

If extensive volcanism recurred on a well-eroded island, the resultant filling of valleys and older surfaces would, if extensive enough, leave large areas of barren lava fields separating small "islands" of forest and could conceivably wipe out many species and subspecific forms and leave small isolated populations to persist in widely separated areas. The subsequent expansion and development of these species populations might be somewhat akin in character to the overseas dispersal heretofore discussed. If the forms of a single species were disposed in a linear manner along a mountain range, as A B C D E, and recurrent volcanism completely covered B, C and D, leaving A and E as distinct and isolated populations with the intermediate forms wiped out, we might have distinct species. Other workers have pointed out that the terminal forms of some species chains act as distinct species, but that through allied links in the chain, the two ends may be traced together by backtracking (fig. 36).

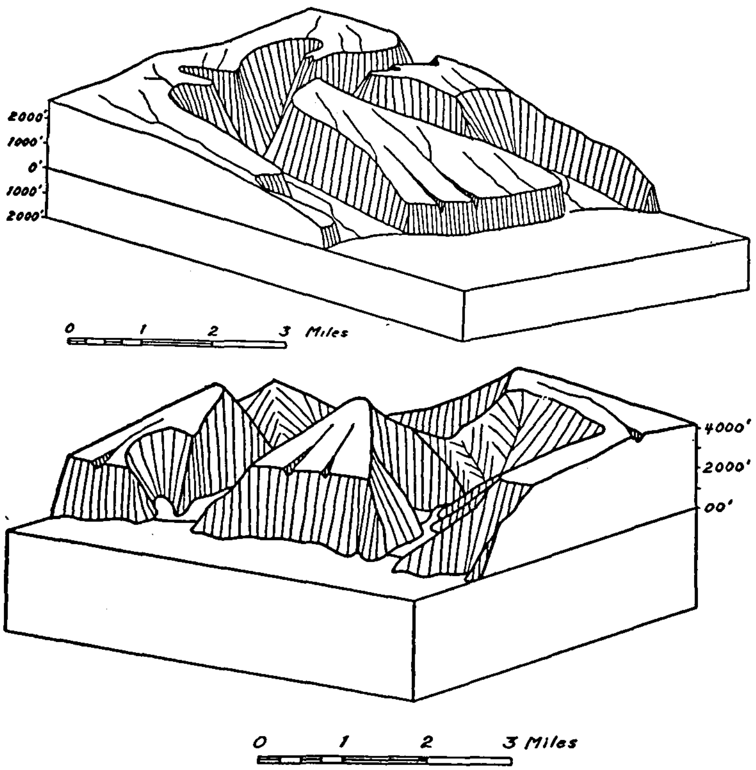

Figure 39.—Block diagrams illustrating erosional patterns in deeply dissected Hawaiian areas. These diagrams illustrate well the profound erosion and stream piracy which have left facet-like remnants of the original cone surfaces isolated by great cliffs and deep valleys. They illustrate also how populations of plants and animals may be isolated by the rapid erosion characteristic of the regions. Note that the facets consist of areas of only slightly altered sections of the original flow slopes of the volcanic mass. The top figure is of Waipio and Waimanu Valleys on Hawaii. The lower figure is of the Pelekunu–Wailau section of Molokai. (After Wentworth, 1928.)

On geologically Recent island areas, such as parts of the great island of Hawaii, many organisms, some birds excepted, have a particularly wide range. However, on the older island areas many species tend to have a much more restricted range. Also, the number of species, and especially divergent or very distinctive forms, are greater on the older areas. It appears that the break-up of some species goes hand in hand with the changes of topography brought about by intense erosion.

We may diagram this viewpoint as shown in figure 38. "A" represents a new, comparatively slightly eroded surface, with a species widespread over it. "B" represents the area after long erosion has cut it up into great ridges and deep valleys which contain isolated, different kinds of derived organisms.

It appears that some species may become widespread on a newly available area; then, because of inherent plasticity or other causes, they divide up into a number of forms which become further modified and isolated until new species are formed.

The rugged topography of our islands is conducive to such speciation. Some of our puzzling, complex species of Hawaii appear to be such forms. At every opportunity new forms appear to be established, and these intra-insular segregates are common in Hawaii.

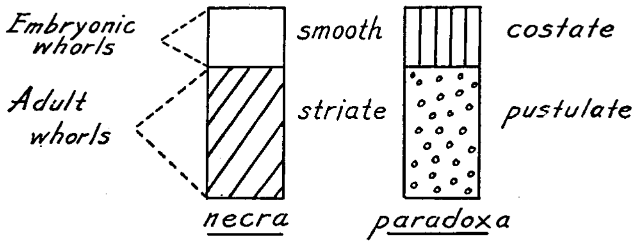

Figure 40.—The characters of *Carelia* used in the accompanying text diagrammed.

When we go into Hawaiian mountains in search of particular kinds of organisms, unless they be common, widespread species, we do not just go into the mountains anywhere. We select certain mountains, certain ridges, certain valleys or particular small areas at specified elevations and exposures in such regions. We know by experience that a given species found on one ridge will not be found on the next ridge across a certain deep valley. In other words, extensive field work has shown that many organisms are remarkably limited in their distribution to small areas in Hawaii. Some forms of Hawaiian land snails can only be found in localities which are to be measured not in square miles but in square yards. If a few species of land snails are brought to the Bishop Museum from a restricted area—from one clump of trees and ferns, for example—it is possible to tell the collector where the specimens came from, not only as to island or mountain range, but definite information on the elevation, side of valley or ridge and the character of the environment at the particular spot where the specimens were collected can be supplied! In some groups it is also possible for the specialist to predict where a certain species may be found when the only specimens known are the types which lack locality data. We take risky excursions to outlandish places because we know that in uniquely isolated, difficult-to-get-to localities we are likely to find peculiar new species. This all leads to the conclusion that, no matter how they act, topographic and geographic isolation do have decided evolutionary significance.

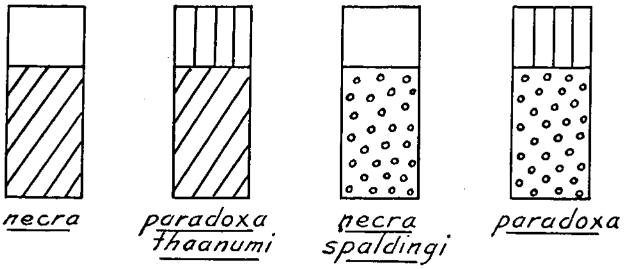

Figure 41.—Diagrams of the characters of *Carelia* and hybrids as explained in the text.

The Carelia paradoxa *Land-Snail Complex.*—On the eastern side of Kauai, at and near the mouth of the Wailua River, four kinds of *Carelia* snails have been found in Recent fossil beds. These four forms present a most interesting problem which has been outlined to me by Dr. Cooke. The four forms are *Carelia paradoxa, Carelia paradoxa thaanumi, Carelia necra* and *Carelia necra spaldingi.* The forms *thaanumi* and *spaldingi* have been called subspecies. The two species, *paradoxa* and *necra,* are separated from each other by the Wailua River. However, the subspecies are each found across the river from the typical forms. Thus, *paradoxa* and *necra spaldingi* are found on the north side, whereas *necra* and *paradoxa thaanumi* are found on the south side. The peculiar thing is not so much the distribution of the shells as it is their puzzling morphological characters. *C. paradoxa* has costate embryonic whorls and pustulate adult whorls. *C. necra* has nearly smooth embryonic whorls and striate adult whorls. These are represented diagrammatically in figure 40.

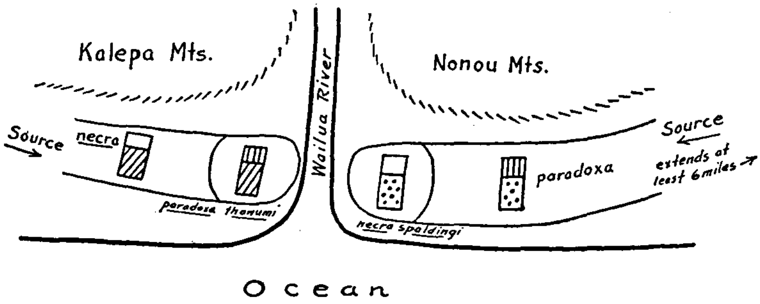

Figure 42.—The distribution of *Carelia paradoxa* and *Carelia necra* and their supposed hybrid forms.

These "subspecies" appear to be hybrids. Their morphological features are peculiar because *necra spaldingi* has the embryonic whorls of *necra* and the adult whorls of *paradoxa; paradoxa thaanumi* has the embryonic whorls of *paradoxa* and the adult whorls of *necra.* These four forms are diagrammed in figure 41 and a diagrammatical representation of the distribution of these molluscs is shown in figure 42.

It is noteworthy that the characters of the embryonic whorls, which are considered basic and most important for use in tracing phylogenetic relationships, are carried

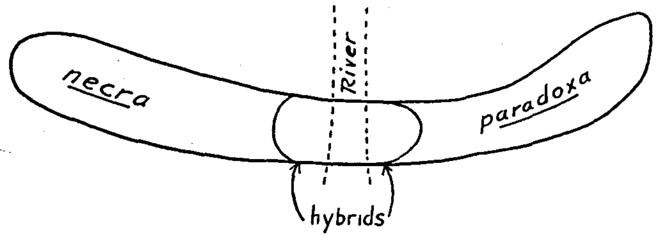

Figure 43.—A diagram to illustrate an alternate explanation of the development of the supposed hybrid populations of *Carelia necra* and *Carelia paradoxa.*

across, whereas the particular adult characters are found on one side of the stream only. Why should not some *paradoxa thaanumi* be found with *necra spaldingi* and vice versa?

There are two explanations for the distribution of these apparent hybrid populations. One is that the species approached the river and some individuals from both sides crossed the stream and mixed with the opposite species. The other explanation is that there appears to be reason for believing that the river once flowed southward (left on the diagram, figure 42) around the Kalepa Mountains and the two species met on undivided ground; then the stream cut through the mountains and separated the zone of hybrids as indicated in figure 43.

Unfortunately, these *Carelia,* and most of the other members of the peculiar genus, are now extinct or apparently extinct, and it is impossible to make as detailed a study of such interesting problems as is desired. There are only certain places where conditions favorable for the preservation of these dead shells obtain. These are in dunes and in sandy areas. Fossil shells do not last long in pure lateritic soil, and where there is no calcareous sand to preserve them, they ordinarily cannot now be found. Therefore, the distributions which I have indicated in the diagrams are partially diagrammatic reconstructions. The *paradoxa* group is considered the most specialized of *Carelia* as based upon the study of the embryos. About 1,000 specimens of the group were examined by Dr. Cooke.

Segregation of Lymnaea *Snails in Different Streams on Kauai.*—Dr. Cooke has supplied some notes which are recorded here as a most interesting case of segregation. A species of fresh-water snail (*Lymnaea*) was found to have both sinistral and

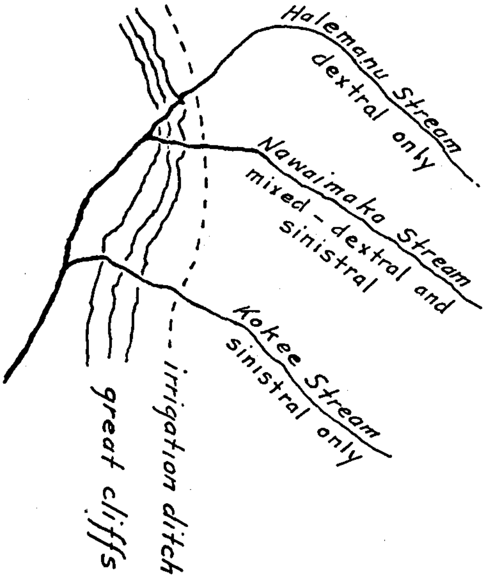

Figure 44.—A diagram to illustrate the distribution and segregation of *Lymnaea* snails in different streams on Kauai.

dextral shells in Nawaimaka Stream, but in the next stream to the south (Kokee) all shells collected were sinistral, and in the next stream to the north (Halemanu) all snails collected were dextral. These streams tumble over a cliff which is about a thousand feet high and then merge in valleys below. Unfortunately, the canyon area below the cliffs has not been adequately explored by shell collectors; it is difficult of access. An irrigation intake ditch has been built above the cliffs and taps each of the three streams mentioned. The most recent collections of snails from the streams show that the artificial breaking of the barriers between the streams has resulted in the mixing of shell types near the irrigation ditch in each of the three streams. It is assumed that the mixing up of shell types will gradually proceed headward until all of the streams are completely occupied by mixed shells. The diagram shown in figure 44 illustrates the problem.

SOME OTHER FACTORS OF SPECIATION

Single rules cannot be made to blanket all evolution. Each particular case must be considered as a separate problem. After proper study of each unit, the grouping of particular kinds or degrees may be made. It cannot be said, for example, that because host isolation has acted in the formation of some species it is the rule that must be laid down for all species. There is no reason why we should consider just one or a few methods as essential to the origin of species. What has taken place in some land snails with their sedentary habits may not be exactly the same in every instance as that which has taken place in volant organisms.

Speciation tends to be held within certain bounds, and it is only occasionally that great breaks occur which set up exaggerated species groups, new genera and the like. The all-important factor is whether or not a new type can survive and reproduce population continua which in turn specifically diverge to form species complexes. There are evidently certain limits of divergence outside of which it appears difficult to go and beyond which success is seldom achieved.

The more we study evolution, the more evident it appears that there are various ways by which new forms arise. We cannot hope to cover all phases of the problem here, but we should call attention to some examples which appear relevant.

There are two fundamentals which have to do with the origins of species upon these islands. One is isolation; the other is small populations. Most of our insular populations are small. Frequently, colonies of only a few individuals are the rule. Isolation is of various kinds and grades, but geographical and host isolation appear to be the types which are the most active or at least the most apparent causative factors here.

The environment, of course, plays an all-important part in the development of species, but there is more than one side to the question. It is generally agreed that profound changes have been effected on organisms by environment. There appears to be another factor involved here, too. From what I have seen in the Pacific, certain organisms appear to have selected certain environmental conditions, rather than being what they are as the result of environmental influence. For example, certain mutant forms which have arisen from causes other than environmental may search out niches best suited to them, and they adopt an environmental category.

One of the principal reasons why there are so many species in Hawaii is the division of the area into several large islands. If the main Hawaiian islands were a single land mass, I believe that species development would not have been what it is today. The division of the group has resulted in the duplication of species. What is now a group of six species which has evolved because of isolation, on each island from Kauai to Hawaii, might be only a single, wide-ranging species if continuous land were available.

The nature of the growth of the islands was, similarly, conducive to the multiplication of species. For example, the two mountain ranges of Oahu were at one time two islands separated by a narrow water barrier. We now find species on one range whose ancestors arose in the opposite range, apparently when the two ranges were separate islands. The faunas of the two areas are distinct, although they are now connected by dry land. The old elements are most distinct; some of the newer ones blend or cross from one range to the other. Molokai, Maui and Hawaii have had similar developments.

The old elements of Maui, Molokai and Lanai are quite distinct, one from the other. The channels between these islands are so shallow that geologists say that the three islands were connected by dry land not so long ago. This is reflected in the insects, because there are a number of forms which hardly differ on these three islands and many species are common to all. In fact, when discussing some groups, we may assemble the species of Molokai, Maui and Lanai and consider them as occupying a single island.

