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OF LIFE
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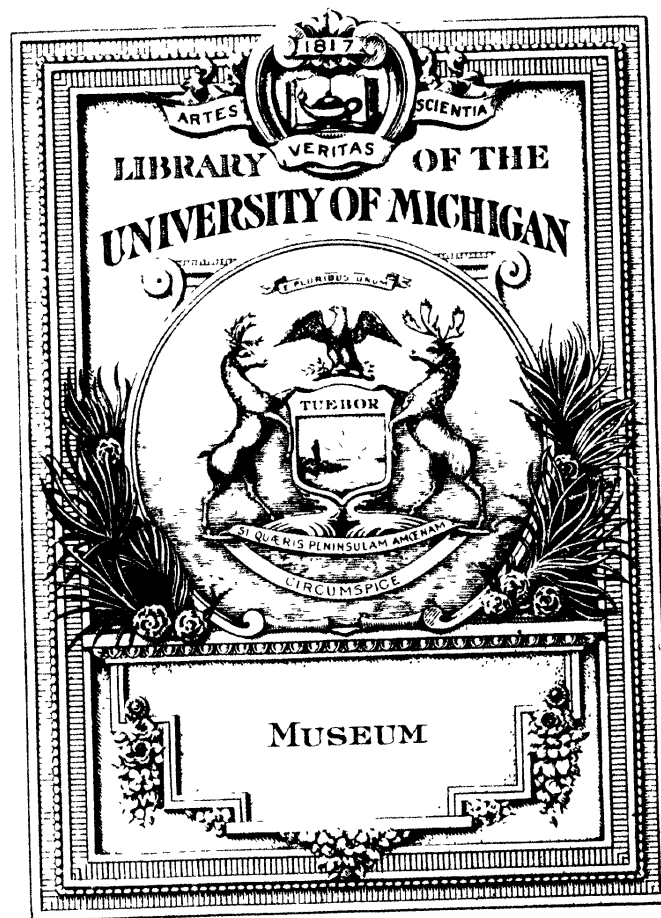
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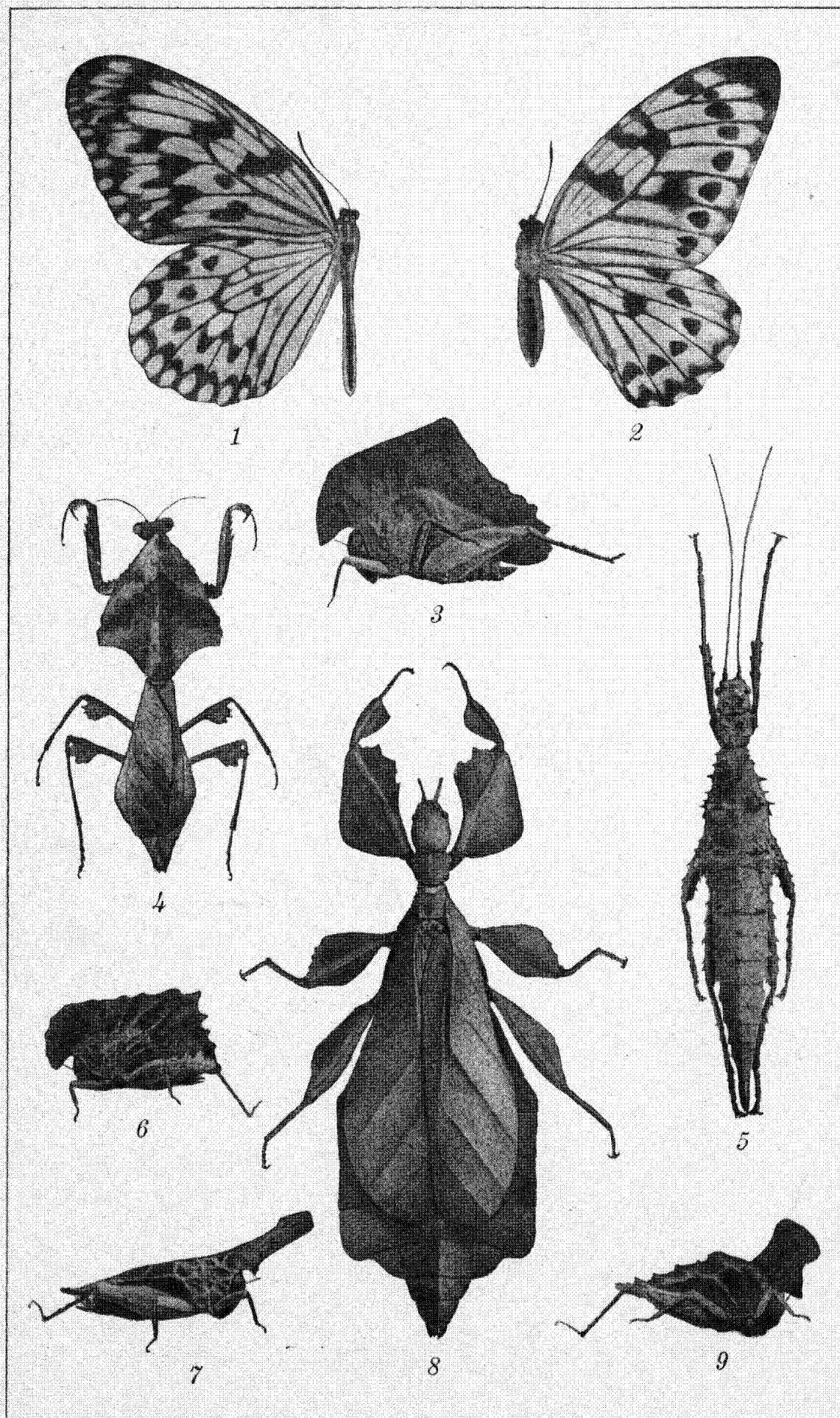
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PHILIPPINE MIMETIC INSECTS.

DISTRIBUTION OF LIFE IN THE PHILIPPINES

BY
revised
ROY E. DICKERSON

IN COLLABORATION WITH

ELMER D. MERRILL, RICHARD C. MCGREGOR, W. SCHULTZE
EDWARD H. TAYLOR, AND ALBERT W. C. T. HERRE



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DISTRIBUTION OF LIFE IN THE PHILIPPINES

**By ROY E. DICKERSON, IN COLLABORATION WITH
ELMER D. MERRILL, RICHARD C. MCGREGOR, W. SCHULTZE
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The Monographs of the Bureau of Science are a continuation of the Bureau's series called "Publications," numbered 1 to 19. The change in designation has been made to obviate the ambiguity of the word publication.

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PREFACE

Primarily, this work is a development of informal conversations upon the broad topic, "the origins and distribution of life in the Philippines." Eventually, a compilation of the data and views expressed in these talks was undertaken, and this book is the product of that effort. The object of the book is to stimulate further study of the distribution of plants and animals, for no more than a beginning has been made.

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During the years 1921 to 1923, several scientists met monthly at the Bureau of Science in Manila to discuss the biology of the Philippines and the possible explanation of the distribution of life forms in the Archipelago. The group included a botanist, a chemist, two zoölogists, an ornithologist, a herpetologist, an ichthyologist, a geologist, a geologist and invertebrate palæontologist, a hydrographer, a seismologist, a protozoölogist, two entomologists, and an anthropologist; so that various branches of the natural sciences were represented. From time to time other specialists and distinguished visitors attended the meetings and made incidental contributions and helpful criticisms. Botany was represented by Mr. Elmer D. Merrill, director and botanist of the Bureau of Science, and the chapter on botany represents his work. He not only contributed from his specialty, the botany of Malaysia, but also aided materially in the preparation of the chapters on characteristic Philippine habitats and on mammals. Mr. W. Schultze, entomologist of the Bureau of Science, contributed most of the chapter on insects. Dr. Warren D. Smith, for many years chief of the division of mines, Bureau of Science, contributed much to the discussion of many of the topics beyond the limits of his own subject, geology. Much of the chapters on geology and palæogeography is based upon his extended exploration in the Philippine Archipelago. Mr. Richard C. McGregor, ornithologist of the Bureau of Science and associate editor of the Philippine Journal of Science, furnished the chapter on birds and a portion of the chapter on characteristic Philippine habitats, and assisted in the editing of this book. Dr. Albert W. C. T. Herre, chief of the division of fisheries, Bureau of Science, contributed the

chapter on fresh-water fishes of the Philippines. Prof. H. Otley Beyer, of the University of the Philippines, was expected to contribute a chapter on the natural history of man in the Philippines. His conceptions coincide, in many respects, with the distributional studies of other life forms; and it is regretted that he submitted nothing for publication here except the map included as fig. 62. Mr. Edward H. Taylor contributed the chapter on the distribution of frogs, snakes, and lizards. The first six chapters, portions of the chapters on characteristic Philippine habitats and on mammals, and most of the final chapter were written by Dr. R. E. Dickerson, who also acted as general editor of this volume. Mr. A. E. W. King, of the Bureau of Science, was of great assistance in making several translations from German texts. Mr. A. v. H. Hartendorp furnished translations of Dutch texts. Prof. Frank G. Haughwout, of the Bureau of Science, a specialist in protozoölogy, aided in editing this book. Mr. Victoriano Elicaño, geologist, Bureau of Science, aided by furnishing valuable geologic data.

The hearty coöperation of the Philippine Bureau of Coast and Geodetic Survey was particularly helpful in the preparation of the maps and charts upon which the hydrography chapter was based. Capt. H. C. Denson, former director of the bureau; Capt. E. H. Pagenhart, director; and Mr. John Bach, supervisor of the geographical division, were always ready to contribute their excellent data.

Rev. Father M. Saderra Masó, S. J., seismologist of the Philippine Weather Bureau, made several valuable contributions which are incorporated in the chapter on hydrography.

Among the other specialists who attended the meetings of the symposium or made incidental contributions were Prof. Artemas L. Day and Prof. S. F. Light, of the department of zoölogy, University of the Philippines; Prof. Charles S. Banks, formerly of the Bureau of Science; Prof. Charles Fuller Baker, dean of the College of Agriculture, University of the Philippines; Dr. H. I. Cole and Mr. Hubert G. Schenck, formerly of the Bureau of Science; and Mr. A. v. H. Hartendorp, former editor of the Manila Times. Prof. D. S. Fansler and Dr. Harriet Fansler, of the English department, University of the Philippines, read portions of the text. Dr. K. W. Dammerman read critically the chapter on mammals and the one on amphibians, lizards, and snakes.

MANILA, September 15, 1923.

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ILLUSTRATIONS

FRONTISPIECE

- FIG. 1. *Hestia leuconoë* Erichson (Nymphalidæ), a distasteful protected species; Luzon. About $\times 3$.
2. *Papilio idaeoides* Hewitson (Papilionidæ), an unprotected species that mimics the one shown as fig. 1; Luzon. About $\times 3$.
3. *Hymenotes triangularis* Westwood (Acridiidæ), mimetic of bark. About $\times 1.5$.
4. Praying mantis. (Mantidæ), mimetic of a dead leaf; Mindoro. About $\times 3$.
5. *Obrimus asperimus* Redtenbach (Phasmidæ), mimetic of bark. About $\times 3$.
6. *Misythus* sp. (Acridiidæ), mimetic of bark. About $\times 1.5$.
7. *Misythus* sp. (Acridiidæ), mimetic of bark. About $\times 1.5$.
8. *Phyllium celebicum* de Haan (Phyllidæ), mimetic of a living leaf; Luzon. About $\times 3$.
9. *Misythus laminatus* Stål (Acridiidæ), mimetic of bark. About $\times 1.5$.

PLATE 1

- FIG. 1. Banisilan, Cotabato Province, Mindanao, looking west across the oldest river bench. Elevation about 375 meters above sea level.
2. A marine terrace in central Bohol. The rounded hills that rise above the general level of this terrace possibly represent a series of stacks or coral reefs, which have been rounded by erosion since the general region was uplifted.
3. Puerto Princesa, Palawan.

PLATE 2

- FIG. 1. Malampaya Sound, Palawan.
2. Saint Paul River, Palawan. Entrance to cave from the sea.
3. Headlands of Saint Paul Bay, Palawan.

PLATE 3

Relief map of the southern half of the Philippines. Palawan trough on the extreme left, Philippine trough on the right; Celebes Sea deep, lower edge center. (Plates 3 to 7 are from a large Coast and Geodetic Survey model.)

PLATE 4

Relief map of the Palawan trough and the Sulu mediterranean sea.

PLATE 5

Relief map of the Palawan trough, the Taal rift, and the Luzon deep.

PLATE 6

Relief map of the Visayan shelf sea, center; and the Tablas deep, left center.

PLATE 7

Relief map of northern Luzon, the Babuyan, the Batanes, and Formosa.

PLATE 8

Relief map of Mindanao; contour intervals, 100 meters. (Coast and Geodetic Survey.)

PLATE 9

Relief map of northern and central Luzon; contour intervals, 100 meters. (Coast and Geodetic Survey.)

PLATE 10

FIG. 1. *Sonneratia caseolaris* Engler, on an open coast, Bongabon, Mindoro.

2. *Sonneratia caseolaris* Engler, showing air roots.

PLATE 11

FIG. 1. Interior of a mangrove swamp near Bongabon, Mindoro.

2. Forest near Agusan River, Mindanao.

PLATE 12

Nipa palm, *Nypa fruticans* Wurmb, showing its habit. (Etching loaned by the Bureau of Forestry.)

PLATE 13

Dipterocarp forest at the edge of a clearing, 450 meters on Mount Maquiling, Luzon. The slender palms in the foreground are *Livistona*. The large feathery leaves near the ground belong to rattans. (Photograph by W. H. Brown.)

PLATE 14

Large dipterocarps in northern Negros. Most of the small trees have been cut. (Photograph by Martin.)

PLATE 15

Pine forests in Benguet, Luzon. (Photograph by Martin.)

PLATE 16

A level area, near the lower limits of the mossy forest, Mount Maquiling, Luzon. (Photograph by Brown.)

PLATE 17

The summit of Mount Pulog, Luzon.

PLATE 18

A part of the shore of Laguna de Bay, Luzon. The checkerboard effect is produced by the dikes of rice fields. The town in the middle distance is Paete. (Photograph by Martin.)

PLATE 19

Rice terraces in Ifugao Subprovince, Luzon. (Photograph by Worcester.)

PLATE 20

A view from Agusan River, in northern Mindanao, showing characteristic growth habit of giant *Pandanus* and the extensive development of prop roots. (Etching loaned by the Bureau of Forestry.)

PLATE 21

FIG. 1. Grassland near Port Banga, Mindanao, showing the effect of clearings and fires. Some molave forest remains, at the left in the picture. (Photograph by Whitford.)

2. Grassland near Balagbag, Rizal Province, Luzon. This type of vegetation is very common in the lowlands wherever the primary forest has been destroyed and the land left uncultivated. (Photograph by McGregor and Cortes.)

PLATE 22

Caiñgins in the mountains of northern Negros, showing typical clearing and cultivation; uncut primary forest on the steeper slopes. (Photograph by the Bureau of Forestry.)

PLATE 23

FIG. 1. A typical caiñgin in Occidental Negros. (Photograph by the Bureau of Forestry.)

2. A clearing on level ground in Mindoro; made by Mañgyans. (Photograph by M. L. Miller.)

PLATE 24

A stand of *Schizostachyum*, a gregarious bamboo. (Etching loaned by the Bureau of Forestry.)

PLATE 25

Heads of some Philippine hornbills, showing the most conspicuous differences, somewhat diagrammatic, about $\times 0.25$. (Drawings by T. Espinosa and M. Ligaya. The colors of iris and of bare skin around eye are not all true to life.)

- FIG. 1. *Hydrocorax hydrocorax* (Linnæus), male; Luzon and Marinduque.
 2. *Hydrocorax mindanensis* (Tweeddale), male; Mindanao and Basilan.
 3. *Hydrocorax semigaleatus* (Tweeddale), male; Samar, Leyte, and Bohol.
 4. *Hydrocorax semigaleatus* (Tweeddale), young.
 5. *Craniorrhinus leucocephalus* (Vieillot), male; Mindanao and Camiguin.
 6. *Craniorrhinus waldeni* Sharpe, male; Negros, Guimaras, and Panay.
 7. *Penelopides panini* (Boddaert), male; Negros, Guimaras, Panay, Masbate, and Ticao.
 8. *Penelopides samarensis* Steere, male; Samar, Leyte, and Bohol.
 9. *Penelopides affinis* Tweeddale, young female; Mindanao and Dinagat.
 10. *Gymnolæmus lemprieri* (Sharpe), female; Calamianes, Palawan, and Balabac.
 11. *Gymnolæmus lemprieri* (Sharpe), young female.
 12. *Anthracoceros montani* (Oustalet), female; Sulu and Tawitawi.

PLATE 26

Parrakeets of the genus *Prioniturus*, upper aspect of males to show similarity and specific characters, somewhat diagrammatic, about $\times 0.3$. (Drawings by M. Ligaya.)

- FIG. 1. *Prioniturus cyaneiceps* Sharpe; Palawan group.
 2. *Prioniturus discurus* (Vieillot); most of the Philippines.
 3. *Prioniturus mindorensis* Steere; Mindoro.
 4. *Prioniturus montanus* Grant; Luzon, interior elevated areas; known from Baguio, Pauai, Polis Pass, Mount Data, and Dupax.
 5. *Prioniturus luconensis* Steere; Luzon, lowlands.
 6. *Prioniturus verticalis* Sharpe; Bungau, Sibutu, and Tawitawi.
 7. *Prioniturus flavicans* Cassin; Celebes.
 8. *Prioniturus platurus* (Vieillot); Celebes and Sangi Islands.

PLATE 27

FIG. 1. *Gekko monarchus* (Duméril and Bibron), a house lizard found in Mindanao, Palawan, and Negros. This species is widely distributed and has been reported from Ceylon and the Malay Archipelago.

2. *Gymnodactylus agusanensis* Taylor.

PLATE 28

FIG. 1. *Gonyocephalus interruptus* Boulenger. This highly ornamented species upon being exposed frequently remains perfectly quiet, trusting to its ability to change its colors and ornamentations to blend with its surroundings.

2. *Gonyocephalus sophiæ* Gray.

PLATE 29

FIG. 1. *Draco ornatus* (Gray), from Mindanao; slightly reduced.

2. *Draco everetti* Boulenger, from Mindanao; slightly reduced.

3. *Draco volans* Linnæus, from a Palawan specimen.

4. *Draco spilopterus* (Wiegmann); a young individual. The flying lizard is unable to rise from the ground, but must start from a tree or other elevated point. It does not fly in the true sense like a bird, but merely stretches the wing membranes and sails from tree to tree. The genus *Draco* is of wide distribution in the Malay Archipelago.

PLATE 30

FIG. 1. *Varanus salvator* (Laurenti); a living specimen in captivity in Manila. This large monitor, incorrectly called iguana, is semi-aquatic in habit.

2. *Varanus salvator* (Laurenti), top of head; after Günther.

3. *Varanus salvator* (Laurenti), side of head; after Günther.

PLATE 31

Ptychozoon intermedia Taylor, photographed from the only known Philippine specimen of this genus. The apparent rarity of the species may be due to its leafy and frondlike appearance. The two other members of the genus are reported from the Malay Archipelago or Formosa.

PLATE 32

FIG. 1. *Brachymeles schadenbergi* (Fisher); Mindanao.

2. *Brachymeles boulengeri* Taylor; Polillo.

3. *Brachymeles bicolor* (Gray); probably Luzon.

4. *Brachymeles eleræ* Taylor; probably Luzon.

5. *Brachymeles burksi* Taylor; Mindoro.

6. *Brachymeles bonitæ* Duméril and Bibron; Luzon. The species of *Brachymeles* show various stages in the process of leg reduction. The burrowing habit of the members of this genus is probably connected with the tendency toward atrophy of the appendages.

PLATE 33

Characteristic species of the genus *Pachyrrhynchus*, showing the very distinctive color patterns; about $\times 1.5$.

- FIG. 1. *Pachyrrhynchus ardentius* Schultze, female; Siargao Island.
 2. *Pachyrrhynchus corpulentus* Schultze, female; Lindabon, Bukidnon Province, Mindanao.
 3. *Pachyrrhynchus decussatus* Waterhouse; Virac, Catanduanes.
 4. *Pachyrrhynchus postpubescens* Schultze, male; Lindabon, Bukidnon Province, Mindanao.
 5. *Pachyrrhynchus absurdus* Schultze, female; Bucas Grande Island.
 6. *Pachyrrhynchus speciosus* Waterhouse, male; Bucas Grande Island.
 7. *Pachyrrhynchus gloriosus* Faust, female; Mount Banahao, Laguna Province, Luzon.
 8. *Pachyrrhynchus gloriosus* var. *abbreviatus* Schultze, male; Bontoc, Luzon.
 9. *Pachyrrhynchus ochroplagiatus* Heller, female; Mount Pulog, Benguet Subprovince, Luzon.
 10. *Pachyrrhynchus argus* Pascoe, female; Mount Santo Tomas, Benguet Subprovince, Luzon.
 11. *Pachyrrhynchus pinorum* Pascoe, female; Atoc, Benguet Subprovince, Luzon.
 12. *Pachyrrhynchus pinorum* var. *transversalis* Heller, male; Atoc, Benguet Subprovince, Luzon.
 13. *Pachyrrhynchus inclytus* var. *modestior* Behrman, female; Mount Santo Tomas, Benguet Subprovince, Luzon.
 14. *Pachyrrhynchus pulchellus* Behrman, female; Benguet Subprovince, Luzon.
 15. *Pachyrrhynchus loheri* Schultze, female; Mount Guinuisan, Bulacan Province, Luzon.
 16. *Pachyrrhynchus igorota* Schultze, female; Pauai (Haight's place), Benguet Subprovince, Luzon.

PLATE 34

- FIG. 1. A timarau near Bongabong River, Mindoro. (Photograph by E. A. Heise, 1921.)
 2. Timarau *Bubalus mindorensis* Heude, from a living animal in Mehan Gardens, Manila. This species is restricted to Mindoro. (Photograph by Cortes.)

PLATE 35

- FIG. 1. Philippine porcupine, *Thecurus*, from specimens in the Bureau of Science. This species is restricted to the Calamianes, Palawan, and Balabac. (Photograph by Cortes.)
 2. Chevrotain, or mouse deer, *Tragulus nigricans* Thomas, from a mounted specimen. This species is restricted to Balabac. (Photograph by Cortes.)

PLATE 36

Scaly anteater, or pangolin, *Manis javanica* Desmarest. In the Philippines, this species is confined to Palawan and Culion. The species was described from Javan specimens.

PLATE 37

Arboreal termite nest hollowed out by a scaly anteater, *Manis javanica* Desmarest.

- FIG. 1. Nest showing the opening made by an anteater.
2. Opposite side of the nest.

PLATE 38

Map of the Philippine Islands, showing seasons and rainfall. (From the Philippine Census, after Coronas.)

PLATE 39

Map of the Philippine Islands, showing the geologic formations. (From Smith, Geology and Mineral Resources of the Philippine Islands.)

PLATE 40

Map of the Malaysian Region, showing the continental shelves and associated deeps. (From Merrill, An Enumeration of Philippine Flowering Plants.)

PLATE 41

Map of the Philippine Islands, showing the provinces and their capitals and the principal cities, mountain ranges, volcanoes, rivers, and islands. (From Merrill, An Enumeration of Philippine Flowering Plants.)

PLATE 42

Map of the Philippine Islands, showing the relief. (From Smith, Geology and Mineral Resources of the Philippine Islands.)

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DISTRIBUTION OF LIFE IN THE PHILIPPINES

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INTRODUCTION

GENERAL DISTRIBUTIONAL CONDITIONS

As long as naturalists believed in the special creation of species, the dissimilarities between animals from different regions appeared curious; but in the light of evolution the perplexing thing is the similarities between animals from widely

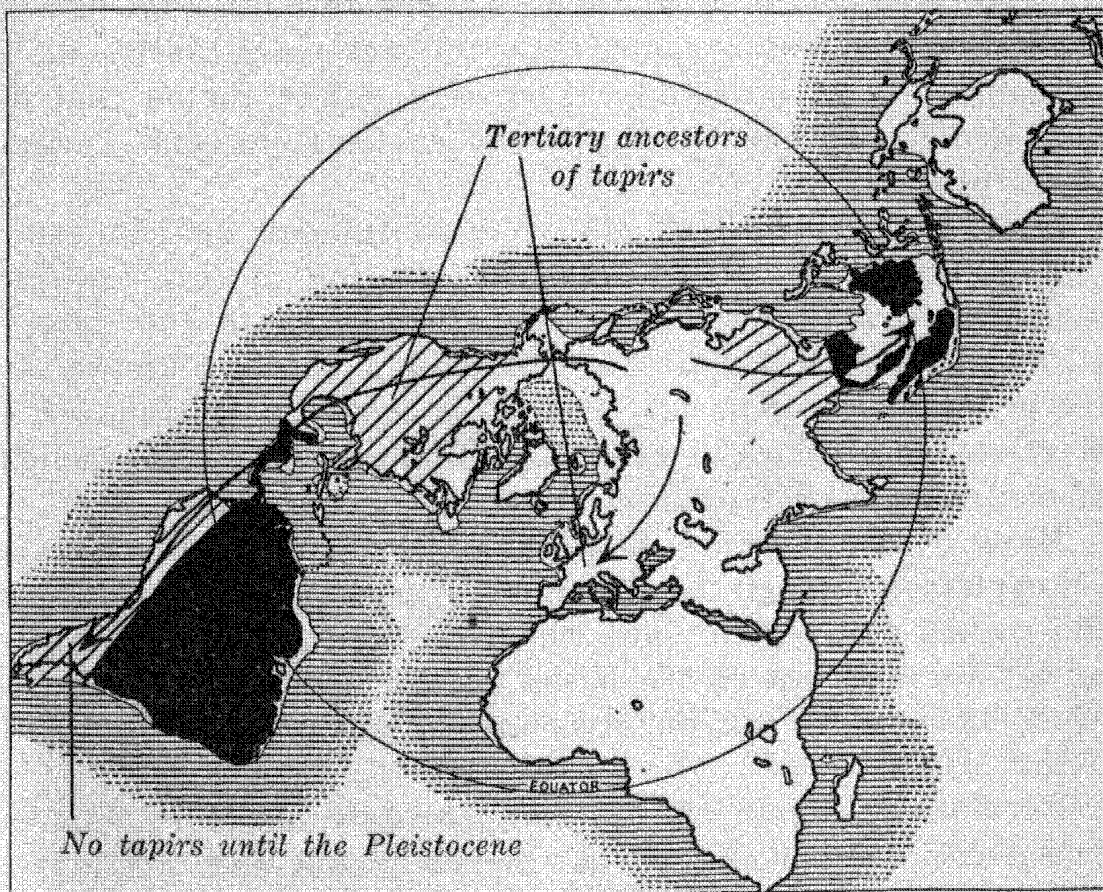


FIG. 1. The distribution of tapirs, living (solid black) and Pleistocene (shaded).

separated lands. For example, the tapirs of Central and South America are strikingly like those of the East Indies, but at present no tapir exists in either continental Asia or North America (fig. 1). To the biologist such puzzling discontinuous dis-

tributions have but one of two possible solutions. Scott* says, in this connection, that "either (1) the American and Asiatic species developed independently of one another from different ancestors, or (2) the regions intervening between these widely separated areas once formed a continuous land, occupied by species of the genus which have become extinct." The evolutionist will reject the first of these two explanations, as being beyond the realms of probability, and will accept the second. This decision places the burden of proof upon him, but in this particular case the load is not an onerous one. According to Matthew† the tapir did not occur in South America until the Pampean (Pleistocene). Tapirs are found also in various parts of North America in Pleistocene beds. In the same continent the direct ancestral forms of the tapir have been traced into the Tertiary to *Protapirus* in the Oligocene and less directly into the Eocene; and in Europe a similar succession has been discovered, except that no ancestral Eocene form is known. The tapir, or its ancestors, apparently did not reach Africa at all, probably owing to inability to cross a desert region that has persisted across the northern part of Africa from early Tertiary to the present.

Another excellent example of discontinuous distribution is that of the horse. The present distribution of this animal is indicated by Matthew in the chart given herewith (fig. 2). Of all mammals, the evolution of the horse is the best known, and the generic succession has been worked out by Matthew, J. C. Merriam, and Osborn in America. Similar interesting examples of discontinuous distribution are found among plants.

Many of the extremely puzzling cases of distribution may be yet explained through the researches of palæontology. Although the realms and regions into which the earth has been divided by Sclater and others are based chiefly upon the distribution of mammals and birds, the divisions apply almost equally well to living plants.

Particularly significant is the apparently direct relation between the development of the higher plants and the highest animals—the mammals. In upper Cretaceous time, the dicotyledons (like the beech, the oak, the walnut, the laurel, the cinnamon, the maple, and the magnolia) were the dominant tree

* A History of Land Mammals in the Western Hemisphere. The Macmillan Co., New York (1913) 137.

† Annals N. Y. Acad. Sci. 24 (1915) 238.

forms, while modern types of grasses and herbs flourished beneath their shade and carpeted the glades and the prairies.

According to Chamberlin and Salisbury,* the changes in plant life during early Cretaceous from ferns, horsetails, cycads, and conifers to a dominant dicotyledonous forest with accompanying herbage of modern grass types influenced profoundly the development of herbivorous mammals by supplying suitable fodder, nuts, and fruits for their growth and later development in the Tertiary.

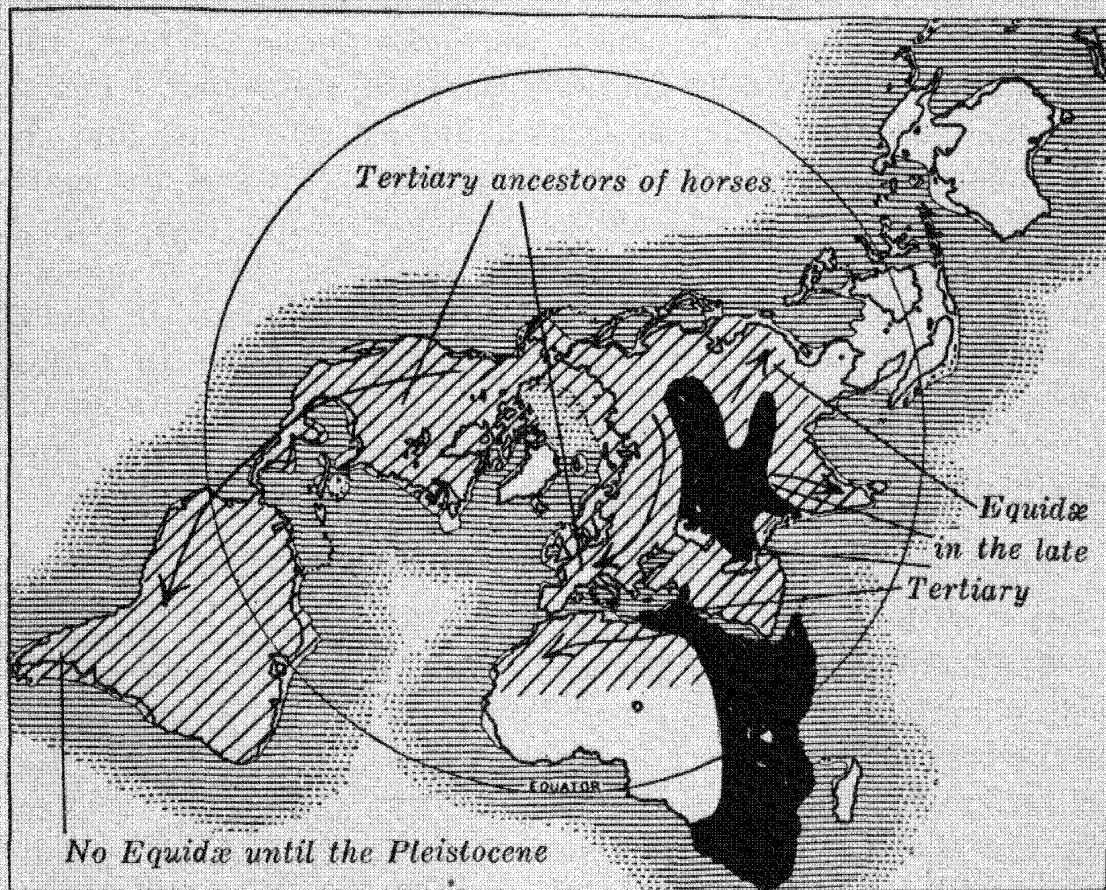


FIG. 2. The distribution of Equidae, living (solid black) and Pleistocene (shaded).

The palæontologic record reveals many examples of the rise and decline of genera. This is a factor that requires consideration when genera in different biologic groups are compared. The rapidity of spread is probably dependent, to some extent, upon the particular grade of generic vigor that a given group has attained at a given time. Thus, if the existence of a given land bridge of the Philippines coincided with the maximum generic vigor of a given set of organisms, this group would be far better represented in the Islands than if the bridge were passable during a period of generic decline only.

* *Geology* 3 (1906) 173-175.

The expansion and development of the modern flora, particularly the grasses and the dicotyledons, took place largely during late Mesozoic time. Modern floral types were well developed in the middle Cretaceous. It is generally admitted that Australia was probably separated from Asia in epi-Cretaceous time; that is, after the deployment of the higher plants. In contrast to the higher plants, mammals did not begin to attain dominance until the Eocene. On account of these developmental differences, botanical and certain zoölogical changes cannot be weighed upon the same scales with those of the higher mammals. Thus, modern genera in plants were, for the most part, well developed while Australia and Asia were still connected. Practically no placental mammal existed during this time, and the mammals were represented by marsupials. Many of the mammalian genera and species of the Pleistocene are now extinct. Change in plant species is probably no faster than in modern mammalian genera. In other words, generic changes in higher mammals may be roughly equal to specific changes in plants. Hence, in dealing with plants, species rather than genera should be used; but, unfortunately, this is impossible, since many plants remain undescribed in Papualand, Sundaland, and Wallacea.*

ZOÖLOGICAL AND BOTANICAL REGIONS

Some of the boundaries of the biologic divisions of the earth are decidedly indefinite. However, the various regions are exceedingly distinct, and the Australian Region is the most distinct. Great geographic separation does not necessarily indicate great separation in the biologic regions of the earth. As Wallace long ago stated, the Englishman is botanically and zoölogically at home in Japan; and, as he discovered, Lombok Strait, east of Java, separates two profoundly different zoölogic regions. Table 1 gives the major zoölogic divisions of the earth, according to Lydekker.† The slight modifications of Dickerson are italicized.

TABLE 1.—*Major zoölogic divisions of the earth.*

I. Neogæic Realm.

1. Neotropical Region: South and Central America, lowlands of Mexico and the West Indies.

II. Arctogæic Realm.

1. Ethiopian Region: Africa south of the Sahara Desert.
(a) Malagasy Subregion: Madagascar.

* Wallacea is defined on page 101.

† A Geographical History of Mammals (1896).

II. Arctogæic Realm—Continued.

2. Oriental Region: Southern peninsula of Asia, Malay Archipelago *including the Sunda Islands and Palawan and its dependent islands.*

(a) East Malayan Subregion (*Wallacea of this book*):
Timor, Celebes, and Philippines in part.

3. Holarctic Region: Northern Africa, Europe, Asia (except southern part), boreal North America.
4. Sonoran Region: Remainder of North America (except lowlands of Mexico).

III. Notogæic Realm.

1. Polynesian Region.
2. Hawaiian Region.
3. Australian Region including New Guinea and its dependent islands.

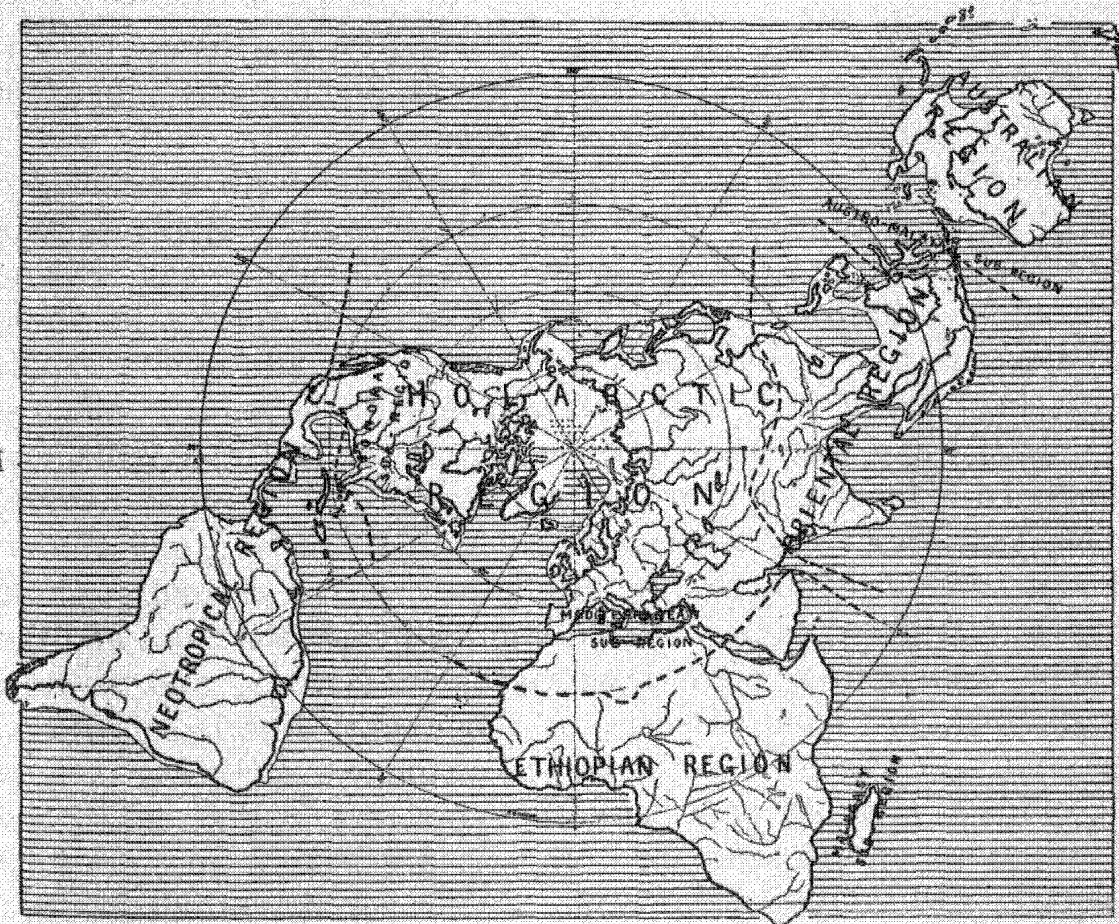


FIG. 3. The zoölogic regions of the earth on a north-polar projection. The areas on the continental shelf (within the 100-fathom line) are unshaded.

These regions and subregions are graphically shown by Matthew in his north-polar projection (fig. 3), which brings out with marvelous sharpness his idea of the vast importance of circumpolar distribution of plants and animals in the Northern Hemisphere. Matthew places the Philippines, an intermediate land connecting the Oriental Region with the Australian Region, as a part of the Oriental Region lying immediately north of his

Austromalayan Subregion. He describes the relations between them as follows:

The Oriental region corresponds in the eastern part of the Old World to the Mediterranean and Sonoran subregions, but, partly because it includes the great East Indian islands and partly because of the barrier interposed by the Himalayan ranges, it is more clearly differentiated from the Holarctic and may best be regarded as a region of itself.

Austromalaya is the debatable ground between the Oriental and the very distinct Australian region; but the consensus of opinion classes it by preference with the Australian. It includes Celebes, the Moluccas, Timor and smaller islands, and is separated from the Oriental region by "Wallace's Line."

The Australian region includes Australia, New Guinea, and Tasmania, and is the most remote and archaic of all the great (continental) regions of the globe. New Zealand is included in the Polynesian (island) region.

More recent researches somewhat modify Matthew's assignment of his Austromalayan Subregion by placing this subregion in the Oriental Region, not the Australian.

The present work is principally concerned with a relatively small area of the world, the Philippines; and if it places this Archipelago more precisely in the great biologic world scheme the effort will have been worth while. The results of these studies on the distribution of life in the Philippines indicate, in a broad way, that Palawan and its dependent islands, Balabac, Cuyo, and the Calamian group, faunally constitute a northern extension of Borneo, which is in the Oriental Region, thus sustaining the deductions of Everett, Worcester, and others. The remainder of the Philippines is the meeting ground of three migration routes; namely, an old dim trail from Formosa and the Asian mainland, a main highway from Borneo, and a good secondary road from Celebes. If a boundary line is considered necessary, Wallace's Line should be extended northerly instead of easterly so as to pass between Palawan and the rest of the Philippines, and to separate Luzon from Formosa upon its final easterly swing into the Pacific. Wallacea is delimited upon the southeast by Weber's Line (fig. 4).

Not every plant or animal requires actual land connections for distribution, but certain species do require such a definite medium before they can spread. Large animals such as the elephant, the rhinoceros, and the buffalo could not migrate from island to island by swimming or by using natural rafts. According to Matthew, it is highly probable that certain small mammals, snakes, and lizards could be transported by natural rafts across considerable stretches of ocean, and he cites the recorded observation of the drifting of a natural raft over a

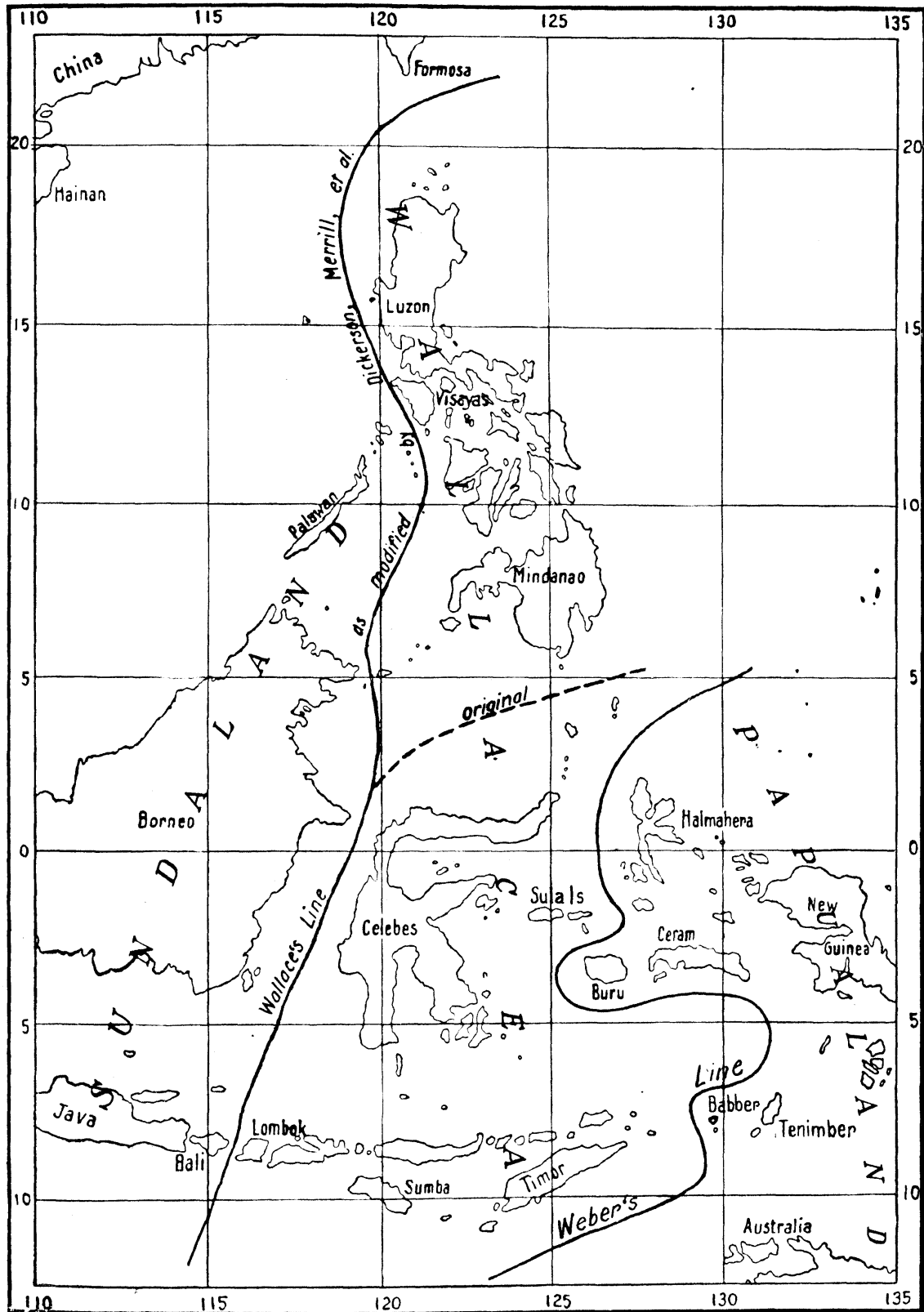


FIG. 4. Wallacea, the unstable area between Asia and Australia.

thousand miles. These natural rafts are nearly always reported from the vicinity of tropical rivers—the Amazon, the Ganges, the Congo, the Orinoco—and they are characteristically tropical. From time to time small animals have been reported upon them, and the distribution of reptiles and mammals upon

oceanic islands is shown by Matthew to be largely according to the size of the island masses.