The separation of the islands brings into play the principles of invasion and re-invasion, (fig. 45). Much of the speciation which has taken place appears to have been the result of single individuals having been removed from one island and

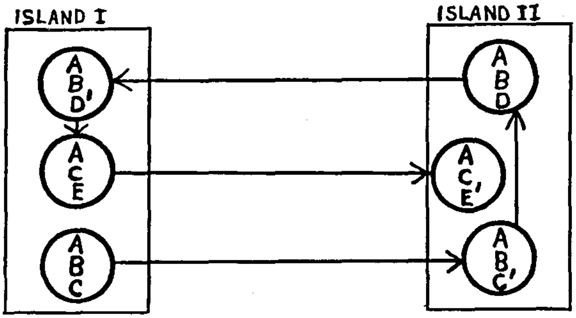

Figure 45.—A diagram illustrating the principles of invasion and re-invasion. The circles represent species, the enclosed letters, their characters. If a single gravid individual of population ABC becomes established on island II, that individual and the new population it gives rise to will not represent the average of all of the characters of population ABC; hence it is represented by ABC′ on island II. A lapse of time and continued isolation of the ABC′ population may give rise to form ABD. If ABD in turn invades island I, it may be so evolved as not to mingle with ABC, its original ancestral stock, and island I will have two distinct forms. This process may repeat itself many times over if conditions are favorable, and, of course, if long intervals of time are involved.

carried across an ocean barrier to another island where a new population was set up. This factor is of utmost importance. The new colony, beginning from one or a few individuals completely isolated from the parent stock, will early display certain differences. The new stock will have part of the characteristics and hereditary units of its ancestral population, but not all of them, and it is not an average of the base stock. It will be different from the average from the very beginning. This changing population might be swamped out if further invasion is made soon from its parent population. However, it may remain isolated for long periods of time, because of the infrequency of successful over-water dispersal. The longer it remains isolated, the more distinct it will become. In time, the new population will be so changed in character that even if another invasion is made by the parent stock, it will remain separate because it has become a distinct species. Over long periods of time, a series of invasions from island "A" to island "B" may be made. If these are made at sufficiently long intervals, then each invasion may set up a distinct species. After island "B" is colonized, the new changed populations may reverse the invasion route and return to the home island "A," where they would maintain themselves as distinct species which would in turn develop into distinct forms. Each of these new populations will, of course, come under the influence of local conditions and may diverge into additional species within each island.

The Hawaiian goose is, geologically, relatively a newcomer to Hawaii, but it remained isolated for so long after its ancestral *Branta* from North America colonized the islands that it developed a distinct form. It is already a widely differentiated goose which in form and habit is so distinct from its forebears that some ornithologists have placed it in a distinct genus.

The giant Hawaiian dragonfly, *Anax strenuus* Hagen, is an endemic offshoot of the wide-ranging Boreal *Anax junius* (Drury). A colony of *A. junius* was established in Hawaii long ago, and this colony remained isolated until it had diverged so much from typical *A. junius* that now it can be called a distinct species, as it really is. More recently *A. junius* has re-invaded Hawaii and succeeded in again becoming established. We now have these two closely allied forms living side-by-side but remaining quite distinct. As a matter of fact, the two forms are known to attempt copulation, but no hybrids are known to have developed, and the populations remain quite distinct and are differentiated easily. The endemic species tends to be more of a mountain species, whereas the later comer, *A. junius,* is mostly a lowland form which only rarely extends its range into the mountains. Perhaps when the islands were wooded to the shore line, the endemic *A. strenuus* was more widespread but adapted to a forest life, and as the lowland forests receded the dragonfly retreated with them. Dean Amadon has called my attention to the fact that the *Phaeornis* thrushes have invaded Kauai twice. An early invasion of Kauai followed by a long interval of time has resulted in the development there of a distinct full species, *P. palmeri.* At a more recent date, *P. obscura,* a species with subspecies on Hawaii, Lanai, Molokai and Oahu, found its way to Kauai and is now represented there by a subspecies.

It appears that most of the endemic groups have established themselves in Hawaii by a single chance invasion. However, there are certain groups which appear to have arisen from two or more invasions. One of these is the *Odynerus* wasp complex. Two lines appear to be represented here: an ancient one composed of about 100 species and a much more recent one represented by *O. nigripennis* and its three allies. The Hawaiian *Nysius* bugs appear to have developed from several invasions.

The developments within the islands reflect clearly the differences in the breadths of the channels separating them and hence the ease or difficulty of over-water colonization. Data on the breadths of the channels are given on page 7. It has been pointed out that some of the groups on the closely associated islands of Maui, Lanai and Molokai (Kahoolawe is included in this assemblage but its endemic biota is unknown because of early extermination) showed close interrelationships. The greatest over-water gap between the main islands is that between Oahu and Kauai (about 75 miles). A more isolated island may be expected to have a more distinctive fauna because it is less exposed to "pollution" by repetition of immigration. Kauai is richly endowed with well-marked and distinctive forms. In many groups, the species found on Kauai are the most divergent. Some birds which have subspecific forms on the other islands have clear-cut species on Kauai. All the *Odynerus* wasps of Kauai are endemic to Kauai, but all the other main islands have an overlapping of species. Some species of bees which are found on several of the other islands are replaced on Kauai by distinct species. A factor which also is involved here is that Kauai is considered the oldest, or one of the oldest areas, of the main islands. Certainly its greater age is reflected in its biota, but its greater isolation also has played a dominant role in its local developments.

Perkins (1913:xl) noted that:

> The extreme sluggishness of so many of the insects and mollusca leading to great restriction of locality, which we observe also in the birds must lead to extreme inbreeding. We have observed colonies of some of the flightless beetles to persist for years on a single tree and where these colonies are isolated from others, no doubt all the inhabitants have resulted from a few stray examples, probably often from one. While the food supply remains in suitable condition these isolated colonies thrive and become very numerous, but they are, doubtless, often totally exterminated when it becomes no longer suitable, unless, by chance, individuals can reach some other tree fit to supply a breeding ground. Obviously this sluggishness and restriction of range must itself diminish the numbers of individuals of a species, and the tendency of island creatures to limit their range and to specialize their habits is a striking feature of the fauna.

We might expect the loss of flight in a group to make it more subject to easy isolation and hence more liable to speciation. However, the presence or absence of wings cannot be correlated with rate of evolution. Of the four genera of insects in Hawaii containing over 100 species, *Proterhinus* with 181 forms is flightless, *Odynerus* with 105 is fully winged as are *Sierola* with 182 and *Hyposmocoma* with 216. Only 2 out of 14 genera containing 50 or more species are flightless.

One of the most wonderful fields of study in Hawaii is the hostplant relationships of the insects. The evolutionary role played by hostplants is a major and fundamental one. Usinger, in concluding his *Nysius* monograph (1942:162), said:

> The conclusion seems inevitable that geographical isolation or host isolation or both may be sufficient to set in operation the processes of species formation, while the biotic environment plays an all important role in determining the rate and limits of this evolution. A disharmonic insular area with great gaps in its environment allows many non-lethal mutations to persist, whereas a fiercely competitive mainland environment rigidly rejects all but the best adapted, thus favoring adaptive evolution by natural selection.

The host-specificity displayed among some groups is astonishing. We find such great host-specificity among the plagithmysine longhorn beetles that if we find borings in a species of tree unrecorded as harboring a species of the group, we conclude that the borings are probably those of a new species. Thus, some new species of these beetles have been discovered, and others are known only from their borings and may be captured and described sooner or later. The same applies to certain genera of leaf-mining moths. Dr. Swezey has described a number of species which were worked out in the field on this basis. We can almost predict from a perusal of the literature where one might go and on what plant he might look to discover new species of some genera.

Perkins (1913:lxvii) says,

> Very often, however, we find species, extremely closely allied, occurring habitually in the same locality and not geographically isolated. Thus, even within a few square yards, the three species of Longicorn beetles, *Plagithmysus darwinianus, P. lamarckianus* and *P. varians* occur. It is hardly conceivable that species can be more closely allied than these and remain distinct. Though so similar, the species keep quite apart. Each keeps to its own food-plant, and though occurring on adjoining trees the species do not mix nor interbreed. *P. darwinianus* has been found chiefly on *Sophora, lamarckianus* on *Pipturus, varians* on *Acacia*. We have observed great numbers of all these species in the field, but have never found even a stray specimen of one frequenting the tree affected by another or in company with it, even though these trees grew side by side. Thus these three species, though not geographically isolated, are isolated by their habits. I know no insects that could be more profitably experimented with by breeding in the field than these and other species of *Plagithmysus.*

The small leaf-mining *Philodoria* moths include at least six which are attached to the widespread endemic urticaceous tree *Pipturus albidus*. Most of these species are not known to overlap in distribution. Thus, one is known from Kauai; three from Oahu, two of which are restricted to small areas in different mountain ranges and one which is widespread; and two from Hawaii, but these occupy widely separated localities in different mountain ranges. Further collecting and study will probably reveal more species of this group localized in various places.

Giffard, in studying our leafhoppers, stated (1922:104) that

> The distribution shows the value of segregation in species formation, which fact is also shown by the lists of food plants. Those species living on two or more plants show much greater variability than those confined to a single host. When we consider the topography of the islands, the isolated distribution of many plants and the fact that so many species are represented only by short-winged forms or only an occasional long-winged form, we can see how isolation can take place even on the same island.

I have been impressed by the adaptation of the color of insects to the color of the plants they frequent. The relationship is not confined to phytophagous species, but also occurs in predaceous species. In Hawaii even predaceous insects are frequently confined to particular hostplants. This color relationship does not appear to be correlated with protection, because for many of the groups in which it occurs we do not know of any particular predatory pressure great enough to have a selective influence. This is a problem about which we have little information. Perhaps predator pressures were greater than we realize in certain groups. However, we feel that some sections of the fauna were never brought under any great pressure by predators.

Near the summit of Haleakala on Maui, I found specimens of the pale, silvery-colored native *Geranium tridens* growing with their branches intermixed with those of the dark-leafed *Coprosma montana*. On the pale *Geranium* were colonies of a very pale *Nesosydne* leafhopper. On the dark foliage of the *Coprosma* was a black species of the same genus! Although the branches of the two shrubs intermixed, the two leafhoppers kept to their own hostplants.

The pale-leafed *Pipturus* has a long list of insects attached to it. Many of these are strikingly pale-colored. On the leaves of the same individual plant at the same time we may find pale delphacid leafhoppers, pale cicadellid leafhoppers, pale mirid bugs, pale psocids and a pale predaceous nabid bug. Near it, and perhaps with the branches intermingled, a dark-foliaged *Metrosideros* tree might be growing. On the dark foliage we may find dark-colored leafhoppers, psocids, mirids and nabids in the same genera. The palest of all Hawaiian nabid bugs is *Nabis kahavalu* (Kirkaldy), a pale-green species. It is found on the pale-green foliage of *Sophora,* and with it on Hawaii are usually found swarms of a mirid bug whose color matches the pale-green of the nabid perfectly. Although predaceous, the nabid is confined to *Sophora.*

Our *Proterhinus* beetles closely match the colors of their hosts. Reddish species are found boring in red fern-frond stalks; dark species are found on dark-barked plants, and pale species on pale bark. The nymphs of the foliage-frequenting *Paratrigonidium* crickets are generally green, but the terrestrial and bark-frequenting species are brownish. Perkins (1913:ccxvii) reported that one of these crickets is so highly host-specific that he found it on only one variety of the multiform tree, *Metrosideros polymorpha.*

Our widespread *Acacia koa* has a remarkable pair of delphacid leafhoppers attached to it. The so-called "leaves" of the *Acacia* are not true leaves but are modified stems, called phyllodes. True leaves are only produced early in the tree's life, or from more or less adventitious shoots. The finely divided true leaves are paler in color than the phyllodes. On the phyllodes we find *Nesosydne rubescens.* A closely allied offshoot species, *Nesosydne koae,* is found on the true leaves. Each of these species is restricted to its particular part of the same plant. Each differs in the color of its nymphs and adults to match more closely the differences in colors between the phyllodes and the true leaves. The adults of *N. rubescens* are a rather greenish-brown when living; those of *N. koae* are pale-green. *N. koae* lays its eggs in young shoots; *N. rubescens,* whose ovipositor differs, inserts its eggs in the edges of the leaves and phyllodes. Here is an extreme case of isolation! These two species, although derived from the same stock, are structurally different; they live side-by-side on the same individual plant, separated only by the type of foliage they feed on; yet they maintain themselves as distinct entities.

A comparable case may be developed when the *Trioza* jumping plant lice (Psyllidae) are more carefully studied. As mentioned under *Trioza ohiacola* in my chapter including the psyllids, this species normally makes galls on the leaves of the hostplant. However, certain "abnormal" specimens have been collected from galls made on the stems. Perhaps the change of food indicates the beginning of a new form.

The long-legged dolichopodid flies are well developed in Hawaii, but they are comparatively poorly known. Dr. F. X. Williams has paid more attention to them than anyone, and the excellent information he has assembled indicates that a vast storehouse of ecological data remains to be uncovered concerning them. The species which hunt on the forest floor, those which are seen often on exposed patches of soil and those found on dull, shady tree trunks are dull-colored, usually brownish, species. The foliage-frequenting species often seen on large, green leaves in bright light tend to be greenish and bright-colored. The species which are found on dripping wet banks are likely to be bright metallic-colored to blend with their glistening surroundings. The species which frequent permanent streams are excellent and agile water skaters; those found on still ponds are fair to good skaters; but the species which hunt about areas where standing water exists only as temporary puddles, and the flies which frequent wet ground in the absence of standing water, are poor skaters.

Muir (1917:298) says:

> I believe that one of the first steps in species formation among Hawaiian Delphacidae is a change of food-plant. In many cases this will lead to isolation and may eventually lead to differentiation of the germ-plasm. Mr. W. M. Giffard brought to my notice the fact that certain species feeding upon more than one food-plant have two or more forms. At Kilauea, Hawaii, *Nesosydne ipomoeicola* is very common on *Lythrum maritimum* H.B.K. and *Sadleria* sp.; specimens from the former plant are on the average much darker than specimens from the latter. In the same locality *N. blackburni* from *Clermontia parviflora* and *Stenogyne* has a distinct green tint when alive which is absent from specimens off of *Pipturus.*

It almost appears that these animals tend to assume a color which blends with the background color of the hostplants because of some inherent, unexplained factor acting within themselves. Some species appear to "feel uncomfortable" when they are on a background other than their chosen one. It is of particular interest that not only do different, but allied, species differ in color on their different hostplants, but that the same species have different-colored populations on different hostplants.

The endemic leafhopper genus *Dictyophorodelphax* is an unusual, aberrant offshoot of a normal type of delphacid leafhopper. The head is drawn out into a great prolongation almost unique among delphacid leafhoppers of the world. No other Hawaiian group approaches them in this development. There are four known species, two on Oahu, one on Lanai and one on Maui. The entire group is restricted to plants of the genus *Euphorbia.* We expect that when other *Euphorbia* plants are examined carefully, especially on Molokai and Hawaii, additional new species will be discovered. Another noteworthy fact is that with one or two exceptions, none of the more than 130 known endemic delphacids is known to feed upon *Euphorbia!* A diverticulum of the gut is known to extend into the cephalic horn. Could this be associated with the type of food obtained from *Euphorbia?*

In the genus *Neseis* (a group of *Nysius* bugs), a compact group of forms has been segregated as the subgenus *Icteronysius.* All of these appear to be attached to the leguminous tree *Sophora.* These are the only bugs of 85 known members of the *Nysius* tribe in Hawaii which feed on a leguminous plant. The subgenus *Icteronysius* contains three subspecies, two found on Hawaii and one on Maui. It is of interest how the one on Maui was discovered. Usinger, in his monograph of the group (1942), stated that members of the subgenus would probably be found on *Sophora* elsewhere, and he left a request with Paul Baldwin, a National Park official, to search for *Nysius*-like bugs on *Sophora* on Haleakala, Maui. Baldwin complied with the request, and during an inspection trip found a new form, as Usinger had predicted. Other groups within the genus *Neseis* appear to have arisen through host isolation. There are four allied species including 12 subspecies all attached to *Pipturus.* A group of four species and six subspecific forms is attached to rubiaceous plants. Two allied species, one on Oahu and one on Molokai, have *Boehmeria* as their host.

Changes in habits may lead to entirely new evolutionary lines. Dr. Cooke tells me that in the highly developed Pacific land-snail family Tornatellinidae, a change from ground-dwelling habits to arboreal habits has almost always established new genera as a consequence. The drastic change from an aquatic to a terrestrial life has produced the most divergent of all the Hawaiian damselflies (see the discussion of *Megalagrion oahuense* on page 145). If this line could survive over a long period, a new order of terrestrial insect carnivores might be produced. The flightless hemerobiids (*Pseudopsectra*), discussed under flightlessness below, is a comparable case. If a population of any species can adapt itself to a new hostplant, it appears that a great advance toward a new form may have been made.

One of the principal facts which has occurred to me during my study of island life is that each problem must be considered as a unit in itself, for "laws" of wide scope do not always cover the multitudes of complex factors one meets. It is vastly different from the chemistry laboratory where we know that when we add "A" to "B" we will invariably get "C." The more years one spends on such study, the more involved the problems become and the more difficult it is to draw general conclusions.

In Hawaii we are dealing with relatively simple, disharmonic floras and faunas established in a favorable environment upon a rapidly changing substratum where environmental pressure (including predacity and parasitism) is reduced to a minimum. Great impetus and momentum have been given to the processes of speciation by the peculiar set of circumstances here displayed. The end result has been great proliferation of species and generic complexes with much radiation and diversification. It is as if a great vacuum existed and species are rushing in to fill every available unoccupied niche. There is even the tendency for some species to enter into environmental categories foreign to their families or orders. New habits arise independently—the non-parasitic bees have developed parasitic species; the aquatic damselflies have produced arboreal species and an astonishing terrestrial species; delicately winged Neuroptera have given rise to flightless "monsters" encased in coriaceous, armor-like, non-functional fore wings, and which creep and leap about in search of prey; the drepaniid birds have rushed in to fill gaps and now are represented by slender-billed nectar suckers, grosbeak-like seed crackers, heavy-billed fruit eaters, sharp-billed insect catchers, those of almost woodpecker-like habits and others almost parrot-like in habit (fig. 46).

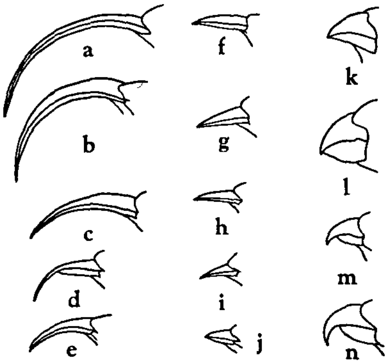

Figure 46.—Sketches of beaks of some drepaniid birds to show remarkable radiation within a single group of animals. *Loxops* (i) is considered nearest the ancestral type. **a,** *Hemignathus* (feeds on insects and nectar); **b, c,** *Drepanis* (nectar); **d,** *Heterorhynchus* (insects and spiders); **e,** *Vestiaria* (nectar); **f,** *Palmeria* (nectar); **g,** *Viridonia* (insects); **h,** *Himatione* (nectar); **i,** *Loxops* (mostly insects); **j,** *Ciridops* (palm fruits); **k, l,** *Loxioides* (mostly seeds); **m,** *Psittirostra* (fruits and seeds); **n,** *Pseudonestor* (wood-boring beetle larvae).

One of the most significant, if least heralded, of all discoveries relating to the Hawaiian biota is the finding of the terrestrial larva of the damselfly *Megalagrion oahuense* by my diligent, modest colleague, F. X. Williams. Who would have suspected that the nymph of this unique odonatan had, or could have, forsaken its ancestral aquatic habitat to take up a life completely foreign to its order and live on land? This species is the most divergent of its remarkable species complex. The nymphs, unlike those of any other known form, have adapted themselves to a life on land. They crawl about in search of their prey in the ground litter beneath dense clumps of fern (fig. 210 in vol. 2). The larvae are morphologically modified for such a life. The species has taken a great step from the typical aquatic habit of the Odonata. Is it not true that this peculiar species shows us how a new order of insects could arise? Here before us we have the essence of evolution. Given time, is it not possible that this unusual damselfly whose nymphs now crawl about on damp ground could give rise to a new and distinct group of terrestrial carnivores? I believe so. To avoid repetition, the interested reader is referred to the section under *Megalagrion oahuense* and to the introductory statements under the generic heading *Megalagrion* in the chapter on the Odonata in volume 2 of this work.

I have studied an undescribed leafhopper from Oahu which carries a complete story in itself, I believe. Although obviously (that is, to anyone thoroughly familiar with the Hawaiian members of the family) it is merely a peculiar specific offshoot of a species of *Nesophryne* (Cicadellidae), this species has developed such peculiarities of its cephalic structure that it can hardly be placed in the same subfamily as the species from which it has been derived! In fact, it cannot be placed in its subfamily by the use of the well-known keys in current use. A new genus may have to be erected for this species, and some workers would probably have to remove it from subfamily association with its progenitors or specific associates, or they would have to modify the existing subfamily characterization. One could hardly blame the taxonomist for following such a course. The "blame" lies with the aberrancy of the species. My contention is that such a specific segregate may carry within itself the potentialities of an entire new group and that these potentialities may be exerted if proper isolation and time factors are brought into play. Within this single species lies a potential new genus, new tribe or an even higher category of an assemblage of diverse forms. Here again, then, is evolution in the act dramatically displayed.

When we study these large species complexes—*Nesophrosyne, Nysius,* land snails and others—we see that there is included a large amount of specific variability of the very characters which elsewhere are taken as generic. There are species which appear to be plastic and unstable. This great insular proliferation is conducive to segregation of atypical forms in what appears to be rapid progression. Most of these changes appear to be nonadaptive. The taxonomist has great difficulty in classifying the species and frequently does not quite know whether he is working with species within a genus or whether he should divide them into groups and call the groups genera. If he starts on the latter course, he may find, when a large amount of material is examined, that the way is blocked by intergrades. It is a puzzle.

A confusing problem confronts the taxonomist when he is faced with the necessity for determining the status of the forms of one species which have spread over several islands too rapidly to have outstanding characters develop on the various islands. For example, certain species of *Oliarus* leafhoppers appear to have occupied several islands in a geologically short period of time, and although the populations of each island are isolated and distinct, the differences between the various insular populations are slight in degree. Other series of forms which are apparently similar in basic make-up are more distinct and are presumed to be older. In the Hawaiian insects all extremes of this development can be revealed by study, for some forms are so distinct that they might be called genera by some workers, others belong to the rank of superspecies, others to species and subspecies, still others are difficult to classify and some may be called "varieties." Many of these complexes defy explanation and definition, and we must ultimately accept the fact that each group, whatever it may be, must be studied and dealt with as a unit or set of units which has acted in its own way upon certain lines, and that general, over-all attempts at definition of evolutionary procedure, "laws" or "rules" are not feasible.

It is noteworthy that in some insect genera which are widespread in the Pacific, those species found in Australia with its continental environment and pressure are fewer in kinds and tend to be more stable and of more conservative nature. Out in Polynesia the multiplicity of species and their radical morphological diversity and aberrancy are astonishing. It appears that once unfettered in isolated insular environments the evolutionary potentials of some of these organisms are unleashed. This is particularly well displayed in the weevil genus *Microcryptorynchus.*

Displayed before us in the biota, there is every degree of differentiation from original ancestral stocks. Forms range from those, such as the strawberry, which have not been in Hawaii for a long enough time to become distinct from their immediate ancestors, to those which have hardly differentiated from their stem species and which may be exemplified by the short-eared owl, *Asio flammeus,* a Holarctic form, whose Hawaiian representative is called the subspecies *sandwichensis.* The Hawaiian hawk has diverged more from its parent stock, and it is considered a full species derived from *Buteo swainsoni.* From these and similar examples in other groups, we might list a whole series of intergrades of increasing distinctiveness to end up with genera which are so unusually distinct that they cannot, with our present knowledge, be allied to any known group outside of Hawaii. The large genus of weevils, *Oodemas,* falls in this category, together with an extensive list of other genera which I shall not attempt to include here. The drepaniid birds, together with the amastrid and achatinellid land snails, were formerly classed as endemic families, but, with our expanding knowledge, we have learned that they belong to known families. However, they are apparently quite distinct enough to be called endemic subfamilies. Several groups are evidently distinct enough so that they may be assigned to endemic tribes.

With basic data from Mayr (1943), we may list some of the birds found in Hawaii in the order of their probable periods of invasion of Hawaii from the most recent to the earliest:

1. Black-crowned night heron, a non-endemic American form, but resident here.
2. Short-eared owl, an endemic subspecies.
3. Hawaiian hawk, an endemic species.
4. Hawaiian crow, an endemic species, but farther removed from its ancestral form than the hawk.
5. *Phaeornis,* an endemic genus of thrushes.
6. *Moho* and *Chaetoptila,* remarkable endemic genera of honey eaters derived from one immigrant.

7. Drepaniinae, a spectacular endemic array of highly evolved, widely radiated genera from a single immigrant.

Such facts as these show plainly that overseas immigration has been a continuous, long, slow process which has extended down to recent time.

Usinger in his study of Hawaiian *Nysius* bugs (1942:160) assembled his notes on this phase very nicely when he said,

> All stages in the process of divergence may be seen at the present time. Thus the various species in the endemic genera fall into a series, ranging from (1) the widespread and variable *Oceanides nimbatus*, not yet broken up into distinguishable forms on the various islands, through (2) the scarcely differentiated *Neseis saundersianus*, to (3) the "polytypic species" (Huxley, 1938) or "Rassenkreis" (Rensch, 1929) *Neseis nitidus*, then to (4) the "supra-species" (Huxley, 1938) *Neseis hiloensis* (at least as regards the Molokai and Oahu forms), and finally to (5) that which Huxley (1938) has called a "geographical subgenus" and Rensch (1929) has called an "Artenkreis," namely the *Neseis mauiensis* and *fasciatus* group with allied species on the older islands.

INDEPENDENT ORIGINS AND DEVELOPMENT

From examples I have seen among oceanic organisms, there appear to be two major "types" of genera. One is a monophyletic line which springs from a single species and diverges from that base. The other is of polyphyletic origin, and the same "genus" may arise in two or more places at different times from different stem species. The monophyletic genus may be a very strong entity. The second type might be called a genus of the taxonomist who must have ways and means of grouping and classifying the myriads of population units confronting him. More often than not, he is unable to ascertain whether a group is monophyletic or polyphyletic. However, I do not feel that these sections are mere products of the taxonomist's imagination. Certainly, they are very real things, but genera vary in intensity as do species. Some genera are very "strong" segregates; others are weakly differentiated. It must be admitted that some are merely convenient, artificial or arbitrary assemblages created by taxonomists to enable them more easily to pigeonhole or separate ultimate units. Long periods of time and extinction of intermediate forms remove such categories as the last-mentioned one. A point I wish to make here is that in our island populations we have examples of both extremes as well as intermediates, that such developments are natural evolutionary products and that they do not exist in the minds of men alone.

As an example of a genus which has arisen from one species, we may cite our wonderfully developed *Megalagrion* damselflies. This local group is presumed to have developed from a single ancestral immigrant, and the descendants of that parent stock now form a local species complex.

The peculiar, flightless hemerobiid genus *Pseudopsectra* (figs. 47 to 51) is a good example of a genus whose members have not sprung from one stock but which have developed independently along similar lines to form a complex of flightless species with certain features in common. Some workers unfamiliar with the unusual local conditions and the history of this group might split several of these flightless forms off as separate genera, but I doubt that such a procedure is necessary or desirable. The intermediate forms cause confusion. There are no intermediate forms between the volant ancestral stocks and the flightless derivatives, however. It is of interest that the name *Pseudopsectra* was chosen because there is a continental genus, called *Psectra,* in which the hind wings of the female have become abortive, indicating a similar trend but with less intensity than in our Hawaiian group.

The delphacid leafhopper genera *Nesorestias* and *Nothorestias* (see under Delphacidae), although making up compact genera, are each polyphyletic. *Nesorestias* contains 2 species, each of which has been derived from a different group of *Aloha* species. *Nothorestias* contains 3 species (one undescribed), and these all have been derived from different ancestral stocks.

H. B. Baker (1941:358) in discussing the development of the Polynesian microcystine land snails said:

> While, in general, their distribution and relationships conform with the theory of evolutionary divergence, certain remarkable convergences almost look as if some branches of their subfamily tree had inosculated and produced stocks of double origin. For example, some species of both *Philonesia* and *Hiona* develop a left shell lobe in the Hawaiian islands, although this structure is not produced in any of the other Microcystinae except *Kusaiea frivola* [from the Caroline Islands] and *Lamprocystis moalana* [from Fiji]. Again, the epiphallus in the species of *Hiona* (subgenus *Insulorbis*) from the Society Islands considerably resembles that in the species of *Lamprocystis* (subgenus *Avarua*) from the Society and Cook Islands and that in the genus *Microcystis* from the Cook and Austral Islands. While the production of a new line by hybridization of such divergent animal stems seems to have happened rarely, if ever, in nature, it might be most apt to occur if members of related island groups were accidentally brought together. Because the forms of each island are geographically segregated, divergence may result from lack of interbreeding but does not require functional inability to produce such crosses.

Usinger (1942:119) notes that in the *Nysius* bugs of Hawaii a "wider range of characters is exhibited . . . than in the combined *Nysius* fauna of the rest of the world. Such characters as form of bucculae, length of rostrum, and shape of costal margins, which are fairly reliable guides to genera elsewhere, break down completely in the various extreme species of Hawaiian *Nysius.*" Similar statements can be made for many of the better-developed groups of Hawaiian insects.

A number of species from several geographical regions, and which have not had a common ancestry, have been assigned to the psyllid genus *Kuwayama.* This genus is obviously polyphyletic, and the species assigned to it appear to have developed their combination of characters independently from the widespread genus *Trioza* or one of its derivatives. Some of the Hawaiian species show a tendency to revert toward the ancestral *Trioza* type.

Parallel development appears to have occurred among the prosopid bees, because it is improbable that the European and Asiatic species which can be assigned to *Nesoprosopis* have the same ancestry as the Hawaiian assemblage.

Among the tornatellinid land snails, *Lamellidea tantalus* from Hawaii has been almost duplicated by a species in Rapa, about 3,000 miles away at the opposite end of the distribution of the family in eastern Polynesia. Although these two species have assumed shell characters which would appear to place them in the same genus, their internal anatomy indicates that they belong not only to distinct genera but to different subfamilies! Both species live under lichens on the bark of trees.

The ground beetle genus *Colpodes* (widespread in the Pacific) has given rise in Hawaii to some species which Dr. Sharp (1903) referred to the non-Pacific genus *Platynus* because they so closely resembled certain American *Platynus*. The superficial resemblance is due entirely to a parallel development, and the two groups have no close affinities.

The only endemic bees found in Hawaii belong to the hylaeid genus *Nesoprosopis*. We believe that the present complex of 55 forms has arisen from a single immigrant Asiatic stock. This local complex has developed species and groups of species which have radiated from the stem form to such a degree that they might have been called different genera had Perkins not assembled such careful data on their interrelationships. However, the most remarkable group is one which has independently developed commensal or semi-parasitic habits. Five allied species which have sprung from a single stem species constitute the semi-parasitic group. The normal-type bees store honey and pollen on which their young feed, but the commensals have lost their industrious habits and lay their eggs in the fully provisioned nests of certain industrious species. The females of the industrious species have well-developed structural modifications which aid them in gathering pollen, but in the commensals these structures are degenerate. Two principal nesting sites are chosen by the industrious species. Some species make their nests in burrows in the ground, others make theirs in hollow stems or in wood and some utilize both situations. Peculiarly, the semi-parasitic forms attack only the nests made in the ground. Although they are not host-specific and may lay their eggs in the nests of more than one host species, they are not known to attack nests other than those made in the ground.