In the Philippines it is highly probable that some of the smaller animals have been transported by rafts. Rafts, in such cases, are moved by ocean currents. The present distribution of certain genera and species in the Philippines is best explained as having resulted from this process. Thus, the nipa, the coco palm, and numerous strictly strand species in other groups, have seeds well adapted for transportation by currents, and for this reason the prevailing ocean currents are briefly described in another chapter. The prevailing winds also affect the distribution of certain plants and small animals. The well-known adaptations of certain plants for wind dispersal need not be described here in detail. Certain of the larger animals, including early man, are notable agents in the dissemination of many plants, insects, reptiles, and mammals.

Even after distribution, the problem of obtaining a foothold in a new environment is not always easily solved by a species. If the soil is sandy and a given plant, such as the nipa palm, has a natural habitat in mud, thousands of seeds of that plant may strand on a beach of coral sand and be unable to germinate. Moisture conditions also control the success of a new arrival. Temperature requirements are, of all necessities, the most important; and the limitation of the spread of animals and plants by this factor is well recognized by C. H. Merriam. According to Merriam, the northward extension of range of southern mammalian forms is limited by the temperature of the breeding season in which the total quantity of heat must reach a certain minimum, and the southward spread of northern forms is restricted "by the mean temperature of a brief period covering the hottest part of the year" in the United States. Similar conditions are encountered in the Tropics, and such distributional barriers as mountains are largely effective through the above-mentioned conditions of temperature, humidity, and suitable food. Of these, temperature is first in importance, and humidity and other causes are second. As is shown in another chapter, temperature within the Philippines varies but little from north to south at sea level, but varies greatly with altitude.

Many illustrations of such climatic changes can be seen in the Philippines, and persistent high altitudes in northern Luzon during late Tertiary, Quaternary, and Recent times have provided a continuous habitat for plants characteristic of temperate climates. A residual flora, chiefly Himalayan in origin,

and a residual insect fauna of Asiatic temperate regions have thus been preserved in this wonderful upland, but their southern migration has been limited by the excessive temperature of the lowlands.

GENERAL PRINCIPLES

Any local study of the distribution of life must begin with a consideration of Wallace's fundamental axioms and general principles;* namely, an adequate knowledge of the fauna and the flora of the whole world; a natural classification of plants and animals; the theory of descent with modification, evolution; the migrations of organisms during the geologic past, through palæontology; historic and stratigraphic geology and palæogeography; hydrography with particular attention to the contour of the ocean bottoms and possible ancient land connections now submerged; climates of the geologic past, their causes and effects; the permanence of oceans and the general stability of continents throughout geologic time.

It is self-evident that an adequate knowledge of the fauna and the flora of a region must be had before it is possible to discuss the origin and the distribution of life in that region, and increasing biologic knowledge of the whole world will aid greatly in placing a given region in its proper setting. Much of this knowledge can never be gained because the destruction of forests and the modification of habitats of many plants and animals have caused their extinction.

Palæontology, particularly that of the Mesozoic, the Cenozoic, and the Pleistocene, has greatly aided in firmly establishing the theory of evolution and in forming a natural classification of plants and animals. Much knowledge has been obtained by recent investigations in central Asia, a probable center of plant and animal evolution during the Mesozoic and the Cenozoic as well as during the Pleistocene and the Recent.

A study of the extent of land and sea during the Mesozoic, the Cenozoic, and the Pleistocene in any given region (that is, palæogeography) is possible only through the details obtained from stratigraphic geology; and more particularly is this true of a study of the marine and land formations within a given region. Closely connected with stratigraphic geology is the portion of oceanic hydrography that deals with the contour of ocean bottoms, since from this type of evidence the later land connections may be discerned, and in certain cases, particularly during the

* *Island Life* (1895) 7-10.

Pleistocene, the former positions of ancient straits and bays can be roughly delimited. Within the Philippines this interesting study yields much knowledge concerning the kaleidoscopic changes of the Pleistocene, through which is attained some idea of the causes of the differences among the faunal and floral areas within the Archipelago.

Cenozoic (Tertiary) and Pleistocene (Quaternary) climates also have had a profound effect upon life within the Philippine Archipelago. Glaciation in the Northern and Southern Hemispheres, particularly during the Pleistocene, and likewise deglaciation, produced great changes in the migration and the extinction of species in the temperate zones and probably indirectly affected life in the Tropics by the withdrawal of vast amounts of water from this region during glacial periods and the restoral of the water during interglacial periods. As Wallace stated, the general permanence of oceans and continents is a fundamental consideration, and the biologic data in the Philippines support this theory. However, his idea, that the greater the depth of a sea the greater the age, does not receive confirmation, since many of the deeps of Wallacea are of comparatively recent origin.

Since Wallace's time knowledge of the world flora and fauna has vastly increased, classification has advanced, and modern biology and palæontology have won almost universal acceptance of the theory of descent through modification. The advances of historic geology and palæontology have added greatly to the knowledge of the distribution of past life and also aided in establishing a natural classification of plants and animals. Hydrographic surveys have clearly delimited the edges of the continental platforms, and many of the depths of the remoter portions of the oceans have been made known. Broad biologic studies have brought to light more evidence of the processes of evolution and have firmly established this theory and its most general explanation, natural selection, in the minds of scientific and lay workers of the world. From such a base we are approaching the problem of the distribution of life in the Philippine Archipelago. However, we are not working under such conditions as did Wallace, a lone scientist who lived upon the local products of the country and traveled among the beautiful and distant isles of the Malay Archipelago in frail native sailboats. We have, as a working base, a modernly equipped building dedicated to Science; and, in the field, we enjoy infinitely better transportation and living conditions than existed seventy years ago.

PHILIPPINE GEOGRAPHY IN ITS BIOLOGIC ASPECTS

The Philippine Archipelago offers a great diversity of tropical habitats for plants and animals. It extends from Sibutu ($4^{\circ} 40'$ north latitude) to Y'Ami on the southern side of Bashi Channel ($21^{\circ} 5'$ north latitude), a distance of $16^{\circ} 25'$ of latitude; and from $116^{\circ} 50'$ to $136^{\circ} 35'$ east longitude. The coast line totals thousands of kilometers. The varying exposures to the shifting trade winds and typhoons, the great heights of mountains, a peculiar distribution of rainfall which is conditioned upon the two factors first mentioned, and the Kuro-Siwo are additional features in a wonderful habitat complex. This tropical archipelago comprises 7,083 islands; 466 of these have an area of more than 1 square mile each, and only 2,441 are named; 4,642 rocky islets and reefs are unnamed. The area of the whole group is 114,400 square miles, which is slightly less than that of the British Isles (121,753 square miles) and slightly greater than the area of the New England States and New York combined. More than half of this area is embraced by two islands; namely, Luzon and Mindanao. The areas of the largest ten islands, in order of size, are given in Table 2. The Philippines are a part of the Malay Archipelago. Some idea of the extent of this great group of islands can be gained from fig. 5, where the entire East Indies, drawn to scale, are superimposed on a map of the United States.

TABLE 2.—*Areas of the largest islands of the Philippines.*

	Square miles.
Luzon	40,814
Mindanao	36,906
Samar	5,124
Negros	4,903
Palawan	4,500
Panay	4,448
Mindoro	3,794
Leyte	2,799
Cebu	1,695
Bohol	1,534

Only 6,628 square miles are included within the seashore limits of all the rest. In round numbers between ten and eleven

million people inhabit these Islands. Owing to the very irregular distribution of the population and its great concentration around the large cities, the centers usually visited by tourists have been vastly altered by man; therefore, the traveling naturalist or the tourist who casually visits the Archipelago is apt to gain the impression that the flora and the fauna are rather poor.

DESCRIPTIONS OF THE LARGER ISLANDS

LUZON

Luzon, the largest island of the Archipelago, is characterized by its great irregularity and diversity of form (Plate 41). It contains a great central plain, which extends north from Ma-

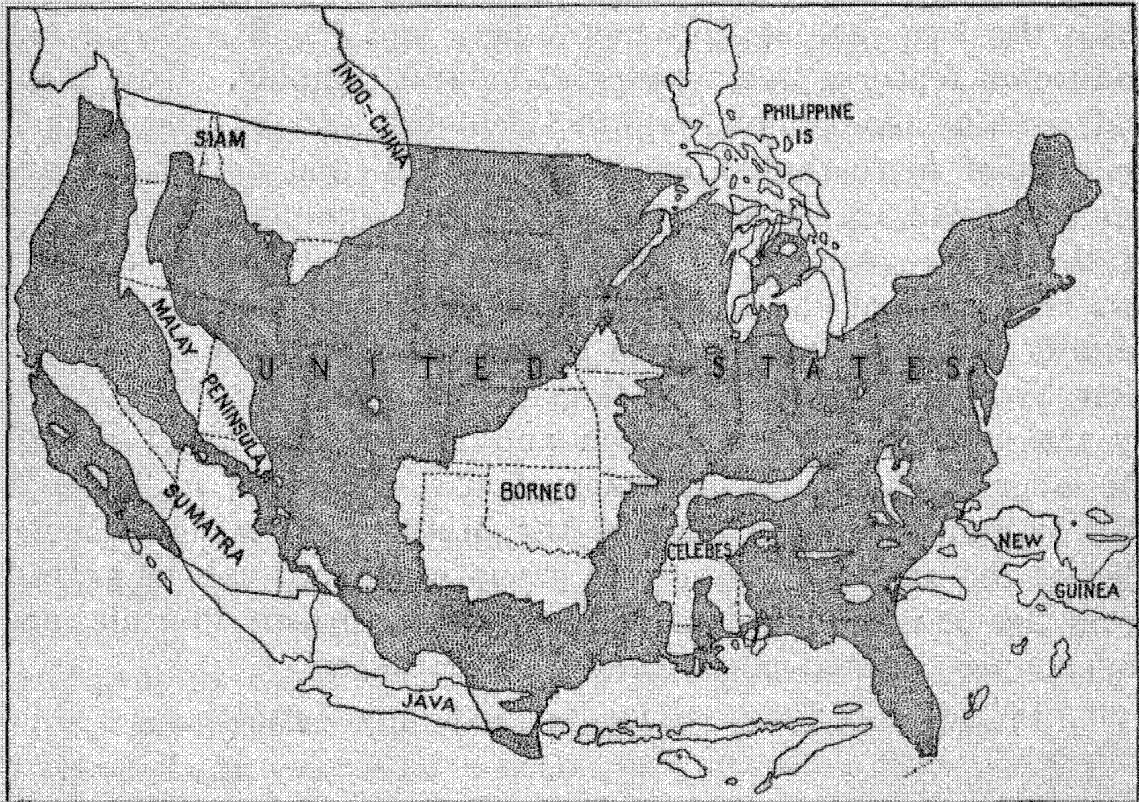


FIG. 5. The East Indies superimposed upon the United States.

nila Bay to Lingayen Gulf; Cagayan Valley, in the northeastern part, is almost as large.

The southeastern portion of the island is broken into a series of peninsulas; Camarines and Bondoc are the principal ones. These peninsulas have a general trend of north 30° west, but they differ markedly in one notable respect. Bulusan, in the southern part south of Sorsogon Bay; Mayon, in central Albay; Isarog, in central Camarines; and Mount Labo, farther north, dominate the scenery of Camarines Peninsula. This prospect

is in striking contrast to that of Bondoc Peninsula, whose low and rugged mountains are composed of sedimentary rocks. Northwest of Bondoc Peninsula and south of Manila the scenery is again dominated by prominent volcanoes; Banahao (altitude, 2,188 meters), Mount Maquiling, and a low but notable volcano, Taal, set in Lake Taal.

In northern Luzon the mountains have a decidedly more northerly trend. The Zambales Mountains, trending north 10° to 15° west, and the Cordillera Central of northern Luzon, trending north and south, are examples of this difference. The Zambales Mountains, which form the western border of the great central plain of Luzon, vary in elevation from High Peak (2,037 meters), the highest mountain, to Mount Pinatubo (1,781 meters), Mount Iba (1,605 meters), and the volcanic peak of Mariveles (1,420 meters). The last-named peak, which forms the north headland of Manila Bay, is a wonderfully beautiful landmark for this vicinity. The Cordillera Central is more notable than is any other mountain mass of the island, because of its uniformly great height. Mount Santo Tomas, near Baguio, has an elevation of 2,258 meters. Farther north, Mount Pulog attains the much greater elevation of 2,924 meters. There are several other mountains in this district that attain a general altitude of over 2,300 meters; namely, Mount Amuyao, Mount Pauai, and notably Mount Data with a plateau top. The last named is at the junction of the three main drainage lines of this region; namely, the Agno; the Chico and the Magat, two of the principal tributaries of Cagayan River; and the Abra.

The geologic recency of the mountains in northern Luzon is well marked. In part they have been sculptured from a great plateau, a few remnants of which still persist, and in part they are fault blocks recently formed. The most noteworthy of these remnants are Baguio Plateau, 1,500 to 1,700 meters in elevation, and Mount Data Plateau, the general elevation of which is approximately 2,300 meters. From the biologic point of view, this extensive uplifted region is important, for in this district a temperate climate prevails and there is a notable amount of temperate-zone vegetation. Northern Luzon, in some portions at least, has maintained heights of 1,300 to 1,600 meters since mid-Miocene time.

However, these heights have never been permanent in one locality, but have shifted from place to place. In other words, mountain-building forces in northern Luzon have been persistent

during a considerable portion of Tertiary time and consequently uplands have been maintained. The land assumed its present shape during the Pleistocene,* as the general evidence in this region indicates that Baguio Plateau was raised from near sea level to its present elevation. Much of this upland region has been deeply dissected by steeply sloping streams carrying the waters of tropical rains that descend torrentially when the typhoons of July, August, and September sweep across northern Luzon or between Luzon and Formosa.

Cagayan Valley extends north and south and occupies the eastern third of northern Luzon. This great broad valley is well watered by its master stream, Cagayan River, which winds in wide and complicated meanders in its lower half. Eastward, this valley is limited by the Sierra Madre Range—an almost unknown region. These mountains descend with great abruptness to the Pacific Ocean, and there are few harbors or possible landing places along that coast.

Owing to the complicated topography of Luzon and the varying trend of its mountain ranges and intermontane valleys, the greatest diversity of climate within the Archipelago occurs in this island. Climate within these islands is largely determined by the distribution of rainfall, which is conditioned by exposure to the prevailing wind and the direction of the mountain ranges that lie athwart this wind direction. A comparison of the relief map and the rainfall map will make these relations clear (Plates 7, 9, and 38).

MINDORO

South of Luzon, Mindoro, a compact island with a general trend of north 20° west, exemplifies the condition just described. Mount Halcon (altitude, 2,580 meters), in the northern part, and Mount Baco (altitude, 2,487 meters), in the central portion, are the principal peaks. Rugged, high-mountain topography characterizes central Mindoro, and only two faint trails, but rarely used, have been made across the island. The northeast trade winds that prevail during January, March, and April yield abundant moisture on the eastern side of the island, and the high central range largely rain-shadows the western half. In June, July, August, September, and October the prevailing southwest winds yield a great rainfall on the western side of the island, making the country well-nigh impossible to traverse

* I should say, during the Pliocene and the Pleistocene.—BAILEY WILLIS.

during those months. The eastern side, on the other hand, is relatively free from rains at that time. Man has made comparatively little progress in conquering Mindoro, and only on the southwestern side is there a large cultivated area. The island is in striking contrast with its southeastern neighbor Panay.

PANAY

The medial portion of Panay is either low, wide-valley land or gently rolling, low upland. The mountains of Antique Province on the western side of the island attain elevations of from 900 to 2,049 meters. The high portion of the range is in its central part; Mount Nangtud is 2,050 meters in altitude; Mount Malinao, 2,049 meters; and Mount Baloy, 1,728 meters. There are few passes across these mountains, through which the moisture-laden tropical trade winds blow. Owing to the north-and-south trend of the principal range, the low central portion of Panay is slightly rain-shadowed; therefore, central Panay has a rainfall well distributed throughout the year, and western Panay has a well-pronounced dry season. On the eastern side a lower mountain range, the peaks of which vary from about 400 to 600 meters, exerts little influence upon the life of the island.

MASBATE

In striking form contrast, the two-pronged island Masbate attracts the attention of even the casual observer. This low-mountainous island marks the junction of two of the dominant orogenic lines in the Philippines, which trend north 30° west and north 25° east, respectively. Since its mountains are of moderate height and in part trend with the prevailing winds, Masbate, like Panay, has a well-distributed rainfall and consequently small differences in temperature.

SAMAR

Samar, which lies east of Masbate, has a general trend of north 30° west, but lacks a well-defined central range. The greatest elevation of this island, 850 meters, is in the north-central part. As the map shows, several of the streams (for example, the Ulut and the Dolores) rise near the western coast and flow toward the east. A great rainfall prevails throughout the year, and consequently this island is heavily forested. The east-and-west-trending rivers would seemingly offer easy courses across the island were it not for their turbulent character during the periods of extreme high water. Samar is, in all

probability, essentially a broad, marine plain (or plains) formed during middle or late Pleistocene time, which has been uplifted and maturely dissected in late Pleistocene and early Recent times.

LEYTE

Leyte, Samar's immediate neighbor to the southwest, has a rugged and dominant central range with a trend of north 20° west. No wagon road traverses it. The only notable plain is that in the vicinity of Tacloban, the capital of Leyte Province. In general, Leyte is low-mountainous. The central range, broken by several passes, does not produce an entirely effective rain shadow, so that this island lacks sharply marked wet and dry seasons; the highest peak is approximately 1,300 meters in altitude.

BOHOL

Bohol has a roughly rounded form and has drainage on all sides from a central height of 800 meters; like Samar, it has a well-distributed rainfall. However, Bohol is less exposed than Samar, being somewhat sheltered by Negros and Cebu on the south and west and by Leyte on the northeast, and its annual rainfall is not as great as is that of Samar. In all probability Bohol, like Samar, has been rather recently elevated from the sea, and the streams have not yet been able to remove completely the traces of marine plains that border these islands.

CEBU

West of Bohol is Cebu, a long and narrow island, which trends north and south and north 5° east. This island has a very definite backbone, which extends from the southern to the northern end; but this backbone range is broken in several places by passes, two of which are traversed by modern mountain highways. Cabalasan (elevation, 1,013 meters), in the central portion, is one of the highest peaks in the island. Most of the other peaks, like Mount Uling, attain elevations of less than 750 meters. Much of this island is fringed by a low marine terrace (or terraces) which varies in elevation from 3 to 30 meters in the vicinity of Cebu city and Mactan Island. There is a marine plateau over 600 meters in elevation in the southern portion of this island. Cebu lies approximately parallel to the prevailing wind directions and on that account has a rainfall well distributed throughout the year and, for the Tropics, very moderate temperatures.

NEGROS

Negros is immediately west of Cebu and parallels that island. Tañon Strait, which separates these islands, is narrow and deep. The principal mountain divide in Negros has a north 5° east trend and lies close to the eastern side; therefore, the longer streams occur on the western side of Negros. These streams suddenly strike a comparatively wide coastal plain upon leaving the mountains. Consequently, they have built alluvial fans between the coastal plain proper and the higher mountains. This piedmont plain and the well-drained coastal region offer particularly fine areas for the agriculturist. The central range of Negros does not produce a very effective rain shadow, since several low passes break its continuity. This condition and the trend of the island, nearly parallel with the prevailing wind directions, give most of Negros an adequate, well-distributed rainfall. Canlaon Volcano, the highest peak in the central range, has an altitude of 2,438 meters.

PALAWAN

Palawan is rugged and elongate. The prevailing trend of the island, north 30° east, strikes even the casual observer. In outline Cebu is suggested, and in certain respects the two islands are similar, as each has a single dominant central range, and because of their central ridges and their narrowness neither has large rivers or river valleys. The detail of Palawan, however, differs from that of Cebu in that numerous excellent harbors (for example, Malampaya Sound and Ulugan Bay) have been produced by the recent drowning of fair-sized river valleys of a former cycle. Mounts Mantalinghan, 2,086 meters; Victoria, 1,781 meters; and Cleopatra, 1,585 meters, are among its higher peaks.