There is a greater development of *Odynerus* wasps in Hawaii than in any one area inhabited by this nearly cosmopolitan genus. Most of our species utilize existing holes, such as old beetle borings and crevices in rocks, for nesting sites or they bore into wood or burrow in the soil. However, *Odynerus oahuensis* Dalla Torre is unique, because it has become an insect potter and has developed the habit of building complete, free, mud cells. "It is distinguished for its architectural ability, standing alone in this respect among the Hawaiian Odyneri whose nesting habits are known. Nor does this habit appear common among *Odynerus* in other parts of the world." (F. X. Williams, 1927:453.) A similar, free, mud cell was found on banana at Kipahulu, Maui, by Dr. Swezey, but its maker remains unknown.

Many insects the world over have developed flattened bodies better to fit themselves to their environment. Fleas are laterally compressed to enable them to slip between the hairs of their hosts. Many kinds of insects are dorso-ventrally depressed to enable them to forage beneath close-fitting dead bark of trees. Among our endemic delphacid leafhoppers, there is one species, *Nesodryas freycinetiae* Kirkaldy, whose nymphs have become independently modified to enable them better to live between the closely fitting leaf blades of the climbing *Freycinetia* vine. Of all of the 139 native delphacid leafhoppers, this is the only one I know which has developed a flattened nymph.

In the crane fly family (Tipulidae), one Hawaiian species has developed a habit which, insofar as is now known, is unique for the entire group. The larvae of our *Limonia foliocuniculator* (Swezey) (Swezey, 1915:87) mine the living leaves of *Cyrtandra* (Gesneriaceae). Tipulid larvae mostly dwell in the soil or in decaying vegetation, and some are aquatic. The leaf-mining habit is a remarkable new development.

A similar abnormal development has taken place in the large weevil genus *Proterhinus*. The normal larval habit of these species is to bore in dead wood or dead bark. However, at least three species have developed leaf-mining habits on Oahu. One of these mines the leaves of *Astelia* (Liliaceae); the other two attack *Broussaisia* (Saxifragaceae). Another species bores in the living stems of *Broussaisia*.

The true bugs of the genus *Saldula* (shore bugs) are mostly riparian in habit. One unusual species is reported to inhabit dry heaths in Europe. In Hawaii, however, species have developed arboreal habits. It is quite a surprise to one who has collected these bugs along stream and lake banks of a continent to come to Hawaii and beat them out of shrubs and trees!

The endemic leafhopper genus *Dictyophorodelphax* is unique in that it has developed a great prolongation of the head (see the figures under this heading in volume 4 of this work). This gives the species the appearance of such fulgorids as *Scolops*, and although the genus is closely allied to other Hawaiian genera, it has quite a different appearance.

The spectacular radiation and development of new types among the drepaniid birds has already been referred to (fig. 46).

It is noteworthy that many of the derived forms of the Hawaiian fauna are much more restricted in range and habit and are much more sensitive to change than are those which most closely resemble or represent the original stock. As an example, the native land birds most successful in meeting changing modern conditions are the *Chasiempis* flycatchers, geologically the most recent of the perching-bird invaders of Hawaii. The old, specialized drepaniids have been vanishing with startling rapidity since white man colonized the islands.

FLIGHTLESSNESS AMONG HAWAIIAN INSECTS

Endemic development of flightless species has occurred in the Orthoptera, Thysanoptera, Heteroptera, Homoptera, Neuroptera, Lepidoptera (?), Coleoptera, Hymenoptera and Diptera. Some remarkable examples of independent loss of the powers of flight exist here. Perkins (1913:xlviii) has given an excellent review of the subject, and I shall refer only to some of the problems and a few of the examples.

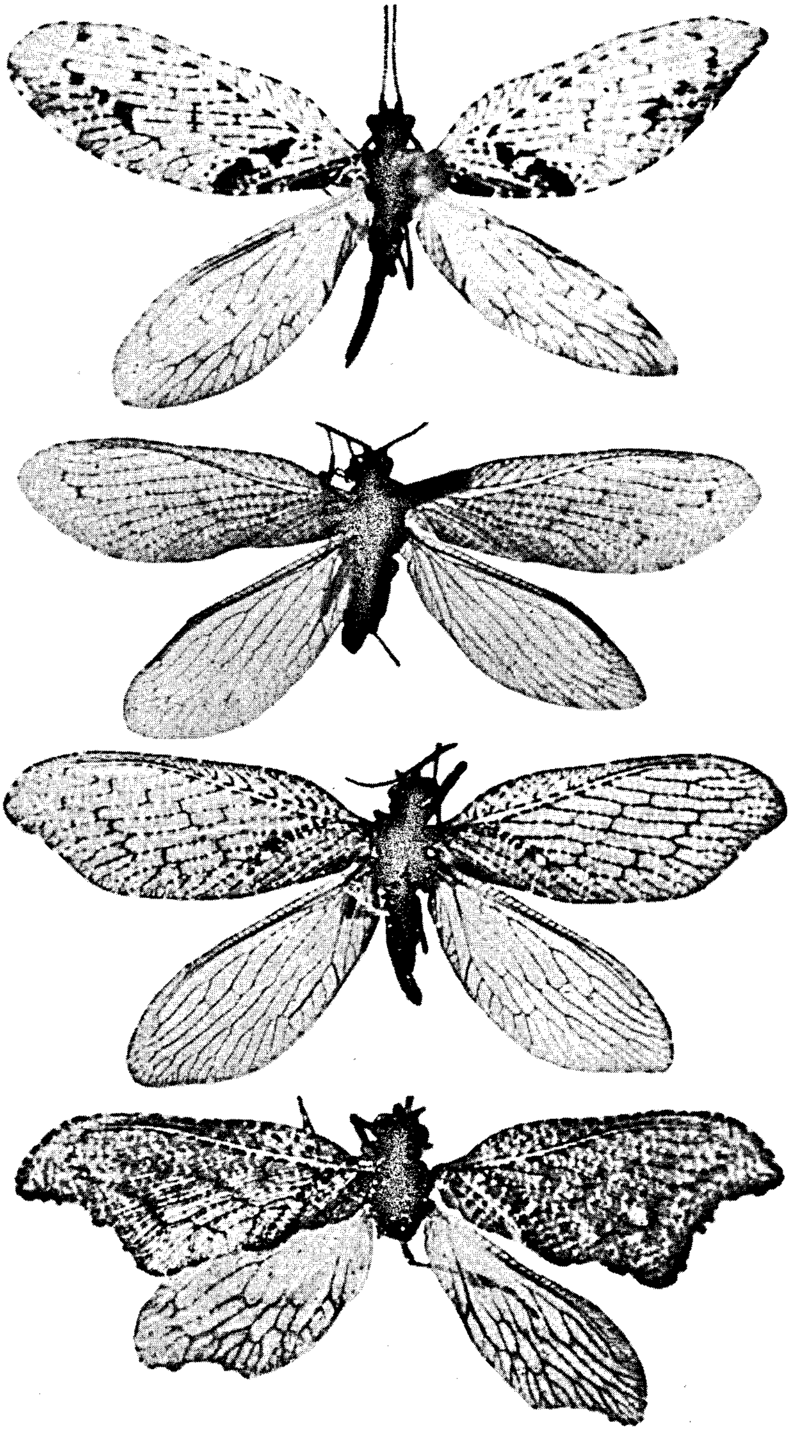

Figure 47.—Four species of *Nesomicromus* to show the transition between the rounded wing tip (top) and the angular type (bottom), for comparison with the accompanying illustrations of the flightless derived hemerobiids. According to the opinion now held, several of the flightless species appear to have evolved independently from such varied types of ancestors as the types figured above. From top to bottom the species are: *Nesomicromus bellulus* Perkins (the right fore wing is slightly turned under at the apex), *N. rubrinervis* Perkins, *N. vagus* Perkins, *N.* species near *drepanoides* Perkins.

I cannot believe that selection has caused the loss of wings because winged individuals are likely to be blown off the islands. These islands are not mere rocks. I concur completely with Perkins' statement (1913:1):

> Nearly all the flightless endemic insects are inhabitants of the forest, or if they frequent exposed situations like some of the Carabidae, they are closely related to species that frequent thick forest and are equally flightless. There is no ground for supposing that in these islands, as has been suggested for flightless insects inhabiting other Oceanic islands, the wings have been lost or degenerated through the agency of natural selection, as being a source of danger, if used on small land areas, where flying insects are supposed to be liable to destruction from being blown out to sea.

The development of our flightless species appears to have come about through the survival of individuals with hereditary abnormalities. They have not been selected because they are better fitted—they have been fortunate in being developed within a friendly environment with quantities of food so easily attainable that the loss of the powers of flight has not been a form of "lethal mutation," and they have had no enemies which might overwhelm them. Certain mutant forms with aborted wings can often survive simply because they do not need wings to get about and to get their food. They need not travel far to obtain what they need and to procreate. It is the ability of certain flightless forms to survive, rather than selection acting against flight. It is probable that had these mutant forms occurred in the rigorous environment of a continental area, they would not have survived. Our present human society harbors, feeds and protects the feeble of mind, the maimed, the chronically ill and the blind. These individuals would have had little or no chance of surviving in environments in which human society existed not so very long ago. The flightless insects of Hawaii are the descendants of cripples which survived only because in these insular environments biotic and environmental pressures are reduced to a minimum, and conditions have been favorable for their survival. They are "hopeful monsters" arisen under circumstances in which there is hope.

Some of these flightless species which were successful under primitive Hawaiian conditions have recently succumbed to new biotic pressure brought about by the introduction of predators which are foreign to the Hawaiian biotal balance. Some of us have searched intensively under the very trees where Dr. Perkins procured a series of the flightless fly *Emperoptera mirabilis* Grimshaw but have never been able to find a single example of the species. It appears that this remarkable fly is now extinct—at least in the type locality—because it was unable to withstand the new pressure created by the invasion of its environment by immigrant predaceous ants.

Flightlessness is not something which has occurred rarely and which developed single lines of flightless forms, but flightless species have arisen within the same group of Hawaiian insects at different times and at different places. Also, flightless species have arisen locally from flightless species whose ancestors in turn were fully winged. The flightless *Emperoptera* fly described from Perkins' Oahu collecting arose independently and from quite a different stock from the one I described from the deep highland rain forest of Maui (Zimmerman, 1938:145). Lamb (1909) described another in the same family from the subantarctic islands of New Zealand. The remarkable flightless *Nabis* bugs appear to have arisen from several local stocks (see the text under *Nabis* and the illustrations in volume 3 of this work). I have chosen the flightless lacewings (Neuroptera: Hemerobiidae) to illustrate this section.

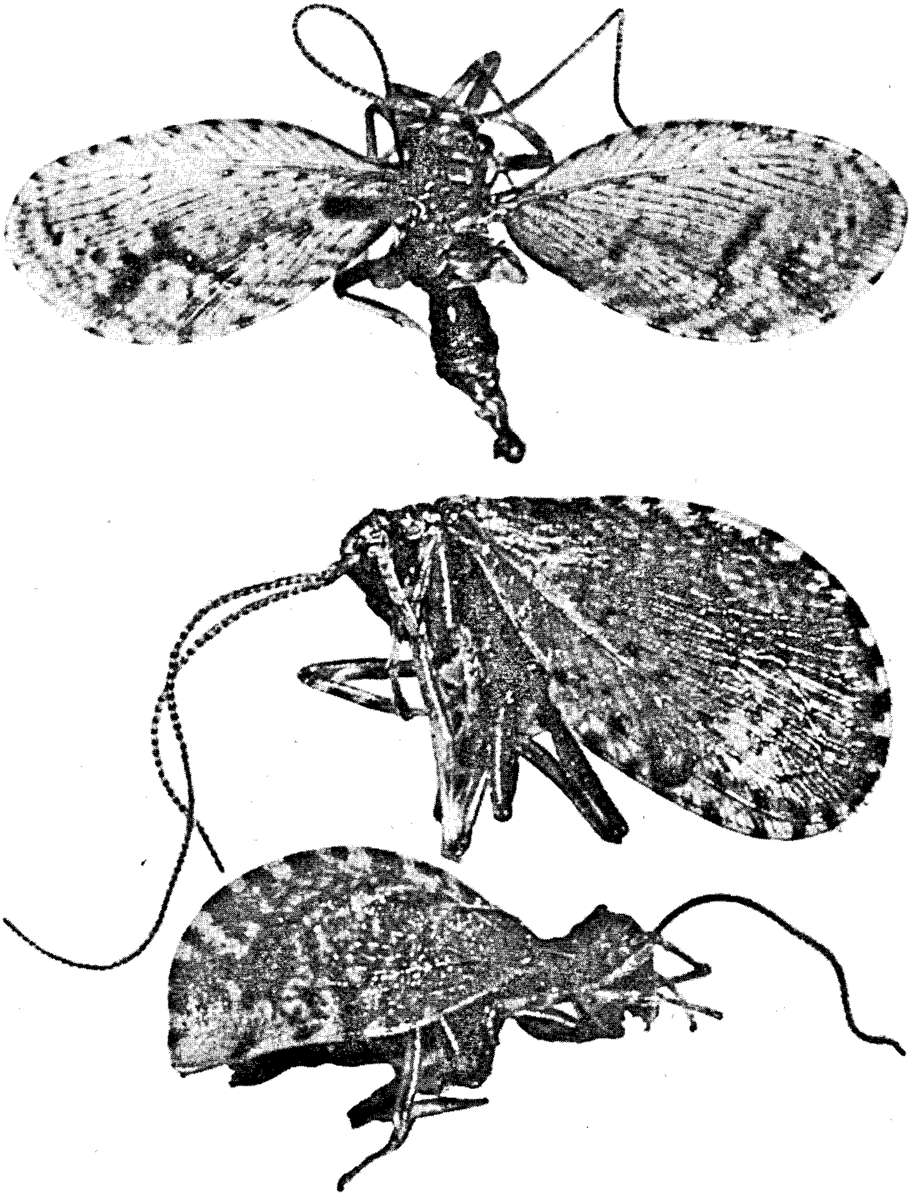

Figure 48.—Flightless endemic Hemerobiidae: *Pseudopsectra lobipennis* Perkins, top and middle; *Nesothauma haleakalae* Perkins, cotype, bottom.

There have been six species of flightless hemerobiids discovered in Hawaii. One of these is from Kauai, one from Oahu (undescribed because the material was lost in the field and it has not been re-collected), three from Maui and one from Hawaii. These species are very distinct, one from the other, and each appears to have developed from a different ancestral *Nesomicromus* (a large endemic genus) at a different time and at a different place. The species of *Nesomicromus* fall into two main groups on the basis of the shape of the fore wings. One group has the

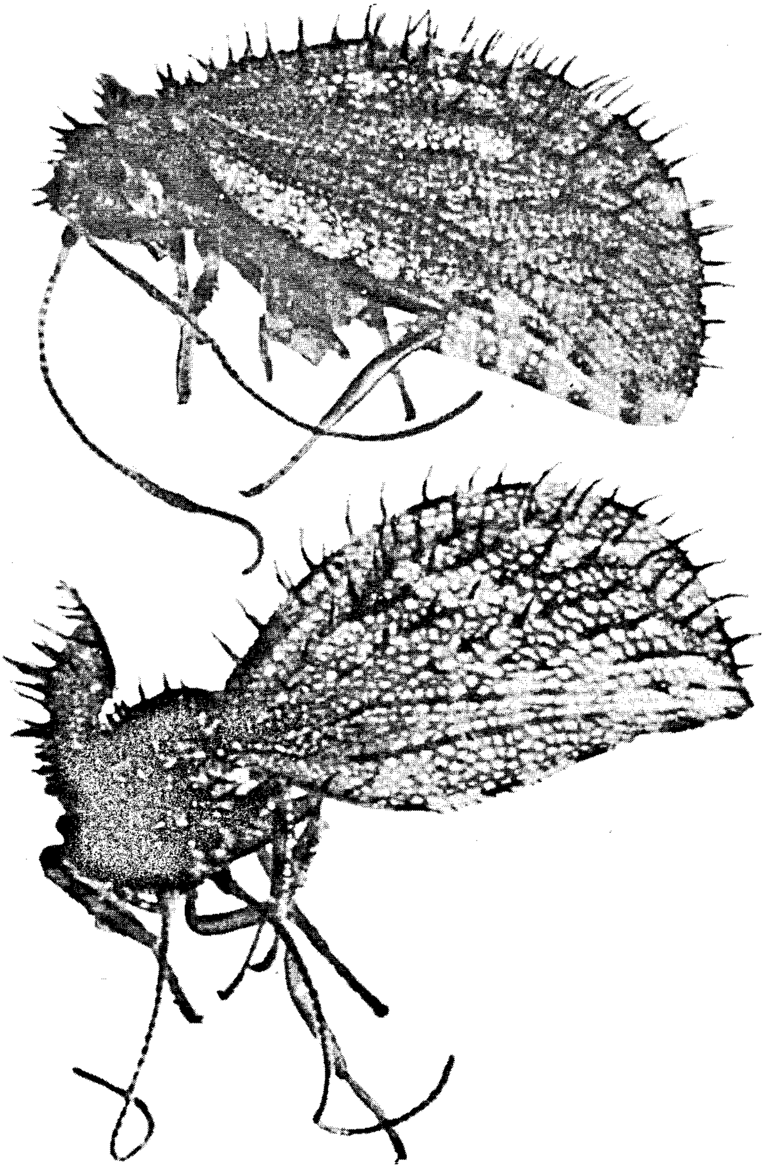

Figure 49.—*Pseudopsectra cookeorum* Zimmerman, a flightless hemerobiid with unusually well-developed, specialized setae.

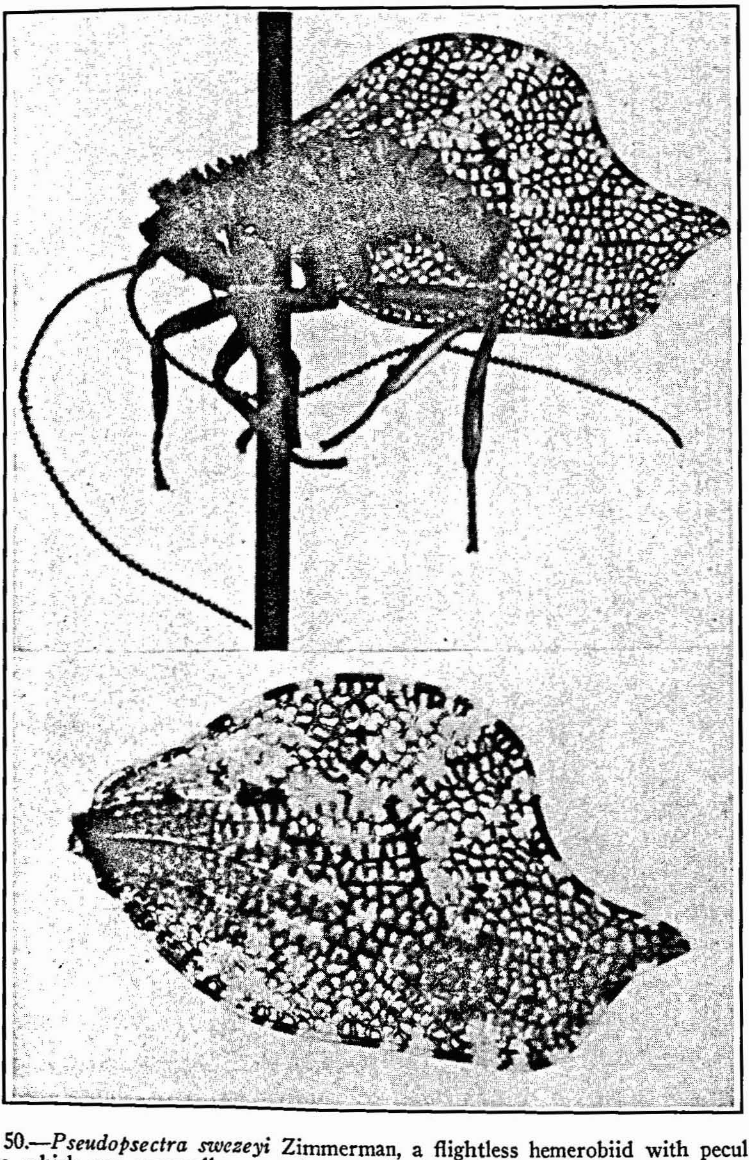

Figure 50.—*Pseudopsectra swezeyi* Zimmerman, a flightless hemerobiid with peculiar angulate wings which are unusually coarsely net-veined.

apices of the fore wings rounded; in the other group the margins are concave, at least at the apex, and some of those with the concave apices also have the posterior margins sinuous. The former group is the more abundant. The illustrations (fig. 47) represent these groups clearly. The remarkable *Pseudopsectra swezeyi* Zimmerman has arisen from an angulate winged ancestor, but all of the other species have arisen from the section with rounded wings. On the five described species of *Pseudopsectra,* the hind wings are reduced to minute fleshy flaps. On the single *Nesothauma,* no hind wings can be found. The length of the hairs of the body and wings varies among the various species of *Nesomicromus.* On some the hairs are conspicuous, but on others they are minute and are hardly discernible. The same applies to the flightless derivatives, but a further advance is made. On *Pseudopsectra cookeorum* Zimmerman the fine hairs have developed into very large, rather grotesque, bipartite spines (see fig. 49).

The volant *Nesomicromus* fly from plant to plant in search of prey. The flightless species crawl about on mossy logs and limbs and frequent low foliage in their food hunting.

The wings of the volant species are delicate and lace-like, but the flightless species, in addition to having their hind wings abortive, have the fore wings

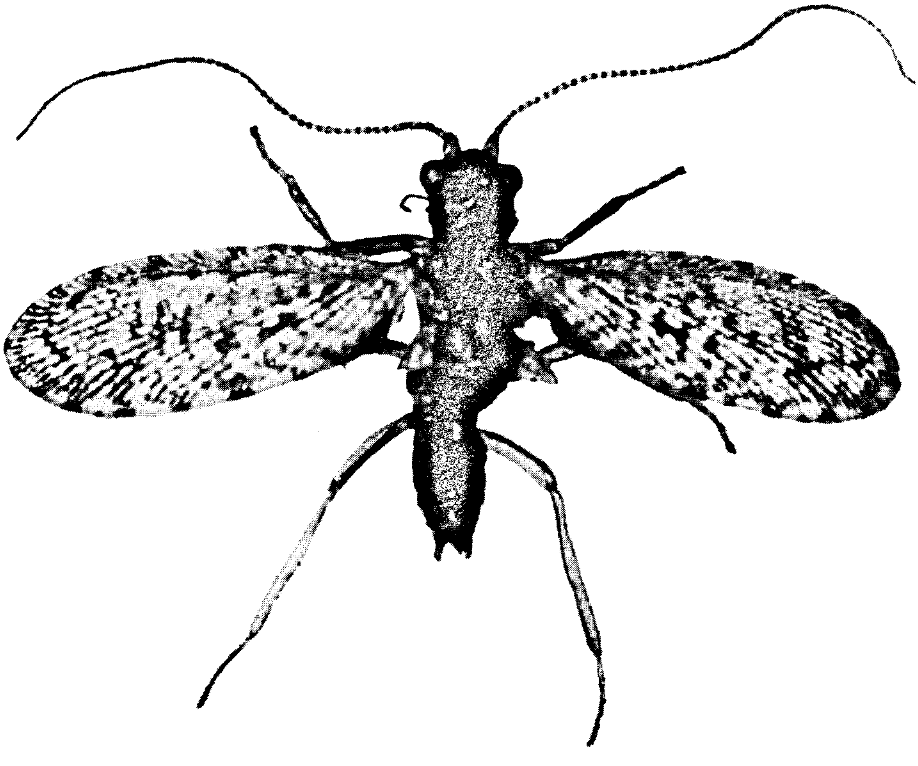

Figure 51.—*Pseudopsectra usingeri* Zimmerman, a flightless native hemerobiid with rounded wing apices.

reduced and greatly thickened. The venation is confused with the veins thickened and with multitudinous cross-veins. The wings tend to be heavy, coriaceous shields for the body and are not a far cry from the elytra of beetles. It is of interest that a rather similar tendency to coriaceous wing development is displayed by our flightless endemic *Nothorestias* delphacid leafhoppers—a group in an entirely different order.

Given time and opportunity, one or more of these grotesque "hopeful monsters" might well give rise to a successful new descendent line which might evolve further into a distinctive new group. One can visualize what might happen if a single gravid example of one of these extreme species were to be carried to and left undisturbed through a long period of time on a new archipelago of high islands which had an array of unfilled ecological niches and was uninhabited by competing groups or overwhelming enemies. Here, again, is displayed before us dynamic evolution carrying the same potentialities which have given rise to the world's floras and faunas, present and past. Here is the way a new order of organisms might arise.

PREDACITY AND PARASITISM IN THE ABORIGINAL FAUNA

As we should expect, the predator and parasite pressure in an insular area such as Hawaii is comparatively low. It is low because of the great difficulties involved in overseas dispersal and colonization. It has been only of very rare occurrence that phytophagous organisms have managed to cross the sea and become established here, and rarer still have been the successful invasions by predators and parasites. The arrival of predators and parasites without the previous establishment of suitable hosts obviously would lead to the early death of any successful immigrants. One would not expect that insect predators and parasites could accompany the original colonizations of their insect hosts for obvious reasons—the most important of these is the small number of hosts arriving at any one colonization period. A single bird immigrant might bring with it lice, mites and worms which could be passed on to its young because of the parental care necessary to rear them, but this would not be true of insects.

There is a sequence of events which much be followed in the population of any new island. Very soon after emergence from the sea, certain of the cryptogamous plants are able to establish themselves. Then, as the rock disintegrates under rain, wind and plant action, higher plants slowly become established as conditions become suitable for their survival. Ecological niches for a large number of kinds of plants do not become available until a long period of time has passed. Conditions change rapidly in the nature and complexity of the new forest as new kinds of plants become established and begin to spread. Only after suitable hosts have occupied the area can animals become established. One would expect that land snails would be among the first land animals which could find food and shelter on a new island. Certain insects, such as some of the small lichen-feeding moths, would be the first to be able to thrive. The speed of development of the biota would increase geometrically with time. Carnivores and parasites could not become established until suitable hosts were fairly well developed in numbers and in area, but it usually does not require much time for a newly immigrant species to increase to large numbers if there is an adequate food supply.

The predaceous groups of insects in the endemic fauna are as follows:—

Odonata: The dragonflies *Anax* (1 species), *Nesogonia* (1) and *Megalagrion* (27) feed mostly on aquatic insects and on insects which accidentally fall into the water. It is improbable that the pressure they brought on the endemic insect fauna influenced speciation.

Heteroptera: *Oechalia* (15 species) (Pentatomidae) prey upon various caterpillars, and some also attack certain leafhoppers. They are a rather restricted group. Only a few (2?) reduviid species are native. The Nabidae, however, contain a large complex of *Nabis* species (25 described) which are the most important of the predaceous Hemiptera. Only a few Anthocoridae are endemic (*Lasiochilus* 5, *Lilia* 1), and these probably prey upon such insects as psocids and thrips. The Saldidae (6 species of *Saldula*) are rather local insects.

Neuroptera: The 26 *Anomalochrysa* chrysopids and the several genera of Hemerobiidae (27 species) feed upon psocids and Hemiptera. It is doubtful that the predator pressure of this group was ever very great.

Coleoptera: The Carabidae (about 215 species), Staphylinidae (90) and Histeridae (35) are the only well-developed predaceous groups in this order, and only a few predators in other families of beetles are native (Dytiscidae, 2 species; Hydrophilidae, 2; and Cucujidae, probably less than 15). The predator pressure brought by the Carabidae and Staphylinidae was a dominant one.

Hymenoptera: The fly-catching Mimesidae and Crabronidae number only about 32 species. The mimesids prey principally upon leafhoppers, whereas the crabronids appear to have fed largely on the calliphorids, the larger *Drosophila*, Dolichopodidae and Anthomyiidae. The eumenid *Odynerus* are numerous both in species and in numbers; their prey consists of certain kinds of caterpillars, and they may have exerted a fairly high pressure on certain moths. It is of interest that these wasps prey almost exclusively on the Pyralidae and certain of the Microlepidoptera; rarely do they attack the Geometridae, which are so abundant in our forests.

Diptera: The only predaceous flies of account are the Dolichopodidae and the *Lispocephala* anthomyiids. There is an extensive series of genera and species of dolichopodids in the native fauna, and they prey principally on larvae of other flies, small caterpillars and perhaps on other organisms. We have little knowledge of their prey. The large genus *Lispocephala* feed as larvae upon the larvae of other flies such as the tipulids, and the adults feed on various insects, even members of their own genus.

Other predators of insects include:—

In addition to the insects, a rather large series of native spiders constituted a general group of predators.

Some of the native birds also fed on various insects. Among the more important insectivorous birds are the five thrushes, which at times feed upon spiders and caterpillars, especially the Geometridae. One of the Kauai forms, though largely frugivorous, hunted *Rhyncogonus* weevils and is the only known bird that fed on these insects.

The three *Chasiempis* flycatchers feed upon a large variety of insects and other organisms including flies, beetles, beetle larvae, moths, caterpillars and even myriapods. They not only catch insects on the wing, but search for them on foliage and on limbs and dead wood. These birds are, relatively, newcomers to the islands.

The drepaniids generally take insects such as caterpillars and moths and some spiders on occasion, and all of them feed their young on insects and spiders. *Loxops, Oreomyza* and *Heterorhynchus* are largely insect-eaters, but some of them also take nectar. *Loxops* and *Oreomyza* feed largely upon caterpillars and spiders and at least an Oahu *Oreomyza* is known to have searched especially for certain carabid beetles. *Heterorhynchus* fed upon spiders and caterpillars and was especially fond of *Oodemas* weevils. *Pseudonestor* fed particularly on the immature stages of plagithmysine beetles on Haleakala, and was specialized for tearing open branches and twigs in search of its prey. *Viridonia* preyed extensively on the cricket, *Paratrigonidium freycinetiae,* on Hawaii.

The Kauai "Oo" (Meliphagidae) fed on caterpillars and the native prognathogryllid and *Paratrigonidium* crickets, and the other species of the genus took insects on occasion.

The single Hawaiian bat is an uncommon species, and almost nothing is known about its food habits.

The only insectivorous plant we have is *Drosera,* which is confined to a few high mountain bog areas. No survey of the insects it captures has ever been made. It is known to trap large numbers of flies.

The parasitic insects in the native fauna are as follows:—

Hymenoptera: In the Ichneumonidae, *Agrypon* (11 species), *Echthromorpha* (1) and *Enicospilus* and its allies (31) are all parasites of moth caterpillars.

The braconids have only a single species of *Ecphylopsis* which parasitizes long-horn beetle larvae, and its endemicity may be questioned.