MINDANAO

The largest compact land mass in the Archipelago is in eastern Mindanao. Western Mindanao, however, is notably broken by several bays which interdigitate with the elongate, mountainous peninsulas. The wide marshy valley of Agusan River, which rises near the southern coast of the eastern portion of Mindanao, is sharply set off from the Surigao coast by the Diuata Mountains. This great fault valley offers a particularly good habitat for the plants and animals of the forested lowland region. In the southern portion of this island the wide flat

valley of Cotabato River, with a great series of tributaries, is a second notable lowland region little disturbed by man. In the north-central portion of the island is the great upland plateau of Bukidnon. Beautiful, lava-dammed Lake Lanao is a feature of this much-dissected lava plateau. This region, which varies from 600 to over 1,000 meters in elevation, is another biologic area intermediate between the lowlands and the true highlands of northern Luzon. Zamboanga Peninsula and dependent peninsulas form the western portion of Mindanao and are almost cut away from the island mass at Panguil and Illana Bays. Zamboanga Peninsula is, on the whole, rugged and mountainous; Mount Malindang (elevation, 2,616 meters), an isolated volcanic mountain, is its highest point. The major portion of Zamboanga Peninsula has approximately the same trend as Cebu, north 5° to 10° east; because of the central ridge, there is neither large river nor river valley in the southern portion. The islands of the Sulu Archipelago are dependencies of this western portion of Mindanao (Plate 3).

Mindanao is the second largest island in the Archipelago, and Mount Apo, a volcanic peak near Davao Gulf, is the highest elevation in the Philippines (2,929 meters). Such a height should afford a place for the preservation of a temperate-zone biota, but from all reports it appears that this mountain attained its present altitude during late Pleistocene and Recent times and hence has had no opportunity to obtain an extensive temperate-zone flora or fauna, or perhaps the small size of the elevated area has been an unfavorable factor.

Outside of northern Luzon Mount Mayon (elevation, 2,421 meters), Mount Banahao (2,188 meters), Mount Malindang (2,616 meters), and Mount Canlaon (2,438 meters) are sufficiently elevated to support temperate-zone species; but with the possible exception of Mount Malindang all of them have attained their present elevations during Recent and even during historic times, for historic eruptions have occurred from Mayon, Canlaon, and Banahao. Of the other notable heights in the Islands, Mount Halcon (elevation, 2,580 meters) and Mount Baco (2,487 meters), both in Mindoro, offer a southern temperate-zone habitat; but through orogenic movements these mountains have only recently attained their present great heights.

CLIMATE OF THE PHILIPPINES

Climate in a given part of the Philippines is largely dependent upon the prevailing wind direction coupled with the trend of the mountains in that region and the rainfall resultant upon the upward forcing of the moisture-laden trade winds by mountain slopes athwart their path. As these warm moist winds are forced upward, their air expands against the lessened air pressure; cooling results from this expansion, and the relatively cool air can no longer hold its former quantity of moisture. Condensation in the form of rain results.

The Philippines lie within the Tropics and consequently within the trade-wind belt and belt of equatorial calms that shift from north to south from the autumnal equinox in September to the vernal equinox in March, and from south to north in April, May, June, July, and August. Chiefly during the latter months the wind system is complicated by the typhoon, a cyclonic wind with a diameter of 500 to 800 kilometers which rotates counterclockwise about an area of low barometric pressure. This low-pressure area travels from east to west across the Philippines (except southern Mindanao) or north of the Islands across Formosa; then it recurves in the China Sea and passes northeast along the Japanese coast or, according to the season, strikes Asia and penetrates the interior where the typhoon is dissipated (fig. 6). When these cyclonic storms sweep across northern Luzon, great indraughts of south and southwest air are whirled upward and cooled, and much rain results (fig. 7). Where these winds strike mountains this effect is reënforced and the uplands of northern Luzon receive rain in torrential downpours of an intensity generally unknown to residents of the temperate zones. Baguio, for example, has an average annual rainfall of 4,597.6 millimeters (181 inches) and holds the world's record (1,168.1 millimeters) for the greatest precipitation during a period of twenty-four hours.

Coronas * recognizes four types of rainfall, and the map given here as Plate 38 is an adaptation of his climatic map. The detailed description of these types is printed upon the map. The relation between rainfall and topography can be seen by comparing Plate 38 with the relief maps.

The typhoons with the accompanying rains and cloudiness exert a marked effect upon the air temperatures. This is the explanation of the July sag in the temperature curve for Baguio

* Census of the Philippine Islands 1 (1918).

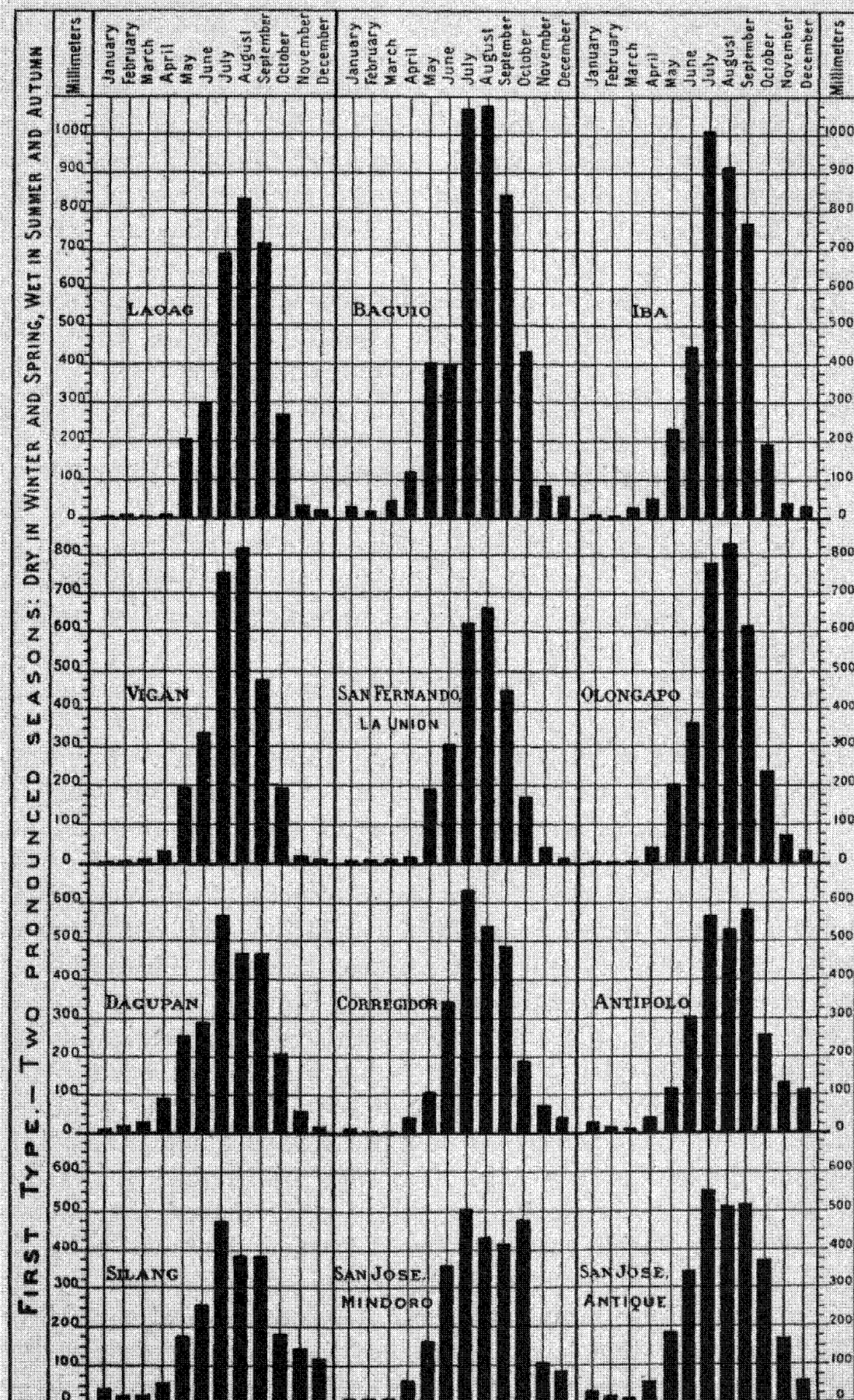


FIG. 7. Monthly distribution of rainfall at twelve stations in the Philippines.

given in fig. 8. During July very few sunny days occur in the vicinity of Baguio, as a great blanket of cloud obscures the sun and cuts off most of its heat. A further study of the annual temperature curves for the principal cities of the Philippines reveals that the usually small ranges of temperature for the Tropics are in marked contrast to the greater ranges for the North Temperate Zone. San Francisco, which has an oceanic climate, is exceptional.

The general evenness of temperature within the Philippines is monotonous to a native of the North Temperate Zone, and it has marked effects upon some temperate-zone plants. The diagrams show that Jolo has a very flat curve in contrast to Aparri, although the difference between annual temperatures at the southern station and at the northern station is but 1.2° C. The annual range at Jolo is in round numbers 3° C., whereas that of Aparri is about 8° C. The increase in range from southern stations to northern stations is progressive and, in general, is characteristic for places in which otherwise similar conditions exist (fig. 9).

Father José Algué, director of the Philippine Weather Bureau, long ago pointed out that in all probability typhoons are intimately connected with temperature and humidity conditions in the region east of the Philippines. Unfortunately, lack of funds has prevented the Government of the Philippine Islands from undertaking any research into the relationship between the temperatures of the Pacific Ocean and the formation of the typhoon. That there is a direct relation between oceanic temperatures and the air temperatures over the Philippines is an entirely reasonable supposition; and the lack of any marked difference between the annual temperature of Aparri and that of Jolo, for example, is very probably due to the equalization brought about by winds blowing across the warm equatorial waters of the Kuro-Siwo that flow northward along the eastern coast of the Philippines (fig. 10). The Philippines and Gilolo act as blocks to the farther westerly progress of the surface waters of the Pacific that are forced toward the equator by the trade winds. Well-marked depths occur off Mindanao, Samar, and northern Luzon, and the shelf seas on the eastern side of the Philippines—that is, the portion of the sea covered by waters 100 fathoms or less in depth—are exceedingly narrow. Probably owing to this abrupt change in submarine topography, the northerly deflection of these equatorial waters is greatly increased. As the relief maps (Plates 3 to 9) show, there are a

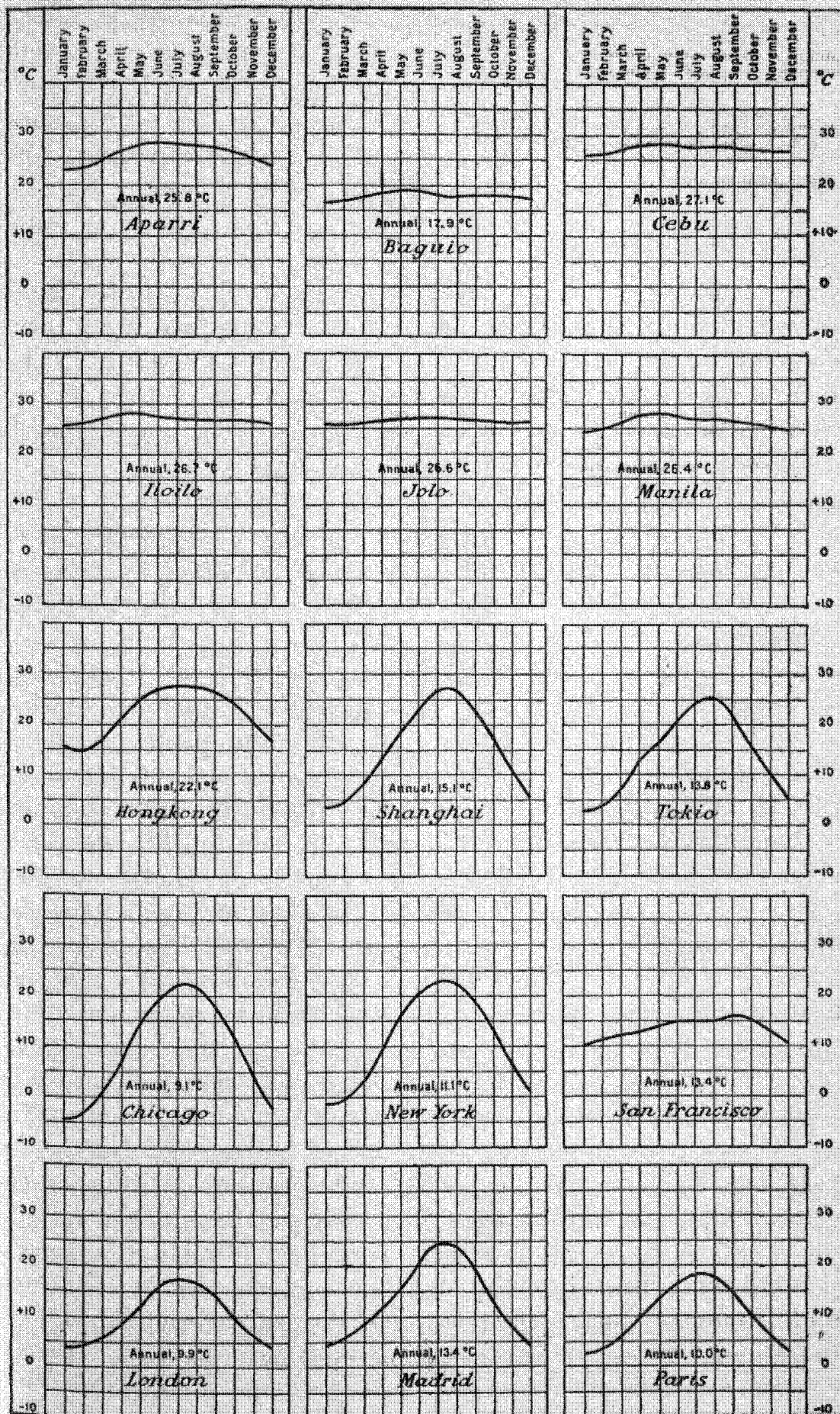


FIG. 8. Temperature curves of some of the principal cities of the world and of some cities in the Philippines.

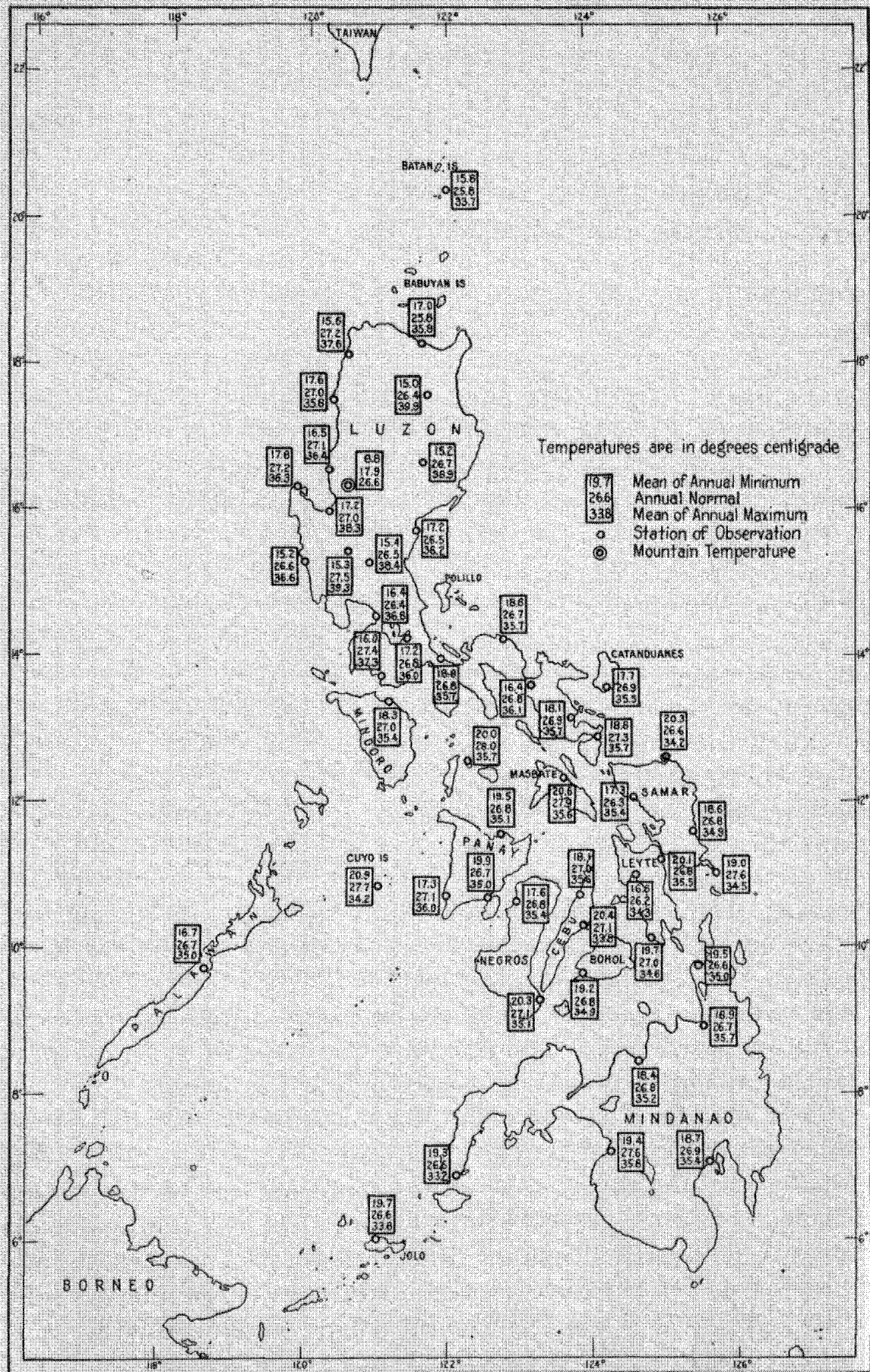


FIG. 9. Temperature map of the Philippines.

few breaks in this deflection wall, but these breaks are not sufficient to dissipate a definite north-flowing current (fig. 10).

Oceanography has been greatly enriched by the careful researches of the Germans in these waters, and most of the knowledge concerning the conditions that prevail in the region east of the Philippines is due to the discoveries of Kurtz and his coworkers during the voyage of the *Planet*.^{*} The temperature readings taken by these voyagers on one trip from Hongkong to Matupi indicate that the waters of the Kuro-Siwo become progressively cooler as they are forced in a northerly direction. This is what one would logically expect, since these warm waters are traveling from the Torrid to the North Temperate Zone and doubtless lose heat to the overlying air and to the water through which they flow. The accompanying map (fig. 11) and Table 3 indicate the magnitude of such temperature changes; the changes are very slight when contrasted with the marked difference between marine temperatures of the waters northwest of Formosa and of those immediately east of Formosa and Luzon.

It is apparent from the conditions described that the Kuro-Siwo forces a marked temperature salient into the chill of the temperate-zone waters. The water temperatures of the Batan Islands for March are decidedly higher than the minimum air temperatures for this region. The map, fig. 9, gives the annual minimum air temperature as 15.8° , which would be far too cold for the growth of corals if the coral polyps were exposed to such

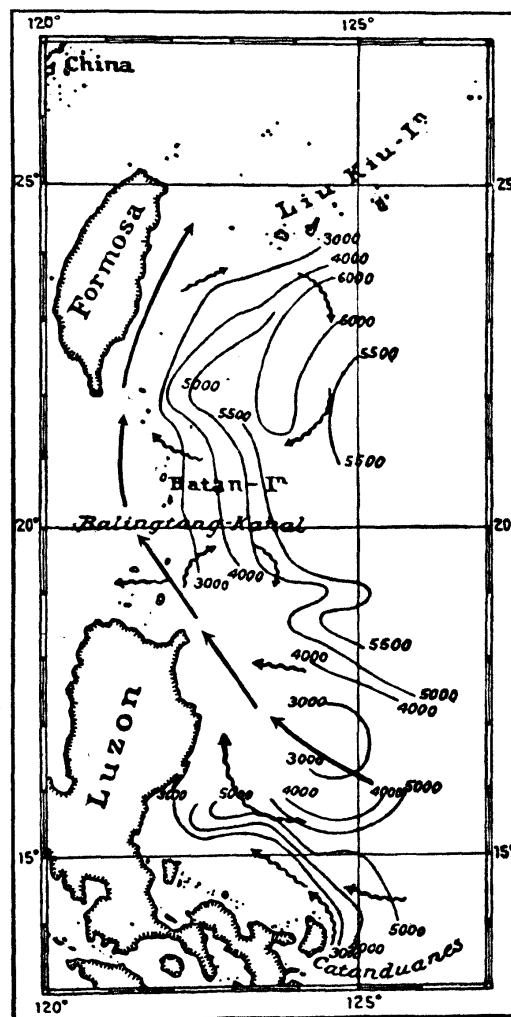


FIG. 10. The track of the Kuro-Siwo, east of the Philippines. Arrows indicate current direction. Isobaths in meters.

^{*} Ozeanograph. Arbeiten S. M. S. Planet und die Reise von Hongkong nach dem Bismarck Archipelago, Annalen der Hydrographie und Maritimen Meteorologie (Oct. 1907) 441-446.