In the Encyrtidae we have a series of *Anagyrus* species (7 described) which are parasites of mealybugs; *Coelopencyrtus* has 4 species which parasitize *Odynerus* wasp larvae; *Hypergonatopus* (7) are hyperparasites of the two native dryinid wasps; *Xanthoencyrtus* (6) are mealybug parasites.

The eupelmids (*Eupelmus,* 54 species, and *Lepideupelmus,* 3) have developed one of our two largest endemic parasite complexes, and they have radiated out to parasitize such varied hosts as Hymenoptera, Diptera, Orthoptera, Neuroptera, Lepidoptera and Coleoptera; some are egg parasites, others are parasites of larvae.

The Miscogasteridae contain about a dozen species about which little is known. One has been recorded as a parasite of a *Dryophthorus* weevil.

The Mymaridae are represented by 16 species of *Polynema* which are, or are presumed to be, parasitic on the eggs of delphacid and cicadellid leafhopper eggs. A species now considered an immigrant attacks the eggs of an immigrant *Nabis*.

The Diapriidae contain 9 species centering around *Phaenopria*, and those which are known are parasites of *Drosophila* larvae.

The Scelionidae include six species of *Prosanteris* and five of *Microphanurus* (endemicity uncertain); at least one of these species has been reared from *Nysius* bug eggs.

Our Cynipidae, *Eucoila* (9 species) and *Cothonaspis* (18 species), are parasites of *Drosophila* larvae.

In the Bethylidae we have 16 species of *Sclerodermus* which are parasites of wood-feeding caterpillars and a few are parasites of certain wood-boring cerambycid and, possibly, other beetle larvae. *Sierola* constitutes the largest complex of native parasites, for it contains 181 known species. These are parasites of moth caterpillars.

The Dryinidae have only two (1?) native species of *Pseudogonatopus*. These are parasites of delphacid leafhoppers. They in turn are parasitized by *Hypergonatopus*.

In addition to these, there are a few species of Spalangiidae, Aphelinidae and Eulophidae which possibly might be native; these are known only from seven species placed in six different genera in the three families.

Diptera: The only parasitic Diptera in the native fauna are the pipunculid flies, 12 of which are known, and these are all parasites of delphacid leafhoppers.

Although much work remains to be done on the relationships of the endemic predators and parasites, particularly by breeding to associate properly the known species with their hosts, some generalizations can be drawn from the data at hand. Some large sections such as the Carabidae, Staphylinidae, Histeridae, Nitidulidae, Elateridae and possibly other groups—over 500 species of beetles alone—are not known to have any insect parasites. Also, these and other families have no known predators in the adult stages, excepting some negligible feeding on occasional species by a few birds and, possibly, damselflies. The large *Odynerus* wasp complex of more than 100 species has some of its species attacked by a few species of *Eupelmus* and *Coelopencyrtus* wasps, and these are the only certainly native parasites known to attack them. Members of the largest complex of Hawaiian Diptera—the Dolichopodidae—have no known parasites, and, at most, only a few predators ever attack the adults (certain crabronid wasps catch some species and others are probably occasionally taken by *Lispocephala* flies and Odonata). I have not found a record of any native parasites of the species of our well-developed *Nabis* bug complex, although Perkins (1913) suspected that one or more egg parasites possibly occurred. If the group has any insect predators, attack must be only occasional. One would expect to find parasites of the exposed eggs of our endemic pentatomid bugs, but none has been found. Only a single parasite species (*Microphanurus*) has been reared from one species out of our nearly 100 endemic lygaeid bugs. Many eggs of various species have been reared without a parasite having been found. The groups which are known to be most subject to the attack of endemic parasites and/or predators are the delphacid and cicadellid leafhoppers, Pseudococcidae, Lepidoptera generally, the wood-boring beetles such as the Anobiidae, Ciidae, Cerambycidae, Aglycyderidae and Curculionidae, the nematocerous Diptera and *Drosophila.*

In the light of present knowledge, it appears reasonable to conclude that parasite and predator pressures have not played a major role in species formation in Hawaii.

CENTERS OF DEVELOPMENT WITHIN THE ISLANDS

One of the most fundamental facts in distribution within the islands is that the various islands have a differential development of species in many genera. Some genera are extensively developed on one island only, some on two or more adjacent islands, or they may be highly developed on one island and become progressively fewer in numbers from one island to the next adjacent and the next. Each of the larger islands has its various developments of different groups of insects which indicate that each island was colonized individually and that different groups arrived at different times on different islands. This is one of the soundest principles which argues against these islands ever having been connected in one mass. I interpret such distributions to mean that the areas of greatest development indicate the place of origin within the Hawaiian Islands of the species complexes in question. For example, genus "A" first became established on Maui where it spread and developed a complex of species. Because of the ocean barriers, few individuals ever became established on the neighboring islands of Hawaii and Molokai. However, through the ages, some forms did become established on these islands, and today we have a large complex on Maui, a smaller one on Molokai, and a yet smaller one on Hawaii. The island of Molokai is closer to Maui than is Hawaii, and hence it was colonized more frequently than Hawaii and now has a greater number of species than Hawaii.

TABLE SHOWING EXAMPLES OF DISTRIBUTION PATTERNS

GROUP	NUMBERS OF SPECIES				
	Kauai	Oahu	Molokai	Maui	Hawaii
Mecyclothorax (beetles)	0	6	20	40	17
Bembidiini (beetles)	14	5	4	5	1
Metromenus (beetles)	3	17	5	1	1
Cossoninae (beetles)	29	22	3	15	6
Achatinella (molluscs)	0	125±	0	0	0
Partulina (molluscs)	0	2	23	44	6
Newcombia (molluscs)	0	0	9	1	0
Carelia (molluscs)	28	0	0	0	0
Rollandia (plants)	1	18	0	0	0
Stenogyne (plants)	4	2	3	14	28
Phyllostegia (plants)	6	12	6	15	9
Psychotria (plants)	3	1	0	0	0

The distribution patterns are not at all similar. In some groups, Maui has the greatest development, in others Oahu is the center, while other complexes are best developed on Kauai, Molokai or Hawaii. Thus, it is apparent that each of these islands has shared individually original colonizations or developments and each has acted independently in this regard. These developments are quite independent of ecological conditions, because for the most outstanding examples of these developments equivalent conditions exist on all the major islands.

The accompanying table was prepared to illustrate some examples of this phenomenon. The islands are listed in order from west to east.

DISTRIBUTION OF SPECIES WITHIN THE ISLANDS

Endemic organisms in Hawaii range in distribution from restricted micro-niches to widespread. Some species occur only in certain valleys or in confined parts of valleys. Some species occur throughout the range of their hosts. The distribution of some species appears quite independent of ecological conditions; other species are distributed in accordance with strict ecological requirements. Questions to make one ponder are such as why the strong-flying Hawaiian crow is absolutely confined to a certain restricted range on part of one island, yet some wingless insects are found widespread on all of the main islands. Why has the Hawaiian hawk restricted itself to the island of Hawaii, and although it occasionally straggles to the adjacent great island of Maui, why has it never colonized that island? (This hawk has wandered all the way to California.)

An interesting fact is that most of our native insects, both winged and apterous, are confined to single islands and most often to restricted ranges on those islands. Some of the newly introduced species, however, whether they be beetles, flies, wasps or bugs, have spread rapidly, not only over entire islands, but have crossed the open-sea channels between the islands and, in many cases, have established themselves on all of our main islands within a few months or a few years. Man has had much to do with this inter-island dispersal.

The remarkable, restricted ranges of most of the native species of Polynesia are in rather marked contrast to the distributions of certain insects which I have studied from the Malay Archipelago. In those continental fragments, I have noted that the insular endemism is much lower than it is in Polynesia and that many species are widespread throughout many islands.

For an example of the distribution of a genus on one island, we may choose the genus *Rhyncogonus,* which is composed of the largest of all Hawaiian weevils. Indeed, they are among the largest, most conspicuous and most sought of all the Hawaiian beetles. They are such prizes that collectors never pass them by; even snail collectors and botanists bring them in for the entomologists. There are few Hawaiian genera which have received such careful attention as has *Rhyncogonus.* Only one new Hawaiian species has been collected in the past 20 years. Dr. Swezey has given the genus special study, and has plotted the distribution of the 13 species found on Oahu. His map is reproduced here as figure 52.

Most of the species have been taken at altitudes between 1,000 and 2,000 feet. Each species occupies a discrete locality, and no two species are known to overlap in distribution. The adults are wingless, and they feed upon leaves of various plants. The eggs are deposited on leaves, and upon hatching, the young larvae drop to the ground into which they burrow (to feed upon roots?).

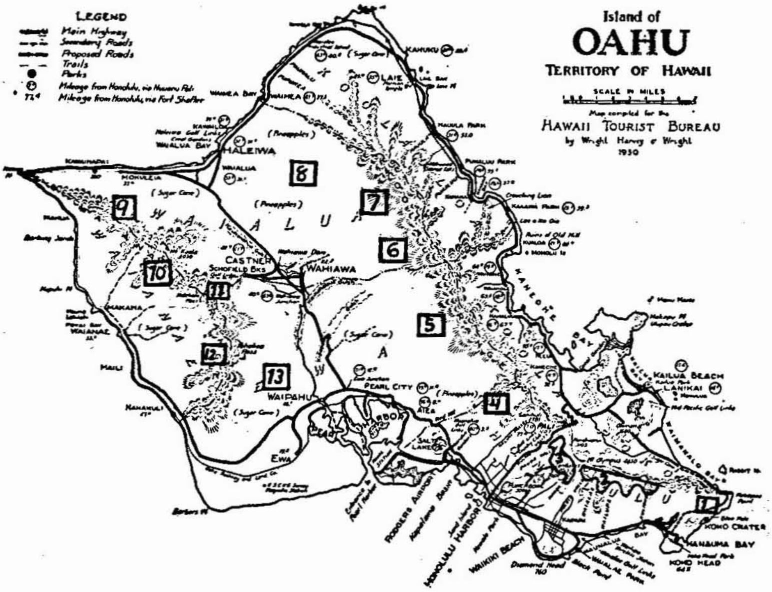

Figure 52.—Map showing the distribution of the known species of the weevil genus *Rhyncogonus* on Oahu. No two species are known to overlap in range. Most of the colonies have been found at altitudes between 1,000 and 2,000 feet. 1, *Rhyncogonus simplex* Perkins; 2, *R. koebelei* Perkins; 3, *R. blackburni* Sharp; 4, *R. mutatus* Perkins; 5, *R. obsoletus* Perkins; 6, *R. segnis* Perkins; 7, *R. freycinetiae* Perkins; 8, *R. oleae* Perkins; 9, *R. fuscus* Perkins; 10, *R. funereus* Perkins; 11, *R. saltus* Perkins; 12, *R. welchii* Perkins; 13, *R. extraneus* Perkins. (After Swezey, 1934.)

ARE THESE INSULAR SPECIES WE ARE STUDYING "GOOD SPECIES"?

Some workers (not systematists) have questioned the "degree" of our species, and they wonder if we are really dealing with "full species" or "good species." It should not take long for anyone who really investigates our species to ascertain that we are dealing with full species and good ones. Many of our groups of species contain such distinct forms that some of them would not be placed in the same genera by workers unfamiliar with the intermediate or connecting species or who might be working with small collections. During the course of this work, an authority examining two allied species of a genus for me stated, after superficial examination, that they belonged to two distinct families. After being informed that our local data indicated that they were allied species, he checked more fundamental characters and agreed with me. One can easily be led astray by these insular products. I have little doubt that if the Hawaiian *Drosophila,* for example, were large animals like birds or rodents, they would be segregated into a large number of genera and even higher categories on the basis of their conspicuous morphological differences. The same applies to most of our species complexes. Our heavy-billed drepaniid birds were once described as finches because of the confusing morphological similarities in form of beak. Although they are not finches, they have taken over the form and habits of finches and have filled an empty niche in Hawaii.

> To take only favourite classificatory characters of Passerine birds, form of the bill and structure of the tongue, we have here forms with long curved bills, forms possessing bills of an average insectivorous shape, thin finch-like bills, bills recalling that of the pine-grosbeak, and heavy haw-finch-like bills. Not less diversified are tongues, from fleshy tongue recalling that of a bullfinch and every kind of gradation towards bifid and fringed tongues. Quite as much diversified is the structure of the nostrils. In all, the diversity is so great that it may seem advisable to separate the long billed genera and to include the others perhaps with the *Fringillidae.* But Prof. Gadow has demonstrated that all these birds form but one family. I came to the same conclusion after my studies. And I consider that all these distinctive characters are adaptive, presenting several widely diverging lines of adaptive radiation, corresponding to great variety of biology and diet of *Drepanidae.*
>
> On the Galapagos we find another peculiar group first discovered by Darwin and described by Gould. At present they are considered as forming one genus, *Geospiza,* with about 25 species. By their rather heavy, short-tailed build, by their colour and patterns, and by colour variations depending on age, they are extremely uniform. But the variety of bills is astonishing and also different is said to be their biology. And at the same time, the gradations of the shape of the bills are such as to make an establishing of divisions quite senseless. (Sushkin, 1929:375–376.)

Many species have outstanding differential characters, but with the multitudes of species, connecting intermediates may, in many instances, be found. Extinction within the ranks would result in large numbers of species groups or genera. It must not be overlooked, however, that various species are known to have large numbers of subspecific forms. Some of these now recognized in lesser categories were earlier classed as species. But we can recognize those groups, and when we now speak of species, I believe that in most cases we know fairly well what we are dealing with. Some groups of allied forms, however, are difficult to understand, and only critical study and experimentation will reveal the true nature of such forms—if they can be understood by us highly evolved human beings so far removed from the creatures we are studying. Since this was written the following material from the pen of Dobzhansky (1944:251) has come to hand and is worthy of being quoted:

> The opinion is often expressed that species and races are arbitrary categories. This opinion is false. If given the opportunity to secure the necessary data, a biologist is able in a majority of cases to decide beyond a reasonable doubt whether the forms under study are distinct species or only distinct races. Lion, tiger, leopard, and domestic cat are species; Angora cat and alley cat are surely not species but races. However, "borderline cases," in which it is impossible to decide whether one is dealing with species or with races, do exist. Indeed, their existence was used by Darwin to demonstrate organic evolution. If species are the primordial units of creation, or else if they arise by sudden leaps (as thought by G. St. Hilaire and recently by

Goldschmidt), then we should be able to find methods to decide whether any two forms are still races or already species. If, on the other hand, species evolve gradually from races, then the decision will be possible only in some, perhaps in a majority, of cases, but at least some instances must be found in which forms are too distinct to be races but not distinct enough to be species.

RATE OF EVOLUTION

The first director of the Bishop Museum, Dr. W. T. Brigham, had so much faith in Dr. Perkins as a collector that he thought that Perkins had collected nearly all the Hawaiian insects. He used to say, jokingly perhaps, that evolution was going on at an extraordinarily rapid rate in Hawaii, because of the numerous new species which were constantly being discovered by Swezey and other workers after Perkins had finished his survey.

It is apparent that the rate of change in organisms does not follow a set pattern; it is a variable. It may be different between various groups of organisms, and it may vary in rate and intensity within groups in different places and at different times.

Evolution in the tropics should be faster than in higher latitudes because we have more generations per year in many groups. Some insects breed almost continually the year around, and several or many generations are produced each year. Likewise, our land snails reproduce almost continually.

We are confronted with extremely difficult problems when we attempt to interpret evolutionary rates, because we are only at the threshold of knowledge concerning such phenomena, and we know little about the causes and effects. From what we have observed, we may venture some remarks upon relative rates of evolution upon these islands.