TABLE 3.—*Temperature observations of the Planet, Hongkong to Matupi.*

Date.	Time.	Position.		Temperature.	
		North latitude.	East longitude.	Air.	Surface water.
1907	a.m. p.m.	° '	°	°C.	°C.
March 18.....	8	22 38	115 40	13.32	16.4
March 19.....	8	23 20	117 20	13.6	14.4
March 19.....	4	23 55	118 0	12.8	12.6
March 24.....	8	25 14	120 3	14.0	13.6
March 24.....	2	25 28	120 51	15.8	13.1
March 24.....	4.30	25 32	121 10	16.5	20.1
March 25.....	8	24 38	122 35	23.2	25.7
March 25.....	4.20	24 18	123 10	24.9	26.3
March 25.....	8	23 55	123 22	25.2	26.1
March 26.....	9	23 15	124 10	25.1	25.3
March 26.....	4	22 49	124 43	25.3	25.3
March 27.....	8	21 42	124 57	25.3	25.2
March 28.....	8	20 29	122 40	24.5	25.2
March 29.....	8.20	19 35	123 25	25.6	25.3
March 30.....	9	19 10	124 45	25.7	25.8
March 31.....	9	17 45	124 49	26.0	26.5
April 1.....	8	16 9	124 45	26.4	26.8
April 2.....	8	14 2	124 26	26.5	27.0
April 2.....	4	14 4	124 49	26.7	27.0
April 3.....	8	14 4	126 6	26.1	26.8
April 4.....	8	13 59	128 2	25.4	26.9
April 5.....	8	13 36	130 7	25.0	27.3
April 6.....	8	13 0	131 51	26.3	27.1
April 6.....	4	12 45	132 27	27.2	27.3
April 7.....	8	11 59	133 16	27.0	27.3
April 8.....	8	11 15	134 30	27.3	27.3
April 9.....	8	9 49	135 59	26.0	27.6
April 10.....	8.45	9 30	137 56	26.2	27.6
April 15.....	8.30	9 57	139 27	26.6	27.8
April 17.....	10.15	(a)	(a)	28.0	28.0
April 20.....	8.30	9 20	138 0	27.7	28.3
April 21.....	8	7 20	135 12	28.2	28.5
April 28.....	8	6 5	138 42	28.8	29.3
April 29.....	8	4 5	138 42	28.8	29.3
April 30.....	8.15	1 44	140 50	25.9	29.3
May 1.....	8.15	0 10	142 30	27.9	28.9
May 2.....	8	0 58	144 40	26.9	28.8
May 3.....	8	1 26	146 27	28.4	28.9
May 4.....	8	1 37	148 42	27.9	28.9
May 7.....	8	4 5	152 10	28.2	29.0

^a In the Ululssi Lagóon.

a temperature. However, fringing reefs are reported by several observers around these islands; their existence would indicate that the ocean waters in this region do not follow air temperatures closely, as a limiting temperature for the reef-forming

coral polyps is 20° C. Reef corals also fringe the islands of the Riu Kiu group as far north as 29° north latitude, which fact indicates that the temperatures of the waters south and east of this region are 20° and above. These oceanic temperatures have a far smaller range than do the overlying air temperatures for this region, and this indicates a well-marked difference between the temperatures of the air and of the surface waters of the Pacific Ocean in this region.

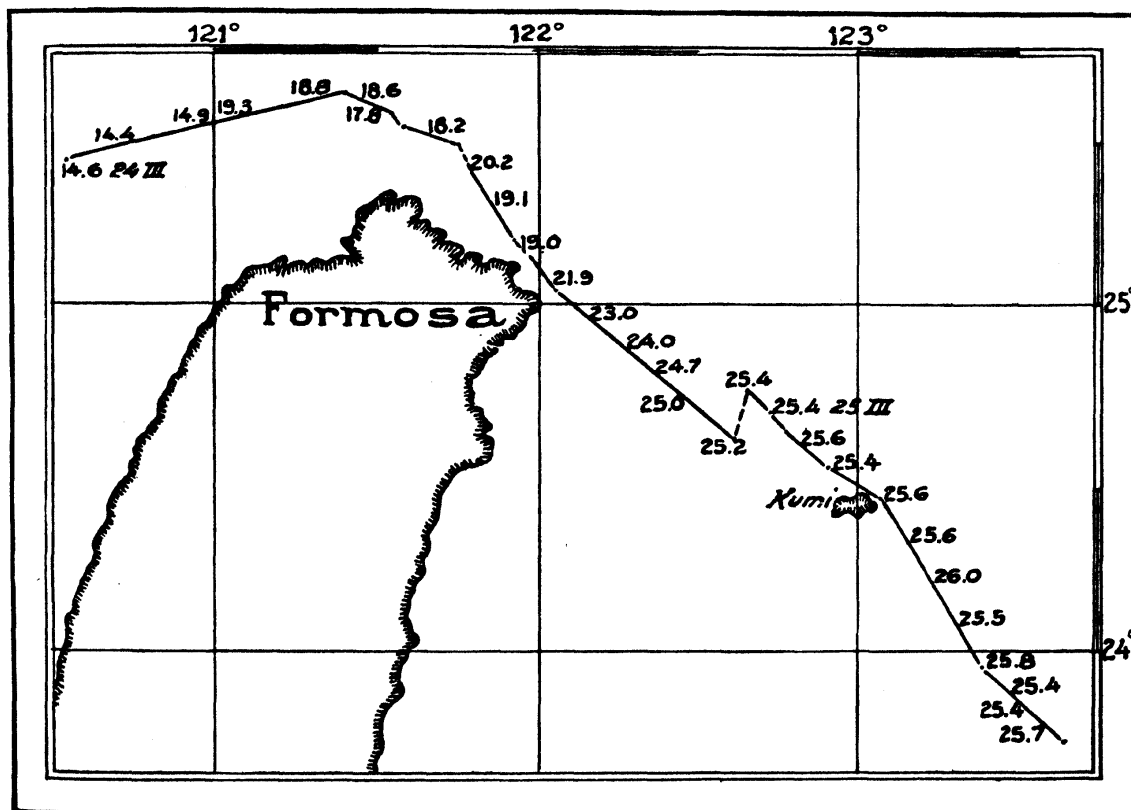


FIG. 11. The temperatures, in degrees centigrade, of surface waters north and east of Formosa.

Nautical charts indicate that the currents in the equatorial regions are deflected in a northerly direction by Java, Sumatra, and the Malay Peninsula into the China Sea, and equatorial temperatures are shifted northward to a certain extent in the waters west of the Philippines. However, this deflected current is by no means as strong as the Kuro-Siwo, since the waters of Hongkong are far too cold for typical reef corals. Such currents in equatorial regions have a great equalizing influence, and the remarkably low range in air temperatures for the East Indies is doubtless due to this tempering effect. This subject is referred to in the chapter on the Tertiary and Quaternary climates in this region. The Kuro-Siwo, owing to its great

uniformity in temperature and its small temperature range, has enabled many of the equatorial marine species to live much farther north than would be possible in the mid-Pacific for similar latitudes. Although the air temperatures do not follow closely those of the waters of this current, the annual temperature of the Philippines is made more nearly uniform than would be possible in a continental land mass. On this account, sea-level floras and faunas in the Philippines from north to south exhibit a remarkable uniformity.

TABLE 4.—*Geologic chronology for North America.*

[Classification based on superposition of strata, and erosion intervals; correlation by means of fossils.]

Era.	Major division.	Period.	Epoch.		Advance in life.	Dominant life.
Cenozoic (modern life).	Quaternary.	Glacial.	Recent (alluvial or post-glacial).		Rise of world civilization. The era of mental life.	Man.
			Pleistocene.	Cascadian revolution.	Periodic glaciation. Extinction of great mammals.	
	Tertiary.	Late Tertiary (Neogene).	Pliocene.		Transformation of man-ape into man.	Mammals and modern floras
			Miocene.		Culmination of mammals.	
		Early Tertiary (Paleogene).	Oligocene.		Rise of higher mammals.	
			Eocene.		Vanishing of archaic mammals.	
		Epi-Mesozoic interval.	Lance.	Laramide revolution.	Rise of archaic mammals.	
					Extinction of great reptiles.	
	Late Mesozoic.	Cretaceous.	Montanian	Coloradian.	Extreme specialization of reptiles.	Reptiles.
		Comanchian.			Rise of flowering plants.	
Mesozoic (medieval life).	Early Mesozoic.	Jurassic.			Rise of birds and flying reptiles.	
		Triassic.			Rise of dinosaurs.	
	Middle Mesozoic.	Epi-Paleozoic interval.			Extinction of ancient life.	Amphibians and lycopods.
					Rise of land vertebrates. Rise of modern insects and ammonites. Periodic glaciation.	
		Permian.		Appalachian revolution.	Rise of primitive reptiles and insects.	
		Pennsylvanian.			Rise of ancient sharks.	
		Mississippian.	Tennesseean.		Rise of ancient sharks.	
			Waverian.		Rise of echinoderms.	
Paleozoic (ancient life).	Late Paleozoic or Carboniferous.	Devonian.			Rise of amphibians. First known land floras.	Fishes.
		Silurian.			Rise of lung-fishes and scorpions.	
	Middle Paleozoic.					
	Early Paleozoic.	Ordovician.	Cincinnatian.		Rise of land plants and corals.	Higher (shelled) invertebrates.
			Champlainian.		Rise of armored fishes.	
			Canadian.		Rise of nautilids.	
			Ozarkian.		Rise of shelled animals.	
		Cambrian.	Croixian.		Dominance of trilobites.	
			Acadian.			
			Waucobian.		First known marine faunas.	

AREAL, STRATIGRAPHIC, AND HISTORICAL GEOLOGY OF THE PHILIPPINES

As Wallace long ago pointed out, the importance of the geologic record in interpreting the life of the present time is exceedingly great. A brief sketch of Philippine geology in its world relation is here given; the subject is more fully treated in the chapter on the palæogeography of the Philippines. Tables 4 and 5, abridged from Pirsson and Schuchert,* can be consulted for more detail. The portion of geologic time known in the Philippines is remarkably small when the general geologic record of the world is considered. The later and better-known half of this record has been in large part deciphered through a study of the remains of life entombed in marine sediments of ancient seas and in land-laid deposits.

Of the record of the geologic chronology (Table 4) only the last quarter is represented in the whole of the East Indies; that is, from Permian to Recent. In the Philippines only a small portion of the Mesozoic era, the Jurassic period, is known; and in the Cenozoic era, only the upper portion, Miocene, Pliocene, Pleistocene, and Recent epochs have been recognized.†

The fundamental datum plane for discussion of the origin of life in the Philippines is at the beginning or in the lower portion of the Eocene. The well-preserved land vertebrate faunas found in beds of this age in Asia, Europe, and North America clearly indicate land vertebrates similar to the marsupials at present existing in Australia. The native fauna of Australia contains no representative of the larger placental mammals except the dog, and the latter may have been introduced by man. Mammals such as the horse, the elephant, the cow, and the buffalo did not attain dominance until the Oligocene and the Miocene in North America, Europe, and Asia. The almost entire absence of placental mammals from Australia indicates that Australia was cut off from Asia and isolated before the present dominant mammalian families attained great importance. Hence, the occur-

* A Text-Book of Geology. New York, John Wiley & Sons, Inc., 2d rev. ed. (1920).

† Possibly the earlier Tertiary is represented.—BAILEY WILLIS.

rence of a single large native mammal in any of the islands of Malaysia is suggestive of probable connections with the mainland of Asia during the Tertiary after the middle Eocene.

That the Philippines had Asiatic connections is shown by the occurrence of the timarau in Mindoro, the chevrotain in Balabac, and deer in many of the larger islands. If the connections with Australia and New Guinea were very strong at any time during the Tertiary, a few marsupial representatives should be expected; but, so far as known, none exists. Of course, in times past the mammals may have been better represented in the Philippines, as indicated by the reports of *Stegodon*, an elephant of Pliocene age, from Mindanao, and of an immature tooth of *Elephas*, from a small island in Lingayen Gulf. The explanation may be offered that had a considerable land mass existed a subsequent extensive drowning would have produced an archipelagic condition, which would have been detrimental to the maintenance of large mammals; but, in such a case, there should be evidence of it in the Miocene, the Pliocene, and the Pleistocene of the Philippines. Such evidence is exceedingly meager.

TABLE 5.—*Geologic chronology for North America.*

Pre-Cambrian history (after Barrell); Archean of earlier authors.

[Classification based on sequence of rocks, crustal movements, and cycles of erosion. Order of events according to Coleman. Correlation without the aid of fossils.]

Great Epi-Proterozoic interval. Over much of the earth unconformity extends to Algomian revolution.

Late Proterozoic (primitive life) age of primitive marine invertebrates (fossils almost unknown). Delimitation of base of this age indefinite.

Ep-Algomian interval. Peneplanation of mountains and continents. Early Proterozoic (primitive life). Age of primitive marine invertebrates.

Ep-Archæozoic interval. Profound erosion of mountains and continents.

Archæozoic (primal life). Age of unicellular life; Protozoa and Protophyta (fossils unknown).

The unrecoverable beginning of earth history.

Cosmic history.

Before an attempt is made to indicate in a geologic time scale the periods of probable southerly connections (and practically all the evidence indicates that the Philippines have within the Tertiary been connected in a southerly direction), a consideration of the known distribution of the Tertiary sediments is necessary. Martin has described an extensive marine invertebrate fauna of Eocene age from Java. Marine Eocene has likewise

been reported from Sumatra, Borneo, Australia, and New Zealand. Eocene is represented in Borneo, according to Martin, by both marine and brackish-water facies; the latter clearly indicates an Eocene Bornean island. Martin has described an extensive fauna from Java which he has assigned to lower Miocene, and recently he has assigned certain strata in Celebes to the Oligocene. Certain strata in Sumatra and Borneo are also referred to this epoch.

The most-widespread horizon is that characterized by *Vicarya callosa* Jenkins and several species of large unicellular forms referred to *Lepidocyclina* of probable upper, middle, and lower Miocene age. Extensive deposits representing this stage occur in Sumatra, Java, New Guinea, Celebes, and the Moluccas, and through recent work the stage is recognized as being distributed throughout the Philippines and in Formosa. In the Philippine Islands this horizon is called the Vigo group. Surely, during this stage Malaysia was, as it is to-day, an extensive archipelago.

The Miocene horizon of *Lepidocyclina* and *Vicarya callosa* in the Philippines is discussed on page 76.

GEOLOGY OF THE PHILIPPINES

THE MESOZOIC

Warren D. Smith first recognized in certain cherts and slates in Ilocos Norte unicellular forms belonging to Radiolaria, which appear to be of probable Jurassic, middle Mesozoic, age.

In certain localities in Borneo, rocks of proved Upper Cretaceous age rest unconformably upon the older radiolarian beds; so that it is clear that the upper possible limit, Lower Cretaceous, is fixed for these cherts. Hinde compared these Bornean species of Radiolaria with radiolarian faunas elsewhere and concluded that their age is Jurassic.

The relations of these radiolarian cherts to the serpentines, schists, slates, marbles, and diorites, which make up a basement complex, is not clear. Smith's opinion is that the serpentines and diorites are intruded in the cherts and schists and are of post-Jurassic age.

THE TERTIARY

The lowest portion of the Tertiary, the Eocene, has not been recognized with certainty in the Philippines, although rocks of this age occur in Japan and Formosa to the north and in Borneo and Java to the south. Likewise, horizons of Oligocene age are not positively known. In certain localities, Eocene and Oligocene times are represented by a mere line of unconformity

between the basement complex of diorites and associated schists and the sedimentary rocks of Miocene age. In other words, a portion of the Philippines was a land mass during the Eocene; therefore, no marine sedimentary beds of Eocene age occur in certain regions.

THE MIOCENE; VIGO GROUP

Rocks of Miocene age have been recognized in most of the larger islands of the Philippines. Because of their widespread occurrence and because of the presence of oil and coal in these rocks, this portion of the Tertiary is best known. The type locality of this group is on Vigo River on the east side of Bondoc Peninsula, Luzon. The oldest rocks here recognized consist of shales and sandstones from 1,000 to 1,700 meters in thickness, the Vigo group and its uppermost member, the Canguinsa formation. The strata as exposed in the vicinity of Vigo River are steeply dipping, black, organic shales, sandstones, and minor lignitic beds, which are unconformably overlaid by the Malumbang formation. The Vigo group, even omitting the Canguinsa formation, is composed of two or three mappable units, or formations, and hence a group name is the correct designation. Detailed mapping immediately west of the type locality and directly connected with it by stratigraphy disclosed these facts.

The conditions of deposition during Pliocene, Pleistocene, and Recent times in the vicinity of Bondoc Peninsula are essentially the same. The deposition during Vigo time was in marked contrast with that of the present in that the contributing land masses consisted largely of diorites, schists, and serpentines or peridotites from which the deposits were probably derived. In some places the material contained in the Vigo sandstones is very coarse, and conglomerates occur locally in Bondoc Peninsula, and on a large scale in northwestern Leyte, east of Tababunga Barrio where they in part closely resemble characteristic desert fanglomerates.

The small amount of Vigo sediments derived from volcanic rocks indicates that during Vigo time volcanism was not widely prevalent, in marked contrast to the prevalence of this phenomenon during the Pliocene, the Pleistocene, and the Recent. However, the Canguinsa formation at its type locality in Bondoc Peninsula and in the northwestern peninsula of Leyte consists of tuffs and tuffaceous sandstones. The time represented since the beginning of the Vigo is evidently long; therefore, and on faunal grounds as well, the Vigo group appears to be as old as

the Miocene,* and the Malumbang probably represents at least a portion of the Pliocene.† The time represented by the unconformity between these horizons was sufficient to allow for the reduction of many of the mountains formed at the close of the Vigo to nearly base level before the region was again gradually lowered to receive its great load of Malumbang coralline limestone and associated marls in the clear, warm, shallow water of a tropical Pliocene sea. Likewise, the orogenic movements that ended the Malumbang were fairly long continued, and the erosion interval that preceded the formation of Pleistocene terraces was not a brief one.

THE PLIOCENE; MALUMBANG AND BANISILAN FORMATIONS

The Malumbang Pliocene is, like the Vigo group, rather widespread throughout the Philippines, and its unconformable relations with the underlying Vigo are apparent at many places. Malumbang has been recognized in the vicinity of Baguio, Luzon, where the limestones of Trinidad Gap and Mount Mirador have yielded pelecypods, gastropods, and corals, which apparently are referable to the same stage as are those of the type locality of the Malumbang formation on Bondoc Peninsula. The Malumbang also occurs in Samar, where its older conglomerates and agglomerates have yielded *Lepidocyclus* remains of reworked Vigo. Schenck's careful study of these rocks of Samar shows that there was an extensive period of erosion between the Malumbang and the Vigo-Miocene; in fact, his rock samples clearly demonstrate this unconformable condition. The Malumbang has been recognized in Leyte, Mindoro, Mindanao, and Cebu. The Malumbang fauna is closely allied to the Pleistocene and the Recent faunas of the Philippines; and, although the corals have not been studied in detail, they are at least generically the same as the Recent corals of the Philippines and apparently most of them are specifically identical. Both lithologically and faunally this formation is in sharp contrast with the Vigo.

As von Drasche pointed out, the great altitude of the coralline limestone near Baguio is very striking, and the amount of move-

* Or even older.—BAILEY WILLIS.

† Judging by the physiographic maturity of the plateau of northern Luzon and the Diwata Range of Mindanao, the uplifts have been exposed to subaërial erosion since early Miocene time. If this be so the limestone involved in the structure of these masses must be pre-Miocene and probably Oligocene.—BAILEY WILLIS.

ment in northern Luzon since these Pliocene coralline limestones were deposited is very great. Mount Mirador is 1,512.5 meters in elevation, and similar limestones are reported from Sagada at 1,372 meters by Smith.*

Apparently associated with these coralline limestones are some fine-grained tuffs yielding a fine flora which Merrill describes as follows:

The fossil remains, mostly remarkably clear leaf impressions, all, or nearly all, represent species still living in the Philippines at low and medium altitudes, and an examination of the material shows that the forest in the Bontoc locality was a typical mixed dipterocarp forest such as is found to-day in all parts of the Philippines, where primeval vegetation persists, from sea level to an altitude of about 800 meters. None of the species is found to-day within the limits of Bontoc Subprovince, and very few of them are to be found in any part of Mountain Province. None of them is found above an altitude of approximately 800 meters, while the present altitude of the fossil-bearing strata is 1,500 meters.

Among these fossils Merrill found specimens of the following living species:

Dipterocarpaceæ: *Shorea polysperma* (Blanco) Merrill; *Shorea guiso* (Blanco) Blume; *Shorea* sp.; *Anisoptera thurifera* (Blanco) Blume.

Lauraceæ: *Beilschmiedia cairocan* Vidal; *Phoebe sterculioides* (Elmer) Merrill.

Guttiferæ: *Calophyllum blancoi* Planchon and Triana.

Tiliaceæ: *Diplodiscus paniculatus* Turczaninow.

Menispermaceæ: *Anamirta cocculus* (Linnæus) Wight and Arnott.

Cyperaceæ: *Mapania humilis* (Hasskarl) F.-Villar.

These species are essentially characteristic of the present low-altitude primary dipterocarp forests of the Philippines; therefore, great elevation must have taken place here since this tropical, low-altitude flora flourished on the present site of Sagada.

The tuffs and their associated coralline limestones are probably equivalent to the Malumbang-Pliocene. Apparently, plants of the tropical regions have changed but little since the Pliocene, thus illustrating the slowness of evolutionary change in these climes.

The Pliocene was marked by extensive lava outpourings, and much of the areas of andesites and basalts and their derivatives was formed during this time. In lower Bued River Cañon in the Baguio district, for example, there is a great thickness, at

* Philip. Journ. Sci. § A 10 (1915) 194.

least 900 meters, of conglomerate, made up largely of andesitic boulders. Luckily, these folded strata yielded coral boulders the components of which are referable to Pliocene or Recent species. This great mass of volcanic conglomerate is associated with andesitic dikes in the same region. The Guadalupe tuffs and the Antipolo basalts and agglomerates, both near Manila, are probably also referable to the Pliocene. The relationships between the Malumbang of Pliocene age and the Banisilan formation of Mindanao are not entirely clear. It seems probable that the Banisilan formation, which typically occurs at Banisilan, Cotabato Province, represents upper Pliocene. The tuffaceous sandstones and tuffs are occasionally interbedded with coralline limestone. Beds of this stage of the Pliocene have also been correlated with those in Agusan Valley, Mindanao, through the identity of molluscan and coral species.

THE PLEISTOCENE

A thorough understanding of the Pleistocene can be had only through a careful study of the physiography of the region, and in this connection a type of physiography characteristic of the Tropics requires specific attention. The conditions of formation of characteristic coral reefs are of great importance to the student of tropical insular geology. The interpretation of the development of land forms and the recent movements and sea withdrawals from portions of the Philippine Archipelago is obtained only through a study of the different types of coral reefs.

CORAL REEFS AND THEIR FORMATION

Coral reefs are characteristic physiographic features in the Tropics made principally through the activities of corals and calcareous algæ. These reefs give excellent criteria concerning changes in the level of the sea or the movements of the land at varying stages and at the same time indicate clearly the limiting temperatures of the tropical waters. How coral reefs may indicate such data will be understood after the growth conditions of reef-forming corals have been stated.

Dana and Darwin determined the suitable conditions for the growth of coral reefs; namely, the water must have a mean temperature of not lower than 68° F. (20° C.), and it must be clear and salty. Therefore, corals do not flourish opposite the mouth of a large river, as the water is too muddy and its salinity too low. Coral reefs develop only in water that is less

than 240 feet (40 fathoms) deep, and corals flourish in water less than 150 feet (25 fathoms) deep. The reef-forming species must be supplied with an abundance of food brought by currents. The ever-changing equatorial currents driven westward by the trade winds produce a notable development of coral reefs on the eastern side of the continental and insular masses in the Pacific Ocean, in contrast with the feeble reef development on the western side. Such, in brief, are the living conditions for modern reef corals, and these conditions doubtless have controlled the growth of coral reefs since the beginning of the Pliocene in the Philippines, as many of the species that flourished during the Pliocene still live in Philippine waters.

The living coral polyp is a simple, fixed, jellylike animal with a skeleton of limestone. The coral polyps, in general, rest first upon a solid substance like rock or, as the coral colony grows outward and upward, upon the skeletal limestone left by their forbears. Owing to the great branching of certain treelike types and the large, rounded coral heads (some of which measure 4.5 meters across), a platform limited in upward growth by the level of the sea is built upward and outward. Gradually the interspaces are filled by the fragments of branches of the tree-like forms broken during storms, by the shells of marine invertebrates, and by the coralline skeletons of marine algæ. The actively growing coral reef is exposed during the lowest tides of the month for short periods. On the outer edge of the reef the reef-building corals flourish best, because the constantly moving water brings abundant food and lime for their skeletons, and because the churning by the surface waves thoroughly aerates the water, thus supplying the amount of oxygen necessary for their growth.

Dana and Darwin recognize three classes of coral reefs; namely, fringing reefs, barrier reefs, and atolls.

Fringing reefs.—Fringing reefs are very numerous in the Philippines and form the shallow-water shore platforms which almost completely encircle some of the smaller islands. The fringe is not entirely continuous, because the portions of the shallow-sea bottom opposite large streams are not covered by the necessary clear salt water. Where shallow water girdles an island for a long distance from the land the reef is wide, as this great area offers suitable conditions for the development of the fringing reef. If the bottom slope is steep the coral fringe is narrow; for example, Tubbataha Reef, with a 30° slope

between the present strand line and points less than 4 kilometers offshore where it is over 1,500 meters deep.

Barrier reefs.—Barrier reefs consist of a series of islands or shoals which are at all points separated from the main land mass by an area of comparatively quiet water. The water between the reef and the main land mass varies from a kilometer to 50 kilometers or more in width, and from about 1 meter to 60 meters (about 200 feet) in depth; a depth of 90 meters (about 300 feet) is exceptional, in channels. All varying stages between the typical barrier reef and the typical fringing reef have been recognized by various writers.

Atolls.—A typical atoll is essentially a ringlike coral reef surrounding a comparatively shallow lagoon, thus differing from the typical barrier reef through the absence of a visible central land mass.

EXPLANATION OF BARRIER REEFS AND ATOLLS

Much study has been devoted to the explanation of barrier reefs and atolls, but no single general explanation of their origin is accepted. Since there are all gradations between the typical barrier reef and the typical atoll, most students of coral reefs have linked the two. How can a coral mantle, 275 meters (900 feet) thick, be developed upon a rock base surrounded on all sides by waters which only 3 kilometers offshore are over 1,500 meters (about 5,000 feet) in depth, when the limiting depth for coralline growth is only 73 meters (240 feet)? Recalling the general explanation of the building up of marine littoral sediments in various geologic formations all over the world, Dana and Darwin early suggested that these formations were due to gradual subsidence of the ocean bottom. The accompanying diagrams illustrate the Dana-Darwin theory. The first stage, fig. 12, represents a volcanic island with two typical fringing reefs built outward nearly to the level of the surrounding sea. By subsidence slow enough to permit the upward and outward growth of the reef to keep pace with this submergence a condition shown in fig. 13 is developed; that is, a volcanic central island surrounded by a ring of barrier reefs. Through a continuance of this process, a condition illustrated by fig. 14 slowly develops; and, finally, a typical coral atoll is developed and the original supporting volcanic rock is now covered by coral limestone and the shallow waters of the lagoon.

Molengraaff has suggested that in the case of such a volcanic island, through the outpouring of the volcanic rock, there

will exist a local area which will gradually yield to such a process of subsidence. This corollary to the Dana-Darwin hypothesis seems to remove certain difficulties which arise from

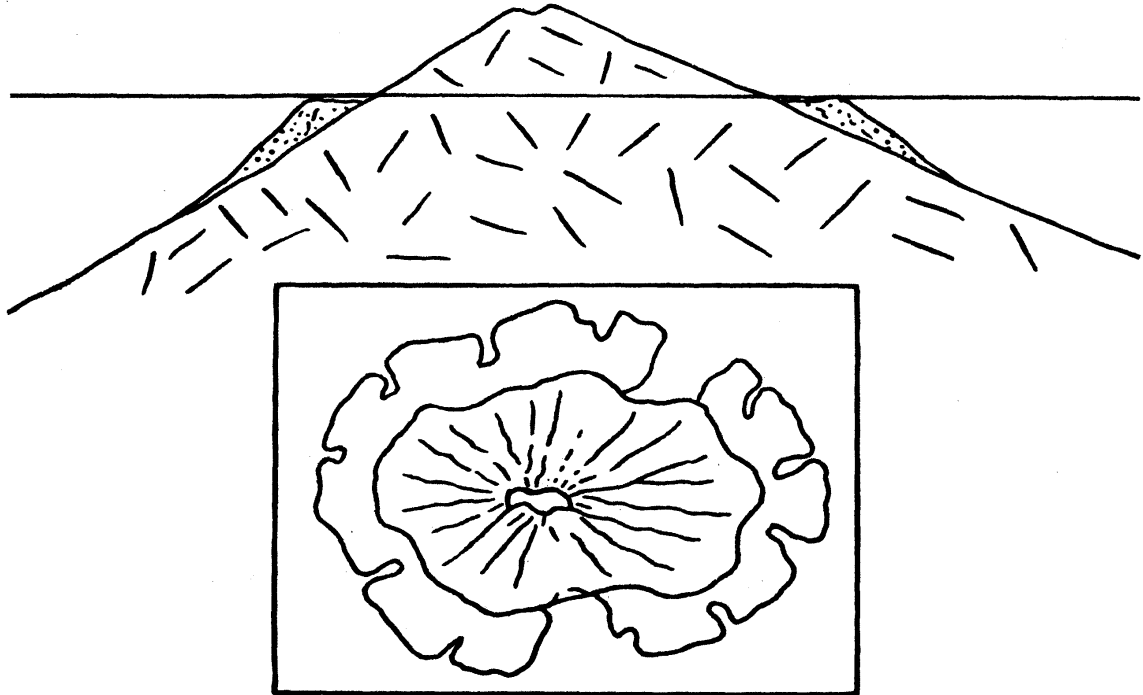


FIG. 12. Fringing reefs formed around a conical volcanic island, in cross section and plan.

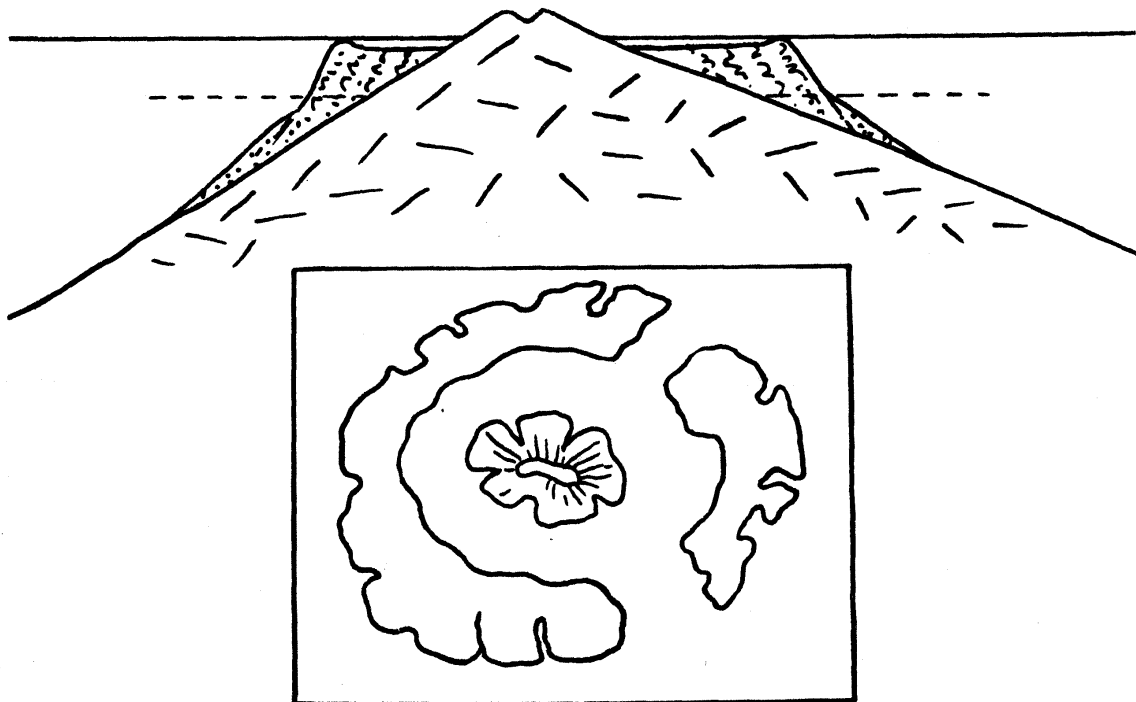


FIG. 13. The island shown in fig. 12, after partial submergence. The upward and outward growth of coral has kept pace with gradual submergence, resulting in an encircling barrier reef.

the postulation of a general sinking of thousands of square kilometers. Various observers have pointed out an objection to this theory; namely, that coral atolls occur in one locality and,

at a comparatively short distance, 50 kilometers, raised coral reefs without bordering atolls occur. However, if Molengraaff's view of local subsidence after a period of upbuilding through active volcanism is accepted, much of the difficulty disappears. The Dana-Darwin theory of reef formation has received support through the studies of Davis, who attacked the problem through physiography.

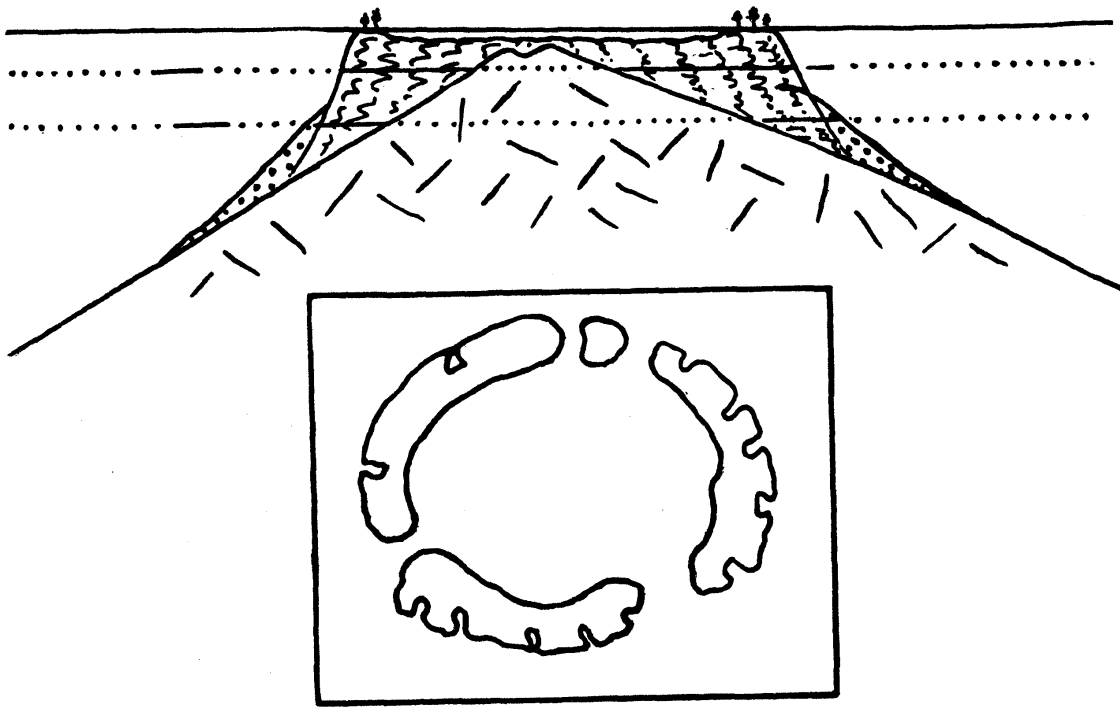


FIG. 14. The island shown in fig. 12, after complete submergence; the resulting atoll developed from a barrier reef, in cross section and plan.

Daly has taken a view somewhat the opposite from that of the Dana-Darwin theory, and he adduces variations in sea level to account for barrier reefs and atolls. Change in sea level, according to Daly, resulted from the vast accumulation of ice in the northern and southern polar regions during the Pleistocene. The withdrawal of a vast amount of water from the ocean and the consequent gravitative effect of this additional mass of matter in the polar regions tended to reduce the level of the water in tropical seas during the glacial phase of the Pleistocene approximately 55 to 60 meters (180 to 200 feet). (See page 65 for further discussion of this subject.) On the outer edges of extensive platforms thus united as coastal plains to the mainland or highland, fringing reefs would start when, at the close of the glacial phase of the Pleistocene, the water became warm enough to support coral growth. As water was slowly restored by the melting ice caps, barrier reefs would be developed and, in the case of small low-lying islands, or shallowly submerged shoals, atolls would be formed. This hypothesis,

like the Dana-Darwin one, assumes an upward growth of coral to keep approximate pace with the increasing depth of water; it accounts quite satisfactorily for the generally prevailing uniform depth of water of the barrier-protected harbors and of the lagoons of atolls.

The solution hypothesis of Murray and Agassiz is generally discarded since it has been shown that calcium carbonate is being deposited in lagoons instead of being dissolved. Moreover, it has been shown that lagoons tend to fill up—not to grow deeper.

Both Vaughan and Wood-Jones have suggested that certain coral atolls have been developed upon shoals on platforms as an incident of the prevailing winds and currents; and in certain crescentic atolls the apex of the crescent opposes the current's direction. There may well be regions in which winds and currents are the prime factors in reef building.

Pirsson and Schuchert * suggest that changes in ocean levels could readily be brought about by slow down warping of the sea bottom, thus resulting in greater deepening. The reverse is also possible. In some areas warping of the sea bottom may well cause changes in the water level, and this may be more or less evident in a given area.

As stated above, no single hypothesis is at present generally accepted, and owing to the vast complications of the problem it is highly probable that more than one method has produced the varying phases of barrier reefs and coral atolls. Molen-graaff in his recent writings accepts the Dana-Darwin and the Daly hypotheses, and he believes that the principles enunciated by Dana and Darwin and Daly's modification of the Dana-Darwin hypothesis are not necessarily in conflict.

In the following discussion the Dana-Darwin hypothesis will be used to explain certain topographic forms, both land and submarine, developed during the Pleistocene. On the other hand, Daly's glacial-control hypothesis will be used to explain certain submarine features in the Philippines.

Much of the detail of the Pleistocene geology of the Philippines is given in the chapter on Palæogeography of the Philippines. Owing to the general unstable character of the Philippine Archipelago, broad Pleistocene correlations from island to island are impossible.

* A Text-Book of Geology. New York, John Wiley & Sons, Inc., 2d rev. ed. (1920) 190.

STRUCTURE OF THE PHILIPPINES

Suess * early recognized the salient tectonics of the Philippines, and he sharply focussed attention upon the dominant tectonic lines in the Islands. He noted particularly the intersection of two systems in Masbate and recognized that island as marking what he terms "virgation" of the Philippines. In other words, the northeast-and-southwest trend of Palawan, the northwest-and-southeast trend of the southern prong of Masbate, Leyte, and Surigao Peninsula clearly indicate dominant lines of folding and faulting. He also recognized that a north-and-south system exists in northern Luzon. A less-definite east-and-west system probably also exists within the Archipelago which is approximately at right angles to the north-and-south system. A subordinate system has a general trend of north 10° east and is rather strongly suggested by the somewhat hypothetical fault along the west side of Panay and the east side of northern Cebu. In the valleylike deep east of Mindoro there are certain faultlike submarine cliffs that suggest a system with a general trend of south 85° east; that is, approximately at right angles to the last-named system. Of these tectonic systems the northwest-and-southeast tectonic line of folding has been existent at least since the end of the Miocene, as the Vigo-Miocene beds have been folded in Bondoc Peninsula, Luzon, and in Leyte along these general lines. Movements along the latter general lines apparently are still continuing, as earthquakes along the Ticao-Masbate line and in Agusan Valley, Mindanao, occur frequently. The early folding in Vigo-Miocene strata in Panay was apparently along the northeast-and-southwest axis. Some suggestion of continued folding along the same axis to the present time is obtained from study of the Sulu deep, which seems quite probably to be the southerly seaward extension of the Panay geosyncline. Movements along the same line seem to be shown by tectonic earthquakes which originated in the region east and northeast of Manila.

Many of the complications in the form of the ocean bottom in the vicinity of the Philippines are undoubtedly connected with these major tectonic lines. The numerous tectonic lines strongly suggest that the Philippines are structurally highly complicated.

* The face of the earth, translated by H. B. Sollas, under direction of W. J. Sollas. Oxford, Clarendon Press 3 (1908) 247.

SUMMARY OF THE HISTORICAL GEOLOGY OF THE PHILIPPINES

The oldest Philippine rocks are cherts and associated schists of probable Jurassic age. Older rocks may occur in the Philippines, but they have not been recognized. After the radiolarian cherts were deposited uplift and mountain building, probably at the close of the Jurassic, occurred. Possibly at that time these schists and cherts were intruded by a great batholith of diorite. During the Cretaceous, the Eocene, and the Oligocene the site of the Philippines was apparently land, as no marine sediments of those ages have as yet been recognized. During the Eocene or the Oligocene this Philippine land mass was connected with Formosa, and it was then or during early Miocene that a characteristic temperate-zone flora penetrated the upland region of northern Luzon. During middle Miocene this land mass was lowered in part beneath the waters of the sea and in the bays and interisland spaces sediments now called Vige-Miocene were laid down. Along the shores of some of these ancient Miocene islands there were rather extensive, low-lying, coastal plains, and in marshy lagoon areas fairly extensive peat bogs were developed. At the close of the Miocene, over large portions of the present site of the Philippine Archipelago, the land was reduced to low-lying plains. In the Pliocene, through comparatively slight submergence of these plain surfaces, extensive coral reefs and their associated marls and sandstones were laid down.

There are recorded in the rocks of the Pliocene many evidences of very extensive volcanism, and apparently during this time many of the present-day volcanoes were built up. During the late Pliocene vast andesitic and basaltic lava flows and extensive mud flows, which may be characteristically seen on the Antipolo Plateau, 20 kilometers east of Manila, covered the Islands. The characteristic tuff-breccia, the Guadalupe tuff, which underlies Manila and its environs, was laid down upon a low-lying coast or in the shallow water of a lake. The Pliocene was ended by extensive foldings, which in some cases were along the same northwest-and-southeast axis as during the Miocene. At the end of the Pliocene much of the mountain land was reduced to low rolling plains and uplands and, in certain parts at the beginning of the Pleistocene, these low plains were completely submerged. During the Pleistocene many complications occurred, the details of which are given in the chapter on Palæogeography. It was during this period that most of the changes that affected plant and animal life of the present

occurred. During the Pleistocene and at its close many of the island masses were uplifted, as is shown by the many series of well-marked step terraces across several of the islands, notably Cebu.

From the middle Miocene to the Recent, mountains of considerable elevation have occupied the present site of northern Luzon. This is shown by a relict temperate-climate flora of Himalaya which reached this land mass via Formosa. Much of this flora, under climatic conditions approximating those of today, could not have survived below altitudes of 1,500 meters; and as is shown in the chapter on past climates of the Philippines climatic conditions have remained essentially the same. This statement is not intended to convey the idea that mountains continued in any one spot in northern Luzon during this long period. It does mean that the various species of this flora were compelled to hop from peak to peak and from range to range to attain their proper temperature requirements. Many species failed to attain proper living conditions and probably many members of the Himalayan flora perished. Only the hardiest survivors remain to testify to northern Asiatic connections.

CLIMATE OF THE PHILIPPINES DURING THE TERTIARY AND THE QUATERNARY

The great influence of climate upon the evolution and the distribution of species is recognized by all students of zoögeography. During the Tertiary in the southwestern United States, the warm, moist subtropical climate of the Eocene changed to the increasingly drier climates of the Oligocene, the Miocene, and the Pliocene.

The influence of climatic changes during the Tertiary is exemplified by the evolutionary history of the horse and of its faunal and floral associates. Similar climatic influences are well known through a study of vertebrate and invertebrate faunas and floras of the Tertiary strata of Europe. Students of the Eocene generally recognize that the climatic zones of that time were far less strongly marked than those of the Recent, since many tropical and subtropical invertebrates and plants of the Northern Hemisphere ranged many degrees farther north than they do now.

During the Quaternary, even more-striking changes in plants and animals of the temperate zones were produced through the alternation of cold and warm phases. Such fluctuations would enable northern species to live in more-southern regions during a cold period, but during the succeeding warm age these boreal types would either retreat to the north again or seek their proper life-temperature zone by climbing mountain slopes, if such existed in the vicinity. Many such "islands of refuge" exist in the southwestern United States, especially along the crest line of the Sierra Nevada of California, and there is an even more striking one upon San Francisco Mountain, an isolated peak in Arizona. In the Appalachians along the eastern coast of the United States and in the mountains of New England notable isolated boreal floras and faunas occur.

The world-wide influence of these changes during the Pleistocene upon life forms necessitates a more-detailed treatment than will be accorded the Tertiary, as the frigidity of the glacial phases in the polar and temperate zones may have produced effects, direct or indirect, upon tropical lands.