The native species we see here are largely those which have developed on these islands. Hence, they are younger than the islands. But we do not know the age of any Pacific island within any but broad ranges of age estimation. Someday when more is known about the age of the land we will know more about possible evolutionary rates. There are few fossils to guide us in our work here, and those which have been found are all of late Pleistocene, or Recent age.

Perhaps the narrowest age range which could be given to an island upon which endemic species have developed would be similar to that of the elevated coral atoll of Henderson (in the Pitcairn group). This island has emerged recently and now stands somewhere near 100 feet above the sea. The endemic plants, land molluscs, insects and birds of that island have developed on it since it rose high enough above the waves to provide ecological conditions suitable for the support of such native organisms. These endemic species are younger than the island as it exists today. It is improbable that these endemic forms developed until the island had emerged for a significant distance above the waves, for none of the many neighboring atolls in the great Tuamotu Archipelago has such a distinctive endemic biota. It appears, then, that the species endemic to Henderson are recent species, and that their age is a matter of a few thousand years at most. Moreover, at the rate natural erosion is progressing on this tiny coral island, it cannot be expected to remain at its present height for very long. It will soon be worn down to sea level again, and, unless the island rises further from the sea, its endemic terrestrial biota perhaps will suffer complete extermination before many centuries have passed.

Here, then, is a base to start on. If species could have developed in geologically very recent times on low, flat-topped Henderson Island with its plain topography and few ecological niches, then some species on other islands are equally as young.

After detailed and careful field work, one of the most astute of Hawaiian geologists has placed the subaerial age of the island of Lanai in the most recent one-fifth of the Pleistocene (Wentworth, 1925). In spite of the small amount of collecting done on Lanai, and in spite of the vast deforestation and extermination which took place before any natural history survey was made, there has been assembled a large suite of endemic species of insects, land snails, birds and plants which have evolved upon Lanai. It appears, then, that a large number of endemic organisms has been evolved on that island in less than about 130,000 to 200,000 years.

Any changes in land and in ecological or other conditions which have influenced evolution are older than the species acted upon. I wish to re-emphasize this point. Any insects which are dependent on plants as factors of speciation are younger than the plants which played the influential roles in their evolution. Unless we are grossly misled, host isolation has played an obvious, dominant role in speciation among Hawaiian insects.

The profuse speciation of *Hyposmocoma, Plagithmysus, Proterhinus* and other insect genera in Hawaii probably went hand in hand with the development of the highly diversified flora. Some groups arrived after the flora was well developed and they also speciated extensively. It is perhaps impossible to say now whether a group "grew up" with the flora or quickly adapted itself to an already diversified flora. It does not appear that any more time than the Pleistocene and Recent periods need be required for many of these specific segregates, as well as numerous genera, to have developed distinctiveness. In fact, it seems that the ages of many of these forms possibly should be measured in thousands of years, rather than the millions some workers believe requisite. Other groups are old, and their ages go back hundreds of thousands or a million or so years. When we begin to speak of "many millions" of years on mid-Pacific islands, we extend our discussions to ages before the present landscapes which have exerted such a profound influence on the development of the biota came into existence, and such long periods of time are largely irrelevant to species formation on these islands. We do take millions of years into consideration when we discuss some stem groups, certain genera and the progenitors of certain groups of our plants and animals. It appears consistent with geological history to conclude that the terrestrial biota of the Hawaiian Islands began its local development in Pliocene time and that its greatest flowering came in the Pleistocene.

It is possible to cite many examples of all extremes in species development among the Hawaiian insects. We have some forms which are so weakly differentiated as to be hardly recognizable as different entities, and forms at the other end of the line which have undergone such profound differences that they are or might be called genera.

It appears that the compactness of the area, its small geographical expanse, and easy availability of food are conducive to speciation. The small sizes of the populations and the ease of isolation contribute to the change. It is believed that isolation of small populations for even relatively short periods of time may lead to inter-colonial differences which may in turn lead to speciation. The small sizes of our insular areas are a very real aid to speeding up of the speciation processes. Moreover, these small populations are isolated from one another, and this contributes to more rapid change than would occur in wide-ranging populations.

Dr. Perkins (1913:ccviii–ccix) said:

> I once examined two large series of *Nesosydne pipturi* from two different stations in the mountains behind Honolulu, where the species is very common. The first lot were taken from a number of trees, growing near together, in a rather open spot, the second lot from an isolated tree distant not many hundreds of yards from the former. Although possible individuals might have been picked from each lot agreeing exactly, yet on the whole the two series were so distinct superficially, that until I examined the genitalia I had great doubts whether those from the isolated tree were not a really distinct species.... In addition to this, a colony of a species infesting one tree sometimes shows considerable differences in appearance, when compared with a colony infesting another tree, even though the distance between the two is small, and these differences are likely to be increased, when colonies from more isolated spots are examined. I have little doubt that any number of superficially distinct forms could be obtained by selective breeding. It is possible that the appearance of individual colonies is often due to the nature of the original parents that colonized the tree, for colonies, if undisturbed, persist on a single tree, as I have experienced, for years.

In certain endemic species or in groups of species which appear to have been, geologically, comparatively recent immigrants, we find that there is considerable variation and it is difficult to decide whether to call the forms variants of a single species or to segregate them as varieties, subspecies or species. I am not familiar enough with birds to pass judgment, but I may call attention to the fact that the California linnet was purposely introduced to Hawaii, and that when a collection of the descendants of the original stock was made some years later, they were found to differ so much from the normal form found in California that they were made the subject of a special report by an eminent ornithologist (Grinnell, 1911). I have been told that individuals making up the Hawaiian population of an introduced Asiatic frog differ from those found in their homeland. If these differences are real, then here are examples of the beginnings of speciation.

A problem of great interest, and one which should receive careful consideration, is that of the leaf-rolling caterpillars attached to banana. These belong to the endemic genus *Omiodes,* which is an ally or segregate of *Nacoleia.* There are 23 described species in Hawaii, and others are known by their larvae only. The group has been studied carefully by Dr. Swezey for 40 years. The larvae of various species feed on palms, grasses, sedges and on certain liliaceous and leguminaceous plants, but there are five described species which appear to be restricted to the banana. These are distinct forms, and they can be distinguished from one another in both the larval and adult stages. If our observations are correct, and if these several species are restricted to banana, and we have no reason to doubt this, then we have here an example of a species complex having arisen within about 800 years. There is no doubt that the banana was brought to Hawaii by the ancient Hawaiians who colonized Hawaii about 800 years ago. There are no bananas anywhere on the islands of the deep Pacific Basin which were not introduced by man. Hawaii was colonized by natives who sailed here from the Society Islands. Neither *Omiodes* nor *Nacoleia* is found in the Society Islands. The Hawaiian *Omiodes* form a closely interrelated, compact group of forms which appears to have originated in Hawaii following a single chance invasion. There can be no doubt that these banana-feeding species have arisen locally from other Hawaiian species. From the data at hand, then, it appears reasonable to conclude that these forms have arisen in about 800 years or less.

When evolution takes place slowly, and/or when extinction is active, many distinct genera and groups of species, frequently isolated by well-marked morphological gaps, are developed. Where speciation is rapid, great species complexes of closely allied or intergrading species in relatively few genera are developed. The Hawaiian plants, land snails and insects definitely fall in the second, or rapid, category.

It has been held by some workers that the center of greatest proliferation of species marked the place of origin of a genus. This "rule" is valueless in the majority of examples of species complexes in Hawaii. Of course, we do have genera which have evolved here and in which the development of species complexes has been entirely local; the "rule" may be applied to such genera. Hawaii probably is one of the most recently colonized places inhabited by the ground-beetle genus *Mecyclothorax,* yet there are 85 known forms in Hawaii but only about 25 in the rest of its range. It had its origin in the Australian Region. Similarly, the *Proterhinus* weevils have explosively speciated in Hawaii, and although over 180 kinds have been described in Hawaii, the genus is an immigrant. The nearly world-wide wasp genus *Odynerus* apparently originated long before the Hawaiian Islands ever felt the air, yet we have the world's greatest single complex of species in Hawaii. (It is particularly significant to this discussion that the vespoid wasps did not develop until Eocene time and that the genus *Odynerus* is much younger. It is not improbable that the more than 100 Hawaiian species are post-Pliocene in age.) The same applies to the *Nysius* bugs, to other insects, to many plants and to land Mollusca. These forms have radiated out to fill the numerous empty niches found upon these islands, and their development can only be described by saying that it has been "explosive."

One might liken some of the speciation in Hawaii to what might happen if one could develop in a laboratory a series of mutant types of *Drosophila* and could release them in a new area and have many of the mutant forms survive as distinct entities which would set up new species because they found conditions favorable to their existence. Or, we might compare certain conditions in Hawaii with those under which we raise prize cattle, dogs, pigeons, etc., which could not for long hold their own in the wild. Some mutant forms get along here which might not stand a chance of survival on a continent.

The rate of evolution among the Hawaiian terrestrial Mollusca appears to be much more rapid than most malacologists will admit. Different rock piles and different shrubs and trees separated only by a few yards support distinguishable forms. The "colony system" of collecting (whereby each colony of shells is sampled and the material kept separate) has been found to be the soundest method of collecting because of the obvious differences between small populations. No rock pile, tree or shrub can be very old on these islands, and the population differences appearing in isolated colonies must be, at least in part, younger than their habitats. The very fact that these differences can be detected so easily is proof of rapid evolution.

It is significant that competition, predacity and parasitism are generally of low grade on islands, and these influences favor explosive types of speciation.

Perhaps it will not be out of place to call attention to Crampton's often-quoted researches (1917, 1925, 1932) on the *Partula* land snails of the Society Islands. Crampton concluded that evolution was proceeding so rapidly there that he not only found significant speciation differences between his material and that collected earlier by other workers, but he also found differences in his own material collected after an 11-year interval. I do not wish to belittle Crampton's outstanding monographs produced after years of concentrated labor, but I must take issue with the above conclusions. We collected in the islands visited by Crampton during the Mangarevan Expedition in 1934 and now feel that some of Crampton's basic data were partly incorrect. Crampton's early predecessors collected at a time when the forest came down close to the beach and when it had not retreated so far or so rapidly as it has before man in more recent times. The early collections were mostly made at low elevations near the coasts. When Crampton collected, his snails were found farther inland. His collections came from other colonies, and hence they showed population differences in his biometrical studies. Furthermore, it is possible that Crampton collected from other populations after his 11-year gap in collecting. When we visited the islands we collected higher up in the mountains and found species and forms never seen by Crampton! These things had not evolved since Crampton's time; they were simply obtained from different populations in different localities.

In almost every section of the terrestrial Hawaiian biota, or in all of it, the primitive groups are conspicuously absent. For example, the gymnosperms are wanting; the primitive orders of insects are either unrepresented or are poorly developed; among the vertebrates there are no primitive forms—the birds are evidently all Pleistocene or Recent derivatives. On the other hand, some of the malacologists are not inclined to concede that the land snails are anything but ancient. However, H. B. Baker, who has made what is generally considered to be one of the soundest and most complete surveys of any group of Polynesian snails yet written, considers the much-speciated zonitid snails to be a comparatively modern group. He says (1941:347) that they are probably "the most advanced families of the terrestrial mollusks which have endemic species in most parts of the Pacific region." Baker also concludes (p. 360) that "their immigrations have probably been relatively recent." He recorded 266 species, 95 percent of which are endemics, from Polynesia. He found that his studies did not support the theories of certain other malacologists who have demanded large land areas of great age in the Pacific, but he emphasized the fact that the group he was working on is a recent one.

If some malacologists are correct in their conclusions that certain of the Polynesian land snails are primitive types, then it appears more plausible to assume that possibly they are derived from primitive stocks through the processes of inter-insular segregation outlined above, and that their present intense speciation is a geologically recent flowering, a resurgence of evolutionary potential. This would bring them more in line with the plants and with other animal developments of Polynesia. It is illogical to suppose that the land snails are utterly out of step with the remainder of the biota. It is of real significance that modern anatomical studies of land snails are bringing to light revolutionary new conclusions which were quite masked when the shells alone were studied. In many groups conclusions drawn from fossils or from shells alone can hardly be used for data applicable to modern studies of relationships and distribution in the light of present findings.

Because many of our groups of genera and species are highly developed, diversified and divergent, taxonomists have been led to overemphasize greatly their peculiarities rather than to emphasize their phylogenetic similarities. Thus, the true relationships of some of our groups have been masked in inaccurate taxonomy for many years. For example, the molluscan groups Achatinellidae and Amastridae have been considered endemic Hawaiian families which are without allies elsewhere, and they have been used by some workers to emphasize especially the peculiarities of Hawaii. The presence of such endemic *families* in Hawaii indicates that the islands are remnants of a great Pacific continent—so some investigators have held. However, more detailed anatomical studies by Cooke and his protégé Kondo indicate that the family Achatinellidae is a local divergent specialization from a basic stock belonging to the widespread Pacific family Tornatellinidae, which is so highly developed, diversified and widespread in eastern Polynesia. Moreover, the two subfamilies of the Amastridae appear to have been derived from two distinct stocks which perhaps will come to be considered as no more than subfamilies in association with the nearly world-wide family Pupillidae. In fact, one of these subfamilies evidently will be merged with the Holarctic Cochlicopinae.

If the remarkable drepaniid birds of Hawaii have evolved and radiated to such an extreme degree and have developed such a large complex of genera and lesser forms in Pleistocene time, then is it not equally possible that our more rapidly reproducing insect and land-snail faunas could have developed their present multiplicity of species largely since late Pliocene time?

EXTINCTION IN RECENT TIME

Before the coming of man, native forest clothed the islands from seashore to timber line as it does today in undisturbed areas of certain other Pacific islands. Isolated lowland pockets of native plants, lowland fossil beds and other evidence support this conclusion. Native animals had a similar distribution. Native drepaniid birds were found at sea level and frequented coconut trees about the native villages when Captain Cook visited the islands, but for probably more than a century these birds have been unable to live at such a low level. After the arrival of the Polynesians, apparently about the twelfth century, the rapid retreat of the forests began. Fires set by the natives, as is still being done all over the Pacific, made great advances through the lowland and dry-land forests. After Captain Cook discovered the islands in 1778 and following the subsequent introduction of cattle, goats, sheep, horses and other domesticated animals (the Hawaiians brought only the fowl, swine, dog and rat with them), and followed in turn by agricultural development by the white man, the forest retreat was alarmingly rapid. The shallow-rooted endemic plants cannot tolerate grazing. When the undergrowth is eaten away, the thin soil dries out rapidly, and, excepting for isolated trees, the forest vanishes.

Hartt and Neal (1940:251) say:

> In 1793 the first cow and bull were landed on the island of Hawaii, at Kawaihae, and were released under a ten-year protective law. They increased rapidly to thousands, and in 1822 they were living in wild herds on Mauna Kea as observed by Goodrich. In 1856 they were so numerous and harmful to vegetation that Hillebrand, according to Judd, wanted them removed. In 1931 they were removed from upper Mauna Kea. Not only wild cattle but wild goats, sheep, horses, and hogs were offenders. By denuding the ground they caused the formation of erosion gulches. Horses were introduced in 1803, and wild ones lived on Mauna Kea until 1932, when they were removed from the upper slopes. Sheep were caught by wild dogs until the dogs were removed; by 1935 they had increased to 40,000. Sheep, largely, have prevented the development of *Sophora* seedlings. In 1909 the Government made upper Mauna Kea a forest reserve, which by March 1936, included 85,000 acres. In January, 1937, a fence 55.5 miles long was completed, encircling Mauna Kea between altitudes 6,000 and 8,000 feet and protecting 88,108 acres of the summit area from sheep, cattle, and hogs. In August 1935, we saw very few seedlings or young trees, but many old and dying trees.