In accounting for the stratigraphy of the Pleistocene in the temperate zones and its accompanying phenomena, geologists of the present day universally accept the explanation of Louis Agassiz that northern and central Europe and northern North America were covered during the Pleistocene by great ice caps similar to those of modern Greenland. Agassiz's glacial hypothesis, first advanced in 1840, has withstood all the criticism of early scoffers and has been greatly reënforced by a careful comparison of the glacial phenomena of the Greenland ice cap and its glacial deposits with Pleistocene deposits in the northern United States and Europe. In addition, geologists have shown the presence of striated boulders and their associated deposits in the older geologic periods, notably the Permian. The sedimentary glacial deposits of the great ice sheets of North America are entirely similar to those of Greenland, and the Pleistocene alpine glacial deposits are identical in character with those of living alpine glaciers.

WORLD-WIDE GLACIATION

The world-wide effects of the glacial phase of the Pleistocene have been well recognized only during the past twenty years. The enormous extent of continental glaciation in the Northern Hemisphere is shown in fig. 15. Daly has estimated that these ice caps were 16,000,000 square kilometers larger than the small residuals that cover Greenland and Iceland to-day, not to mention the great amount of ice in the large alpine glaciers that occupied the valleys of all the higher mountain ranges in the Northern Hemisphere.

In the Southern Hemisphere, the glaciers of the Andes were much larger than they are now. South of the Strait of Magellan, a small ice cap covered Tierra del Fuego, and the great Antarctic ice cap was more extensive and much thicker. The alpine glaciers of New Zealand covered much greater areas of those islands, and in places piedmont glaciers, formed by the union of alpine glaciers, covered the coastal regions. In Australia notable glaciation is reported, from New South Wales (35° south latitude) and western Tasmania Island (42° south latitude), by Australian geologists. The highlands of South Africa (28° south latitude) were also glaciated. Such, in brief, was the great extent of the ice covering during the Pleistocene epoch (fig. 15).

Whether the Southern Hemisphere was glaciated at the same time as the Northern Hemisphere is a moot question, since little proof of synchrony has been found. In connection with this important matter the complications of the Pleistocene will be briefly stated. The phenomena of the Pleistocene were not simple; great alternations of climate during this period are recorded by the morainal deposits of successive ice sheets and interglacial deposits. Much study has been given to these deposits in North America and in Europe. In Europe, Penck divides Pleistocene time and estimates the length in years of each division as shown in Table 6.

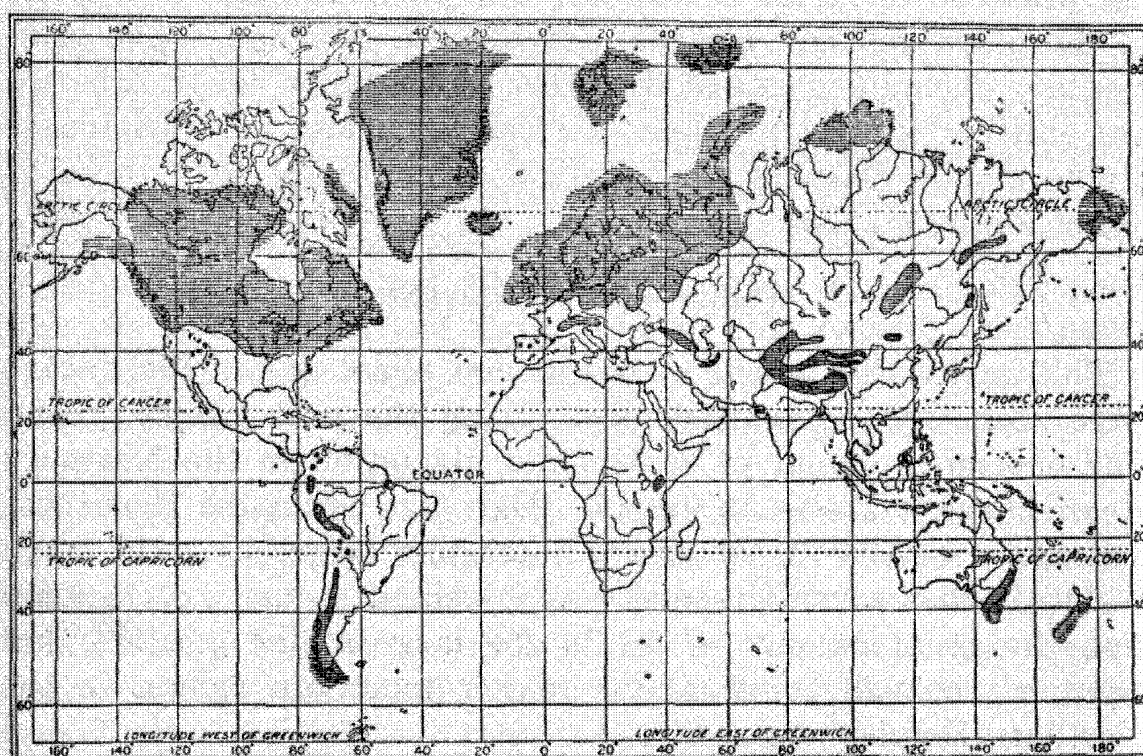


FIG. 15. The world, showing Pleistocene glaciation.

Any measurement in years is of necessity only an approximation, but the relative lengths of the various epochs shown in Table 6 have a distinct value. American authorities, in general, recognize more intervals; but Leverett correlated the Nebraskan with the Günz, the Kansas with the Mindel, the Illinoian with the Riss, and the Wisconsin with the Würm, and recognized corresponding interglacial epochs. Other authorities have modified these estimates, but in nearly all cases the last, or post-glacial, epoch is used as the unit of measure. In America, the time interval is based upon the rate of retreat of Saint Anthony Falls and Niagara Falls since the ice receded from their sites. In Europe, Penck and Brückner based their estimates of this

epoch in years upon the rate of formation of certain lignite and delta deposits.

For the purpose of this work, the irregularity in the length of time of the various epochs is the important feature. That interglacial epochs such as the second one are estimated as twelve units in length indicates a great climatic change. That the interglacial epochs were warmer than the glacial and, in certain cases, warmer than the Recent is shown by the occurrence of a fossil flora obtained from interglacial beds in Ontario, Canada, by Penhallow, who referred the plants to species now living much farther south, in Virginia.

TABLE 6.—*Penck's estimate of the duration of his divisions of the Pleistocene.*

Estimated time of—	Units.	Years.	Total.
Post-glacial.....	1	20,000	20,000
Würm glaciation.....	1	20,000	40,000
Third interglacial epoch.....	3	60,000	100,000
Riss glaciation.....	1	20,000	120,000
Second interglacial epoch.....	12	240,000	360,000
Mindel glaciation.....	1	20,000	380,000
First interglacial epoch.....	5	100,000	480,000
Günz glaciation.....	1	20,000	500,000
Pre-transitional.....	1	20,000	520,000

Penck determined the positions of the snow line for the four glaciations in the Alps and found that the Günz was 1,200 meters; the Riss, 1,300 meters; the Mindel, 1,350 meters; and the Würm, 1,200 meters lower than the present. He found that the snow line for one of the interglacial stages was approximately 300 meters higher than the present one. He also determined that in the Alps to lower the snow line by 200 meters would require a lowering of the temperature 1° C.; hence, the temperature was only from 6° to 7° C. lower during glacial time than at present. From these data he concluded that a decrease of 6° C. in the present temperature would result in another glacial epoch. Abundant evidence of glaciation in equatorial regions has been found upon the slopes of such high mountains as Kenya and Kilimandjaro in central Africa. Mauna Kea, in the Hawaiian Islands, also has distinct evidences of glaciation at 3,600 meters. A further discussion of this subject is given on pages 69 to 71 in connection with the effects produced in warm-temperate and tropical regions.

TERTIARY CLIMATES IN THE PHILIPPINES

The work of Martin upon the Eocene and the Oligocene invertebrates of the East Indies and upon the Miocene strata of the Dutch East Indies indicates clearly that tropical climates existed during the Tertiary and the Quarternary. The presence of what he identified as reef corals, interbedded with marine Pliocene strata unconformably beneath the Kendeng beds at Trinil, Java, the celebrated horizon which yielded the remains of *Pithecanthropus erectus* Dubois, testifies to temperatures for the shallow tropical seas of above 20° C. (68° F.), since typical reef corals cannot survive in colder waters.*

Evidences as to climate during the Eocene-Oligocene in the Philippines are lacking owing to the absence of, or the failure to recognize, strata of the periods involved. The first clear record is obtained from beds of Miocene age, known as the Vigo group in the Philippines. A study of the invertebrates obtained from the Vigo indicates that faunal changes from the Miocene to the Recent were far less rapid in Philippine waters than in the United States and Europe, since at least 75 per cent of the species obtained from the Miocene beds still flourish in Philippine waters. One of the great factors that promote the evolution of pelecypods and gastropods is change in temperature. From the evidence afforded it appears probable that there was no well-marked temperature change during the Tertiary and the Quaternary in the Philippines.†

Merrill, in litt., contributes the following illuminating note upon Pliocene climate in the Philippines:

As indicating very slight temperature changes in the Philippines since Pliocene times the fossil deposits at Sagada may be considered. These deposits as previously pointed out, present the constituent species of the typical, living, low-altitude dipterocarp forests of the Philippines. In this connection, the fact that practically none of the living dipterocarps is found to-day at above an altitude of 750 to 800 meters or 1,000 meters at most should be emphasized. A very few species of the genus *Vatica* are the only ones found at approximately an altitude of 1,000 meters.

The Sagada deposits present fossil remains of species in such dipterocarp genera as *Shorea* and *Anisoptera* and remains of species in such genera as *Diplodiscus*, *Beilschmiedia*, and *Calophyllum*, in other families, the various species being identical with those associated with the dipterocarp forests of to-day. This very clearly indicates that the temperature and other climatic conditions of Pliocene times in the vicinity of what is now Sagada were approximately identical with those now existent through-

* Martin, K., Die Tertiarschichten auf Java. Leiden (1880).

† Dickerson, Roy E., Philip. Journ. Sci. 18 (1921) 17-19.

out the Philippines at low and medium altitudes where the dipterocarps are dominant.

After a careful consideration of all factors in the case no reason whatever for considering that there has been any marked change in the climatic conditions in the Philippines since the Pleistocene and Pliocene can be seen; in other words, the present-day flora is practically identical with those of these two epochs, and generally speaking the temperature in the Philippines at least at low and medium altitudes was practically unaffected during the period of glaciation in the North Temperate Zone.

Similar conclusions are obtained through a study of the Pliocene strata of the Philippines. From 95 to 100 per cent of the species collected from the Pliocene beds are Recent. No extinct form has been recognized among the Mollusca collected from the marine Pleistocene terraces in the Philippines. From such study the obvious conclusion is that life conditions for marine Mollusca since middle Miocene time have remained practically the same. Since change in temperature is one of the dominant factors in promoting the evolution of gastropods and pelecypods, the conclusion follows from this line of evidence that the climate of the Philippines has altered but little during the Neocene, the Pleistocene, and the Recent.

QUATERNARY CLIMATE IN EQUATORIAL REGIONS

The evidence given above is admittedly quite different from that obtained from certain other portions of the tropical regions during the Pleistocene. Mount Kenya, in central Africa, almost on the Equator, has the great altitude of 5,195 meters (17,040 feet) and even now is sufficiently cold for small glaciers to exist in the valley heads on its slopes. Well-marked evidences of glaciation were obtained 1,620 meters (5,400 feet) below the ends of these modern glaciers and, apparently, Pleistocene ice capped the entire mountain during that period. Klute * describes his investigations upon the glaciated and still higher peak of equatorial Africa, Mount Kilimandjaro, about 6,000 meters (19,710 feet). He found the present snow line to be about 600 meters (2,000 feet) lower on the southern and southwestern sides than on the northern and northeastern quarters. During the Pleistocene, as now, glaciation was developed on a vaster scale on the southern and southwestern sides of the mountain than on the opposite quarters. From this fact, Klute concluded that the wind system of the glacial period must have been the same as that of the present and, therefore, any shifting

* *Ergebnisse der Forschungen am Kilimandscharo*. Berlin (1920).

in the position of the poles or continents cannot be adduced as explanations of the incidence of the ice age. He says:*

From November to February Kilimanjaro is swept by the northeast monsoon: from March to October by the southeast trades. The summits of Kibo Shira and Mawensi rise well into the antitrades which here as elsewhere in this part of Africa blow from the northeast. The southeast trades are locally deflected so as to blow up the southern slopes of the mountain from the southwest * * * The distribution and character of precipitation upon the mountain sides is determined in large measure by these winds and in turn the details of surface morphology, glaciation, and vegetation cover depend upon the precipitation. In general it may be said that the highest parts of the mountain, like the steppes which surround it, are relatively arid. Maxima of precipitation are found at middle and lower altitudes, and in a belt of heavy precipitation which encircles the mass if the greatest quantity of rain falls along the southerly and south-westerly slopes brought by the trades from the Indian Ocean * * *. The snow line is some 2,000 feet lower on the southern and southwestern sides of the cone than on the northern and eastern. The southerly side is not only less exposed to the dry antitrades but is also open to moisture brought by the deflected southeast trades which blow up the slope from the southwest * * *.

On the slopes of Mauna Kea in the Hawaiian Islands, Daly recognized distinct evidences of glaciation at the 3,600-meter (12,000-foot) level.† Concerning this Daly says:

A fall of only half a dozen degrees in the average temperature of the intertropical seas would make an enormous difference in the distribution of the stenothermic reef-corals, which can not withstand a winter temperature below 20° C. The February marine isotherm of 20° lies but a few hundred miles north of the large Hawaiian Islands. We may be certain that these islands were not bordered by living reefs at a time when 4,000,000 square miles of ice capped the neighboring continent.

In a later publication, Daly‡ makes the following statement upon Pleistocene temperature of the tropical oceans:

Remembering the 20° lower limit for reef corals, the reader observes that a mere general fall of only 6° C. in the minima must cause a very extensive destruction of the living animals. Further the favorable temperature conditions of the western tropical Pacific and western tropical Atlantic are partly due to the westward driving of abundant warm water by the trade winds. In the Glacial period the trade-wind belt must have been much narrower than now, and the effect of these winds correspondingly less.§ At the same time the general storminess, correl-

* Op. cit.; review in *Geog. Rev.* (July, 1922) 495.

† *Am. Journ. Sci.* 180 (1910) 303-304.

‡ *Proc. Am. Acad. Arts and Sci.* 51 (1916) 169.

§ The trade winds, on the other hand, may have been stronger, as higher barometric gradients probably were present between the torrid and temperate zones than now.—R. E. DICKERSON.

ated with rapid shifts of cold currents, was greater than at present. Finally, the Pleistocene extension of the Antarctic ice-cap must have caused some narrowing of the sea south of Cape Horn, with the probable result of increasing the volume of the cold Humboldt current, which now distinctly lowers the temperature of the central Pacific.

For various reasons, therefore, the temperature conditions for lusty coral growth during the Glacial period are not fully suggested even by the statement that the mean annual temperature was then lower than at present by a half-dozen or more degrees. That lowering was but one of several associated causes for the inhibition of coral-reef growth. The writer believes it is not an extreme view to hold that practically the entire area now occupied by the oceanic archipelagoes and by the great barrier reefs of Australia and New Caledonia was, during the maximum Pleistocene glaciation, bereft of reefs growing rapidly enough to resist destruction by the waves. Though meager, slow growth of corals may have been possible in the open ocean, especially those along the eastern continental borders within the tropics. In these localities the corals perpetuated their kind, rendering possible a future, more favorable existence in the open ocean. The resulting Pleistocene reefs are, of course, now completely submerged. A likely place for their development was in the southern part of the Red sea, which, in the Glacial period as now, was doubtless particularly warm. The vast, rough plateaus at 60 m. to 120 m. below the surface of that sea, may represent places where reef corals then flourished.

This admirable statement seems extreme, in connection with East Indian and Philippine conditions, for the reasons set forth below. Various other authorities make similar statements concerning the effect of Pleistocene glaciation upon the Tropics. Chamberlin and Salisbury * state that even in tropical regions glaciation occurred on mountains where it did not exist before and does not now exist, and on mountains now glaciated the ice descended to 1,500 meters (5,000 feet) or more below its present limit.

Some of the results of the Selenka Expedition, through a study of the floras associated with Trinil man, *Pithecanthropus erectus* Dubois, indicate similar conclusions for Java. Schuster † states these conclusions as follows:

PHYTOGEOGRAPHICAL RESULTS

A result of the preceding examination is of interest from the points of view of plant geography and of geology. As a result of the proof here produced for the first time on a palæontological basis, there are indications that in the ancient diluvial (Pleistocene) time there prevailed a period in Java that was characterized by a more temperate and rainier

* Geology 3 (1906) 327.

† Monographie der fossilen Flora der Pithecanthropus-Schichten (1911) 1-70, pls. 1-27, reprint from Abhandl. Akad. Wissensch. München 25 (1911). Translation, pages 54 to 59, by A. E. W. King.

climate than exists at the present time. Just how far the cooling off of this period proceeded may be deduced from the fact as a result of this period there was a dislocation of the vegetation amounting to an entire height zone.

SUMMARY OF GENERAL RESULTS

1. The fossil flora of the *Pithecanthropus* strata belongs to one and the same epoch without essential variation in climate.

2. It contains only species which are still living to-day and is, therefore, not older than the diluvial.

3. It corresponds in general to a cooler and rainier climate at the time of the deposit in comparison with that prevailing in the same region at the present time.

4. It may be classified for that reason as belonging to the "Mindel-Ice Time" corresponding to the culmination point of the great pluvial period.

5. Its composition is constituted of various elements depending upon the region.

6. The results 1 to 5 are corroborated by the fossil flora of Lasen coming from an indubitable diluvial (Pleistocene) stratum.

As a result, the following weighty facts are proven:

- I. The ancient diluvial (Pleistocene) age of the *Pithecanthropus*.

- II. The pluvial time in Java.

- III. The mixed characters of the "Malayan" flora.

Merrill, in litt., recently reviewed this excellently illustrated work, and from his extensive knowledge of the Malaysian flora concluded that Schuster's general conclusions concerning climatic conditions are unwarranted. He states:

The climatic conditions existing in Java at the time the Kendeng beds were laid down were not radically different from the climatic conditions as they exist there to-day. There is certainly little or no evidence that the climate was cooler there at that time than it is at present. That during the Pleistocene the forests in this part of what is now Java were typical rain forests of the temperate zone is a conclusion that cannot be drawn from the data available.

Practically none of the species enumerated is found in the temperate zone; on the other hand, practically all of them are found to-day at low altitudes in the Malay Archipelago. Judging from the types of vegetation preserved in the Trinil formation and eliminating a few species regarding which there is more than a reasonable doubt as to the correctness of the identification there is certainly no evidence that the climate was cooler then than it is at the present time.

Making due allowances for possible errors in identifications, I can see no reason for believing that the fossil flora of the *Pithecanthropus* horizon represents other than elements from a single forest type; namely, a tropical forest very similar to that occurring to-day at low altitudes in the entire Malay Archipelago.

The point of special interest brought out by Schuster is that the flora existing in Java several hundred thousand years ago is not radically different from that existing in Java at low and medium altitudes to-day. This

indicates strongly that, at least so far as tropical vegetation is concerned, a very high percentage of our species are constant in their specific characters and have been constant for a very long period of time. I should draw the general conclusion that the vegetation and the climatic conditions existing in the Malay Archipelago as a whole during the Pleistocene were practically the same as those existing to-day.

Conclusions derived from a study of the general distribution of coral reefs in the Philippines, Formosa, and the Riu Kiu Islands are in agreement with Merrill's comments. Uplifted Pleistocene coral reefs occur at many elevations within the Philippines and, in all probability, represent varying phases of the Pleistocene. Similar conditions are reported by Yoshiwara * in his study of the Riu Kiu Islands, where he describes reef corals veneering marine terraces of several generations, and he reports that fringing reefs encircle those islands as far north as 29° north latitude. This evidence indicates a condition very different from that of the Hawaiian Islands of the mid-Pacific.

The existence of a Pleistocene Japanese current is highly probable, as the great distribution of Pleistocene corals indicates. It is well recognized that the Japanese current is a trade-wind effect, and it is highly probable that a tropical temperature was maintained in the Philippines, Formosa, and the Riu Kiu Islands during the entire Pleistocene. If this line of reasoning be correct, then the neighboring tropical waters off the eastern coast of New Guinea were probably even warmer than the waters of the Philippines. On this account Daly's conclusion that the equatorial waters off the eastern New Guinea coast during the glacial phases of the Pleistocene were too cold to support active coral growth is not substantiated.

Likewise, the flora of the Kendeng beds of Java of lower Pleistocene age, according to Merrill, flourished under climatic conditions essentially the same as those of to-day. Daly's picture of a narrowed trade-wind belt in the Tropics and stormier weather during the Pleistocene appears to be entirely logical. With a greater temperature gradient between the North Temperate Zone and the Torrid Zone, and a consequently greater barometric gradient, the trade winds of the Pleistocene, although restricted to a narrower belt, may have been stronger than those of the present and, likewise, the tropical waters would have been shoved northward in the Japanese current with greater force than to-day.

* Journ. Coll. Sci. Imp. Univ. of Tokyo 16 (1901-3) article 1.

The evidence in hand indicates that the direct effects of the glacial chill of the Pleistocene were almost entirely damped in the Philippines and the East Indies, although it is recognized clearly that the equatorial African mainland was considerably colder.

Although the direct effects of glaciation did not influence life in the Philippines, the indirect effects of the great accumulation of ice in the Northern Hemisphere exerted a great control upon it. The first scientist to suggest a definite connection between the height of the sea level in the Tropics and glaciation of the Pleistocene was Penck.* His statement, translated, is briefly set forth as follows:

The causes of the general rise of sea-level in the latest geological time might perhaps be connected with those climatic changes which the earth underwent in the Glacial Period. If during that time, northern Europe, northern North America, and the Antarctic regions were simultaneously glaciated, a considerable mass of water must have been removed from the ocean, and, if the thickness of the ice be assumed as 1,000 meters, the sea-level must have been 150 meters below its present position.