The introduction of nematodes and plant diseases of various sorts speeded the destructive processes. Introduced grasses and other plants smother young growth and prevent the reproduction of forest seedlings. Today there are several million acres where hardly a native plant can be found. Not one-quarter of the original forest cover remains in these islands. Fortunately, however, during the last quarter of a century steps have been taken to safeguard our dwindling segments of this marvelous heritage. By legislation, by scientific planning, by fencing, by the control of feral animals and by development of forest-reserve areas, the extreme rate at which our forests were disappearing has been decreased markedly. In fact, some forest areas are coming back slowly. But much remains to be done, and it is too late to save what has been lost. At the present time, about one-fourth of the total land area of the main Hawaiian Islands is classed as forest reserve. Not all the forest reserve is clothed in native forest, however. The conservation program has been carried on because of the realization that forest cover is essential in the preservation and protection of the most valuable mineral resource in the islands—water.

The changes wrought on the natural balance of plants and animals on these lands has been tremendous. Extermination has been extraordinary. We lost forever—before a scientist ever had an opportunity to examine the area—almost all data concerning the true character of the lowland flora and fauna. Here and there in small pockets we have found vestiges that give us a few clues. We find Recent fossil terrestrial molluscs which tell us much. But we know next to nothing regarding the prehistoric lowland insect and bird faunas. There is not an area in the world where so many birds have become extinct in so few years as has been true here. We can tabulate some of the extinct birds because we have a few specimens collected long ago, but we have no idea of the numbers—probably many hundreds—of kinds of insects which have become extinct since man appeared on the scene. There has not been an endemic insect described from the islands of Niihau or Kahoolawe. There is a remote possibility that some few still exist in nearly inaccessible cliff areas on Niihau, but the endemic plants and animals of Kahoolawe have long since been extinct. Cattle, sheep and goats ate the native vegetation off that island long ago, and for years it has been literally blowing out to sea. It is now almost divested of its soil and is uninhabited. What a pity that we know nothing of its indigenes!

If it were not for the introduction of numbers of predatory and parasitic insects, many of our endemic insects might still exist in lowland areas. The introduction of a single species of ant, the voracious *Pheidole megacephala,* alone has accounted for untold slaughter. One can find few endemic insects within the range of that scourge of native insect life. It is almost ubiquitous from the seashore to the beginnings of damp forest. Below about 2,000 feet few native insects can be found today, and those which are found there belong to a few species which form an unusual small assemblage of forms which have been able to withstand the changing environment, or have adapted themselves to new hosts.

Perkins (1903:393–394) said:

> Although the destruction of the lowest belt of forest over by far the greater part of the islands has, in my opinion, been a most efficient cause of the destruction of native birds, many other causes have been at work, all of which are due to the occupation of the islands by white men. Such causes are the introduction of cattle and goats, which have extirpated or very much thinned out great portions of the native forest; of cats, foreign rats, and the mongoose (which are direct enemies), as well as the mynah, which not only attacks and drives away other birds, but also devours their eggs and young. The disturbance caused by the entrance of cattle into untrodden forest appears to be alone sufficient to scare away some species. Thus, on a very

> rough lava-flow on Hawaii in 1892, the "Oo" (*Acrulocercus nobilis*) was very numerous, and as many as a dozen of these birds could be seen in a single tree, making, with hosts of the scarlet "Iiwi," the crimson "Apapane," and other birds, a picture never to be forgotten. A few years afterwards, on revisiting the spot at the same season, although the trees were, as before, one mass of flowers, hardly a single "Oo" was to be seen. The only noticeable change was that cattle were wandering over the flow and beginning to destroy the brushwood, just as they had already reduced the formerly dense forest bordering the flow to the condition of open park-land.
>
> Cats were introduced into the Hawaiian Islands at a very early time, and, no doubt, increased excessively, while, as their owners moved from place to place, many strayed into the woods and began to feed on mice, rats, and birds. They are now found wild on all the islands, apparently only the wettest portions of the forest being free from them. On Lanai, in walking up a single ravine, I counted the remains of no less than twenty-two native birds killed by cats, and these must all have been destroyed within two days as previously the whole gulch had been washed out by a heavy flood. Two cats were actually shot on this occasion as they were devouring their prey, and several others seen, but, owing to the fact that they are extremely shy and mostly nocturnal in habits, few people who have not lived much in the woods have any idea of their numbers. The common rat is also quite at home in the forests and is decidedly arboreal in habits, feeding on fruits, land-molluscs, and no doubt on birds. The mynah, which I have myself seen devouring both young and eggs of other species, has increased prodigiously, and probably exceeds in numbers the whole of the native land-birds put together. It has greatly extended its range through the forest since 1892, and on some of the islands it is now ubiquitous.

Many favorite collecting grounds—type localities—for workers active before the turn of the century are now devoid of native plants, insects and land snails, and are cultivated or are covered by city streets and buildings. Patient, repeated search in type localities in the lower forests has failed to recover a number of species especially sought after, and many of these are certainly extinct. Even in high mountain areas where cattle have run we now have great difficulty in finding many plants and insects. In some places where we can find a steep little gulch which contains a bit of native brush which the cattle have not yet destroyed, we find new kinds of insects on rare plants. Some of these species are on the verge of extinction, and some have become extinct recently.

In Perkins' time, some species of *Odynerus* wasps were common in populations of "millions." Swezey collected nine species in Iao Valley on Maui when he first visited the valley about 35 years ago, but in more recent visits he found them to be rare. Today one must work hard to capture a small series of examples in a day's collecting. *Odynerus* feed upon certain kinds of caterpillars, and probably one of the factors influencing their decline has resulted from the wholesale slaughter of caterpillars by the immigrant and introduced caterpillar parasites. These parasites have created a profound pressure on the native caterpillars. The *Omiodes* caterpillars, a favorite food for some *Odynerus,* were once common in the mountains. Because of the new parasitism, these moths are now rarities or have not been seen for years. The ramifications of influences brought to bear by new, aggressive introductions to insular faunas are frequently appreciated by only a few workers who by chance of interest have been made aware of them. Many of the moths collected early in the century by Dr. Swezey have not been seen for years. Time and again we bring in caterpillars from the forest and rear out not the fine adult moths but introduced foreign parasites. Three introduced continental ichneumonid wasps have by themselves played the dominant role in this great reduction or extermination. These are *Casinaria infesta* (Cresson), *Cremastus flavoorbitalis* (Cameron) and *Hyposoter exiguae* (Viereck). These are general parasites on whole series of moths, and if one moth species becomes rare, the parasites can keep up their numbers on other species. Hence, there is always an abundance of the parasites, and extermination of precinctive, small populations of particular endemic moths is quite possible. If the parasites were specific, host extinction would probably not come about because when the host became rare, the parasite would also decrease in numbers.

Perkins (1913:cxvi) found about 90 percent of the larvae of the endemic longhorn beetle *Clytarlus fragilis,* and over 90 percent of those of *Plagithmysus solitarius,* parasitized by foreign *Ischiogonus* wasps. These wasps also attack our other species of remarkable plagithmysines and probably account for the rarity of most of the species today.

Perkins (in a letter) stated that on Hawaii one year he had observed cicadellid leafhoppers "dead of some fungus disease in countless thousands in the Kona district, and in a few minutes I remember filling several pill boxes, as they stuck dead, but lifelike, on the trees. No doubt these were mostly one species. I never saw another epidemic like this, and if the fungus attacked the species indiscriminately, it would go hard with the rarer ones on such an occasion!"

Dr. Cooke has told me of an early record of a disease which attacked the now scarce native Hawaiian duck. It was said that the duck died by the thousands at Pearl Harbor.

The lowlands used to teem with certain delicate and beautiful native damselflies. After the introductions of fresh-water fishes such as top minnows, the native damselflies, whose ancestors never had to protect themselves from fishes, became scarce.

Rock (1913) held that the dry, lower forest areas of the lee sides of the islands were the richest in varieties of trees, and said that in certain of these regions a botanist could collect more different kinds of trees in a day than he could find in a week or two in the rain forest. He stated that 60 percent of all the indigenous trees in the islands could be found in the leeward dry regions. If this be true, then the amount of extermination must have been great in these regions, for most of these areas are now practically stripped of native vegetation to 2,000 to 5,000 feet or more. Limited areas of dry forest are preserved best on Hawaii, Lanai and part of Maui. These may be of great interest botanically, but they are now mostly so overrun by myriads of immigrant ants that they are largely barren of native insects. We do not have a true picture of what the magnificent dry-land fauna of these islands was. What riches might the naturalist have found when such areas as the Lualualei region of Oahu, the lee side of Kauai, western Molokai, the plain of Lanai, the vast region between the isthmus of Maui to above the Kula and Ulupalakua regions and the wide expanses of leeward Hawaii were in their natural state! We do not know how much we have lost.

The remarkable endemic genus *Carelia,* which contains the largest of all Hawaiian land snails, consists of 29 described forms. The genus is a lowland group, and probably most of the species lived below 500 feet. Of these 29, only about 7 have ever been taken alive, and of these only 2 have been taken during the last 10 or more years. From evidence presented by beds of thousands of dead shells, it is obvious that the shells once swarmed over the lowlands.

There are a number of fine trees and shrubs which are extinct and others which are on the verge of extinction in Hawaii. Some are known from small groves or from one or two existing plants only. Unfortunately, a list of these is not available, but when one is compiled, it will be rather lengthy. Some of my friends have seen destruction by cattle of the last survivors of unique, localized, native plants when a short length of fencing could have preserved the species.

> Above the lower dry mountain slopes, at elevations varying usually from 1200–3000 ft., one reaches the belt of continuous forest. Where undisturbed by man or beast, this is often so dense as to be impenetrable without cutting a pathway, or at least breaking through by force. Luxuriant growths of Ieie (*Freycinetia*) in many localities and in others wiry-stemmed ferns (*Gleichenia*) make progress difficult. The width of this forest-belt varies very greatly according to the locality and according to the destruction that has been the work of man. In some places no such forest-belt exists, in others it has been reduced to an open timbered country, covered with foreign grasses. This is the last stage preceding destruction, when the remaining trees produce their seed in vain, for the thick growth of grass prevents any young trees springing up to replace the old. We have known a forest so dense that it could be traversed only along a narrow made path, generally knee-deep in mud, to be reduced to open woodland by the ravages of cattle within a period of about fifteen years. (Perkins, 1913:xxvii.)

Rock (1913:43), speaking of the middle forest zone on Mauna Loa, said:

> The *Ohia lehua* gradually passes into the *Koa* forest, if such it can still be called; for nowhere has the writer found such a pitiable sight as the *Koa* forest presents in this district at about 3000 feet up to 5000 feet elevation. Here 90 per cent of these giant *Koa* trees are dead; their huge limbs dangle in the air on pieces of fibrous strings of bark, ready to drop, if stirred by the slightest breeze. The remaining 10 per cent of the trees are in a dying condition, and in a very few years the country will be entirely denuded. Huge masses of trunks and limbs are scattered over the ground, and it is really difficult to ride through this remnant of forest.... Trees reach here a height of 80 feet or more. This condition is mainly due to the cattle, which have destroyed all the undershrubs and also injured the trees, which are then readily attacked by insects.

On the "great central plain" of Hawaii, Rock (1913:46) noted that

> On this plain are scattered many volcanic cones, mainly composed of black cinder and covered with dense vegetation. But especially on the crater bottoms one is likely to find interesting plants which have disappeared from the open plain, where they are eagerly devoured by cattle and goats, while at the bottom of these craters they are safe from their ravages. Anyone collecting on this plain should direct his steps to all these cones, as it is here only that he can obtain things of interest.

On Maui, Rock (1913:70) found that

> The forests spoken of by Hillebrand at Ulupalakua have entirely disappeared and only remnants of them can be found. *Cheirodendron Gaudichaudii* is still common, besides Suttonia, and *Ohia lehua*; numerous still is the araliaceous *Pterotropia dipyrena.* The undershrub is again mainly *Rubus hawaiiensis.* The species of Cyanea found by Hillebrand are gone forever; and where they once reared their proud palm-like crowns toward the sky there is now only grassland, with herds of cattle and ugly Eucalypti. The writer was fortunate enough to find a specimen of the long-sought-for, gorgeous *Cyanea arborea* in that locality in a small gulch inaccessible to cattle. It was the last of its race. He scoured the country for miles searching for the handsome *Cyanea comata,* but his searches were in vain: it has vanished forever.

We know that dense forest covered the area between Makawao and Ulupalakua not so long ago, because one "used to ride through the jungle on the trail" between the two points. Other stories handed down mention horses "bogged down" in the mud on the trails in the Kula region. Today there is not a patch of native forest in the entire area, and water is so scarce in the Kula district that it must be brought by a pipe line that runs for many miles to the intake in the Olinda forest reserve on the other side of the mountain; but the draft is so great that water must be rationed on occasion and expansion of agriculture is limited.

Each native plant in Hawaii supports a lesser or greater assemblage of associated insects. Many insects are absolutely host-specific. When their hostplants become restricted in range, the range of the insects shrinks accordingly. Deforestation and extermination of various trees on our islands have accounted for the extinction of an untold number of associated insects. Some insects which were at one time abundant on certain trees back of Honolulu are now no longer found, because, for many years, we have been unable to find a specimen of their hostplants.

There are many references in earlier Hawaiian literature pertaining to the abundance of various native insects, but we cannot find these insects in such abundance today. Extinction and great reduction in numbers are very real occurrences in Hawaii. There is no way of knowing what part of the insect fauna existing in Hawaii when man arrived has been exterminated, but I believe that to say a third or more of the species are now extinct would be no exaggeration. One should not forget that the living native insects we study today are largely confined to less than one-quarter of the area once available to the fauna.

ECOLOGY

This subject has been so well covered by other workers who have had an opportunity to spend much more time than I have in the forests of the Hawaiian Islands that it is appropriate for me to refer the reader to their published works for detailed accounts. Hillebrand, Perkins, Rock and W. A. Bryan have given extensive discussions of the vegetation from which the interested person may obtain an excellent picture of local conditions in their day. Henshaw (1902) has outlined the faunal zones in relation to birds. Recent workers, such as F. X.

Williams (in his series on water insects), Hosaka (in his paper on Kipapa gulch), Ripperton and Hosaka (on vegetation zones), Usinger (in his *Nysius* paper) and Hartt and Neal, have included discussions of ecology, and these authors refer to a number of other published works. An account of the climate, prepared by S. B. Jones, is included in the Ripperton and Hosaka discussion (1942).

Any area in which one can pass within a few miles on a single mountain mass from a seaside semidesert to a rain forest receiving over 50 feet of rain in a year, or from lush, steaming tropical jungle to a perpetual, subpolar desert (mean minimum July–August temperature at 13,000 feet of 0° C. or less) where snow on occasion lies on the ground the entire year at nearly 14,000 feet, and which has such a spectacular, rugged topography clothed with dense vegetation containing about 2,000 known native higher plants making up one of the most distinctive botanical provinces of the world, cannot escape having an unusual range of ecological conditions. The remarkable thing is that so many different types of ecological niches are available in such limited areas. The proper treatment of the subject of ecology in Hawaii would require a book by itself.

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ERRATA
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p. 74, line 8, for "two" read "three" and add *Pseudocymus* after *Sephora.*
p. 78, after "8 Caloptilidae" add "*Philodoria,* 14 species and."
p. 79, after "17" read "3" instead of "2."
——— line 6, under "19" remove "endemic" after *Hypenodes.*
p. 93, at *Parectopa* in the Lepidoptera, add "*Philodoria* 14 species."
p. 124, end of line 3 in figure legend, add "*Amastra (Heteramastra) hutchinsonii* (Pease)."
p. 157, line 6, read "four" for "five."
p. 158, paragraph 4, line 1, read "must" for "much."
p. 189, under the Van Dyke entry, read "89–129" in place of "1–129."
p. 205, remove "Variation, 52."

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