According to Daly, the ice sheet at the 49th parallel of latitude near the southern limit of the cap was over 6,000 feet in maximum thickness, with an average of 2,000 feet. Daly† regards Penck's estimate as somewhat too high. He says:

The removal of enough water to form these great sheets of ice would tend to lower sea-level all around the globe by the amounts here approximately stated:

<i>Estimated average thickness of ice (in feet)....</i>	3,000	3,600	4,000	5,000
<i>Corresponding decrease of ocean's depth (in feet)</i>	125	150	167	208

Woodward, Hergesell, and others have shown that a second cause for a negative movement of sea-level in the equatorial zone is to be found in the gravitative power of ice. Using Woodward's formulas, it may be calculated that, if the ice had an area of 6,000,000 square miles and an average thickness varying from 3,000 to 5,000 feet, the attraction of the ice would lower the level of the equatorial sea by amounts ranging from five to eight fathoms.

Taking the two effects together, the formations of the ice sheets (which have since disappeared) would produce a negative movement of sea-level in low altitudes to an amount ranging between twenty-five and forty-five fathoms. Assuming 3,000 feet as the average thickness of the ice, the shift of level in the equatorial sea would be about 30 fathoms.

The successive withdrawals and restorals of tropical waters through these indirect effects of glaciation and deglaciation

* *Morphologie der Erdoberfläche* 2 (1894) 660.

† *Am. Journ. Sci.* IV 30 (1910) 299.

during the Pleistocene had a profound effect upon the distribution of life in the East Indies and the Philippines. The shallow seas were laid bare and larger islands were united during the glacial phase, and during the succeeding warm phase of the Pleistocene a reversal of these events occurred. This successive opening and shutting of many portals resulted in great diversity in the flora and the fauna of the Philippines, as relatively rapid biologic adjustments were necessitated; first, by the enlarged habitats and, later, by the restricted habitats of the warm phase. The reader will appreciate these Pleistocene events more fully after reading the chapter upon Hydrography and the succeeding life chapters.

TERTIARY AND QUATERNARY PALÆO GEOGRAPHY OF THE PHILIPPINES *

THE PHILIPPINES DURING THE EARLY TERTIARY

The lack of any early Tertiary sedimentary record leaves this important portion of the period in which modern life had its beginning largely blank. Present-day knowledge concerning conditions that prevailed previous to the Miocene is largely inferential, and is based upon study of the character of Miocene sediments and upon indirect palæontologic evidence concerning Formosan botanic affinities. The sedimentary rocks of Vigo-Miocene age, which are characterized by the presence of *Vicarya callosa* Jenkins and of various species of *Lepidocyclina* and associated Foraminifera at various horizons, contain coarse detrital material which has obviously resulted from the erosion of the basement complex of cherts, schists, serpentine, and diorite. Coarse materials constitute portions of the Vigo strata west of Baguio and in Cagayan Valley in northern Luzon, and in Leyte, Panay, Bondoc Peninsula, and Mindanao. Such materials could not have been transported great distances, which fact indicates the existence of a land mass composed of the rocks of the basement complex. The sedimentary record of Formosa for early Vigo time is, in part, the same as that of the Philippines. Eocene has been recently discovered in the so-called clay-slate strata of Formosa. Cretaceous has not been reported there, but it must be remembered that this large island, like the Philippines, has not been studied in detail. Palæozoic rocks occur in the central part of Formosa, according to Dr. S. Nakamura, of the Imperial University of Kyoto. As far as present knowledge goes, all of the Tertiary previous to the Vigo-Miocene can be recorded by the unconformity between the Vigo and the basement-complex rocks. In other words, Formosa and the Philippines may have been a united land mass (fig. 16).

* For a more-detailed paper see R. E. Dickerson, Philip. Journ. Sci. 25 (1924) 11-50.

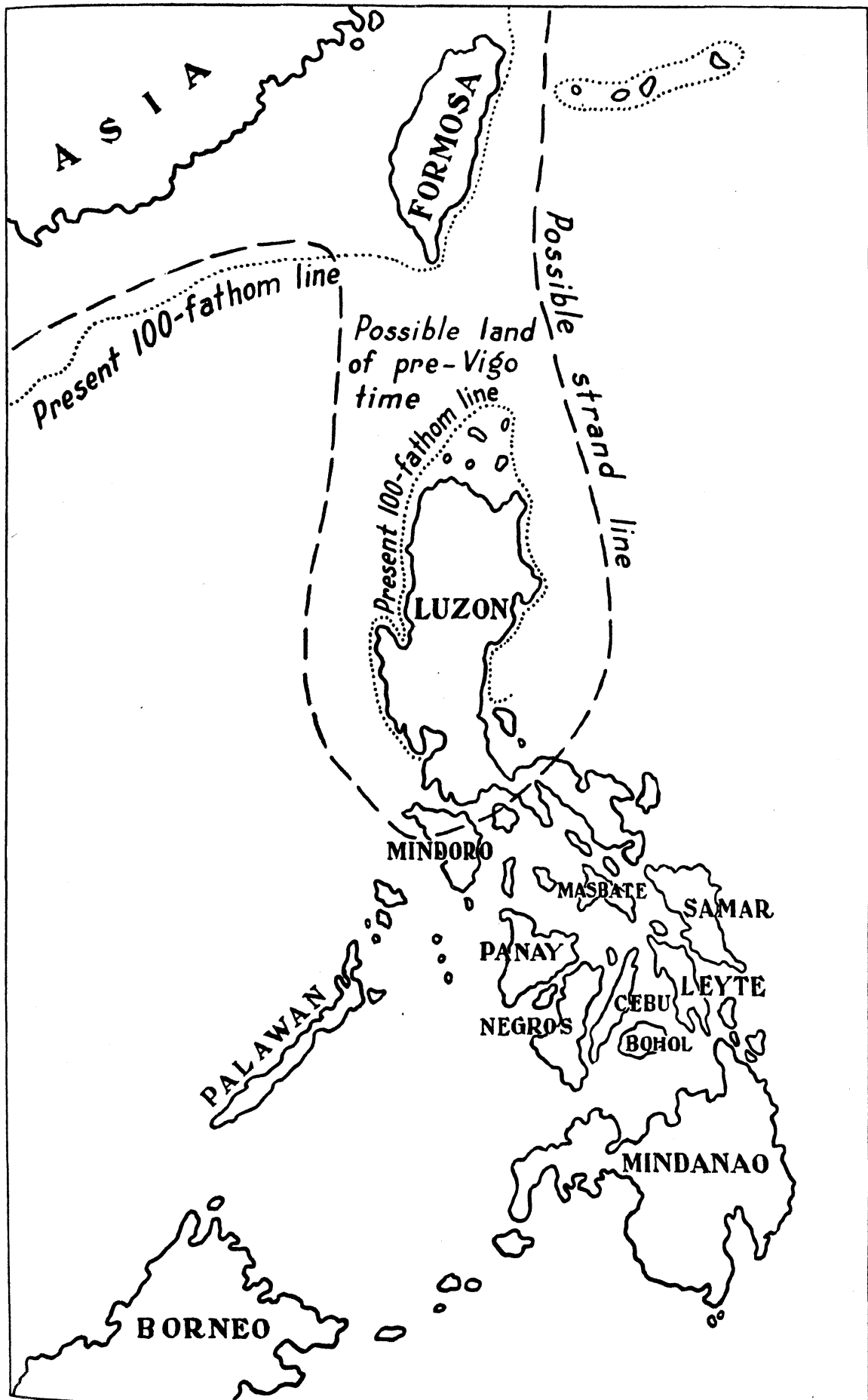


FIG. 16. Hypothetical connections of the Philippines during early Tertiary (pre-Vigo) time.

The other evidence pointing in this direction is supplied by Merrill and by Smith.* At Sagada, in northern Luzon, at an elevation of 1,500 meters, Father John A. Staunton discovered and collected a fossil flora which was determined by Merrill. Among these fossil plants were characteristic dipterocarps, at present living only at elevations below 600 meters. This flora is stratigraphically connected with Malumbang-Pliocene coralline limestone at this place. The point of this matter is that no dipterocarps occur in the present flora of Formosa. According to Merrill, the climate and the soil of that island are not unsuitable for dipterocarps, and he can see no reason for their absence except long separation of Formosa from the Philippines. The lack of dipterocarps in Formosa leads to the conclusion that Formosa was not connected with Luzon during the Pliocene. Unfortunately, no decisive palæobotanic evidence from Formosa is at hand; but the study of the distribution of marine sediments of Vigo age, both in Formosa and in the Batanes and Luzon, indicates very clearly that much of the present site of Formosa and northern Luzon and the intervening Batanes region were covered by waters of the Vigo-Miocene sea. Herre's investigations of the fresh-water fishes of the Philippines show that none of the species has any affinity with Formosan fresh-water fishes. All Philippine true fresh-water fishes are allied to Bornean species. This evidence is in entire accord with the known geologic data. In view of all of these facts, a connection between Luzon and Formosa during the Vigo-Miocene seems highly improbable.

At various places erosional contacts between the Vigo and the basement complex indicate that a great period of subaërial erosion preceded the deposition of marine Vigo-Miocene. It is highly probable that Formosa and northern Luzon were firmly connected during the early Tertiary, and it is even probable that the plants common to the two islands spread southward from Formosa at that time. Definite evidence of the precise stage at which such floral occupation occurred is lacking, but it was probably during the interval between the Oligocene and the Miocene; that is, Ep-Oligocene. This opinion is based upon the probable rate of evolution of plants. It seems highly improbable that about forty present-day plants common to Formosa and northern Luzon could have persisted in both Formosa and Luzon for a greater period without specific change. This

* Philip. Journ. Sci. § A 10 (1915) 195-197.

idea is tentatively set forth on the accompanying map (fig. 16). Just how far south this probable pre-Vigo land mass extended is problematic, as the present-day high-altitude flora does not persist farther south than the present high mountains of northern Luzon; other guides are lacking, as probably all of this southern area was under the sea a portion of the geologic time after the beginning of the Vigo.

THE PHILIPPINES DURING THE VIGO-MIOCENE

In certain localities the Vigo sedimentaries are conglomerates and coarse-grained sandstones derived from the basement-complex rocks, in marked contrast with great thicknesses of shale and limestone which accumulated in deeper waters. After a study of the distribution of these two types of rock some conclusions will be possible. The basal member of the Vigo group in Leyte near Tabubunga on the northwestern coast is a thick fanglomerate (?); which evidently was deposited either as land-laid material or close to the shore, since some of the boulders are more than 1 meter thick. These beds contain thin strata of arenaceous *Lepidocyclina* limestone. On the other hand, the prevailing sediments in Cebu at the base are coal seams associated with *Lepidocyclina* limestones, which are in turn overlaid by fine-grained shales. While the coal may be regarded as of lagoonal or shore-marsh deposition, the *Lepidocyclina* limestone indicates deposition in water offshore; that is, the deposits are not strictly littoral. Samar, likewise, is characterized on the whole by shales and *Lepidocyclina* limestone. *Lepidocyclina* limestone is found above the coal on Batan Island off the east coast of Camarines Peninsula. West of Camarines Peninsula is Bondoc Peninsula, the type locality of the Vigo group, where the Vigo is, in general, represented by shales—sediments probably deposited in the deeper waters of a Vigo inland sea. Farther north, coal of commercial value is reported by W. D. Smith, on Polillo; thus a shore-line condition is indicated. The connection between that island and the central highland of northern Luzon was probably broken by relatively recent movements along the northern end of the Taal fault, which now marks the continental shelf along the steep eastern coast of northern Luzon. In all probability, Vigo sediments have been dropped upon the eastern side of the Taal fault, whereas the older basement-complex rocks have been upthrust to form the steep-cliffed, east-coast mountains, the wild Sierra Madre Range. The Vigo sedimentaries of Cagayan Valley are in general coarse-grained sandstones and lignites, and apparently represent shallow-water

deposition in a marked geosynclinal trough that was bordered by land on either side. On the northwest coast of Luzon the great section of the Vigo group exposed along the Naguilian Road west of Baguio indicates littoral deposition.

The distribution of sediments, as briefly outlined above, indicates that an elongate Palawanlike island existed, which stretched from the eastern coast of Mindanao through central Leyte, through Camarines Peninsula, across the enbayment on the eastern side of Polillo, and northward on the east side of northern Luzon (fig. 17). In all probability there was an island mass in Abra Province and in western Kalinga and Apayao Subprovinces during Vigo time. The great amount of coarse sediments exposed along the Naguilian Road west of Baguio indicates that land was close at hand. Whether or not, in addition to this smaller island through north-central Luzon, there was another, 65 to 80 kilometers west of northern Luzon, in the China Sea site of to-day is hypothetical; but the great thickness of the Vigo group and the coarse character of these sediments indicate a neighboring land mass larger than the narrow island or peninsula that separated the Cagayan Vigo embayment from the basin of deposition west of Baguio.

The ocean contours delimiting the western side of northern Luzon might well be interpreted as indicating a continuation of the great Formosa fault which delimits Formosa on its eastern side, and movements along such a fault may have carried that western island of Vigo time beneath the sea.

The great amount of coarse sediments described by Abella, in the basal Tertiary beds in Iloilo Province, Panay, indicates that the material of Vigo-Miocene age was derived from a considerable land mass entirely or in part to the west of Panay Island. The orientation of Tablas and the western coast of Panay lends some support to this hypothesis, and it is possible that such older land mass is now covered by the waters of Cuyo East Pass. In other words, there is a dropped block west of Panay. It is entirely probable that connections existed to the south, from Mindanao to Celebes, during the Vigo-Miocene; and from the biologic evidence Celebes may have been connected, either directly or indirectly, by a stepping-stone bridge or by a more-continuous land structure, with this elongate, north-and-south, Palawanlike Miocene island. Information concerning palæogeographic details of the Philippine Archipelago during the Vigo-Miocene is hazy, but all the evidence at hand indicates that an archipelagic condition prevailed during that period (fig. 17).

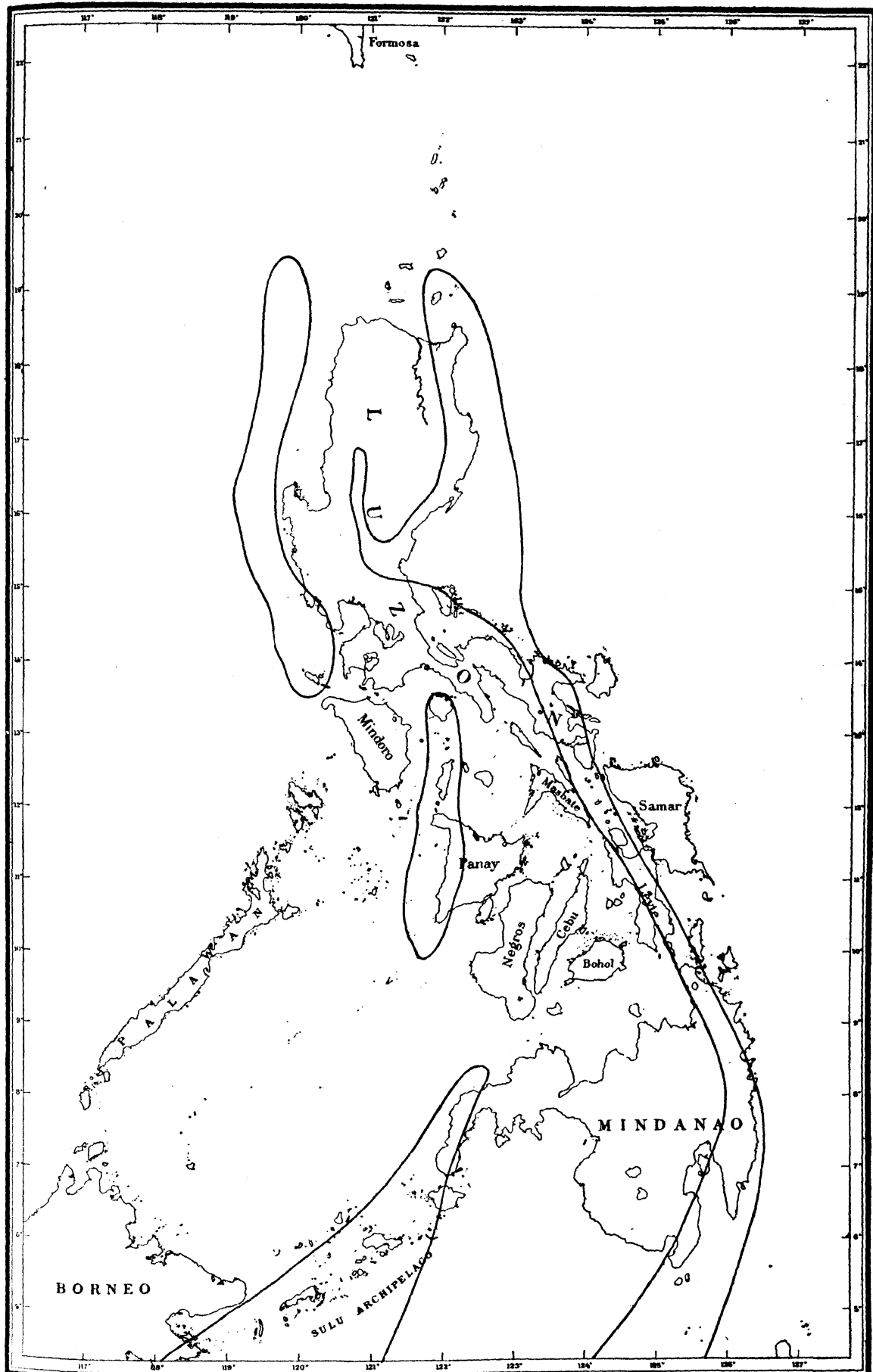


FIG. 17. Some probable islands in the Philippines during Tertiary-Miocene time.

SOME POSSIBLE PLIOCENE PHILIPPINE ISLANDS

The Vigo-Miocene sediments were evidently derived from erosion of an older land mass composed of diorites, slates, schists, and cherts; but a study of the Pliocene beds as exposed in the Philippines indicates that the dominant processes during this stage were the accumulation of organic sediments and volcanics. However, this is not wholly true, as Schenck and Moody have demonstrated the presence, in Pliocene strata of probable Malumbang-Pliocene age, of *Lepidocyclus* limestone boulders of Vigo-Miocene age. Such evidence indicates that the Vigo sediments have been consolidated, faulted, and eroded in part to form the sediments of the Pliocene sea. There is a remarkably small amount of quartzitic or dioritic rock fragments in the sandstones of Pliocene age. The abundance of andesitic boulders and fragments of coral rocks containing species closely related to or identical with those living in the Philippine waters of the present day, is a notable character in the Pliocene sediments about Baguio. However, Smith reports much sandstone of upper Pliocene age associated with coralline limestone in the Banisilan beds in the region north of Cotabato River.

In most of the larger islands of the Philippine Archipelago coralline limestone of Pliocene age is common, and the corals composing it are typical of the fringing reefs now bordering the Islands. It is well known that such reef corals are limited to waters of less than about 70 meters in depth. This widespread occurrence of coralline limestone, which indicates shallow-water deposition, is further evidence of an archipelagic condition in the Philippines during their deposition.

The location of land masses during this stage is indefinite and vague. A portion of the present site of Samar was probably land during Malumbang time, as the Malumbang on that island is derived directly through erosion from previously formed *Lepidocyclus* limestone of Vigo-Miocene age. The present site of Agusan Valley, Mindanao, was occupied by the shallow waters of a Pliocene sea, as is indicated by the presence of fossils at several points in Agusan, Saug, and Tagum Valleys. These sediments are all of the inshore type, and it seems probable that an island occupied the eastern side of Mindanao of to-day and, possibly, extended several kilometers east of the present shore line. A study of Malumbang-Pliocene in the northern and the southern peninsulas of Leyte indicates that most of that

island was covered by shallow water at this stage. Most of Bohol is composed of Malumbang-Pliocene limestone, and the presence of the same rock in Cebu is notable. North of Cebu apparently all of Masbate of to-day was covered by a shallow Pliocene sea, and a striking unconformity on Ticao between these rocks and the rocks of the basement complex was found by Dr. A. N. Kryshtafovich. The wide extent of Malumbang limestone in Bondoc Peninsula, Luzon, as indicated by Pratt and Smith, demonstrates that this site was likewise beneath the waters of the sea at this stage. Owing to the great amount of volcanic rock and rocks of the basement complex in Camarines Peninsula, but little is known concerning the presence of marine sediments at this stage; and, although lack of evidence is no adequate proof, it seems possible that Pliocene Samar extended northward, covering a portion of that peninsula. In northern Luzon, however, the evidence is far clearer, and island masses or a single large irregular island covered the present site of northern Luzon. As has been indicated briefly in the discussion of the distribution of the dipterocarps, land-laid tuff found at Sagada in close association with coralline limestone demonstrates the presence of neighboring land. In Cagayan Valley Kryshtafovich found a fossil dipterocarp flora associated with Malumbang strata, and upon these two bases the presence of a large irregular island or islands in this region is indicated.

Rocks of Malumbang-Pliocene age occur in Negros and also, in great amount, in central Panay. In southern Mindoro, rocks referred to this age were discovered by Moody and Kryshtafovich. Coralline limestone is reported at a few places upon Palawan. Such evidence indicates that in the Pliocene a Philippine archipelago existed with, in all probability, the same elongate series of islands or a single irregular island as probably occurred in Vigo-Miocene upon the eastern side of this group. Certain other well-recognized island masses existed in northern Luzon, and it is quite probable that a rather large island or islands occupied portions of the present site of Panay and Negros. It is exceedingly important to grasp the significance of this continued insular condition during the Miocene and Pliocene periods and of the persistence of the elongate island on the eastern side of the Philippines when considering the questions of distribution of plants and animals (fig. 18).

The apparent scarcity of large mammalian remains in the Philippines is possibly a reflection of this persistent insular

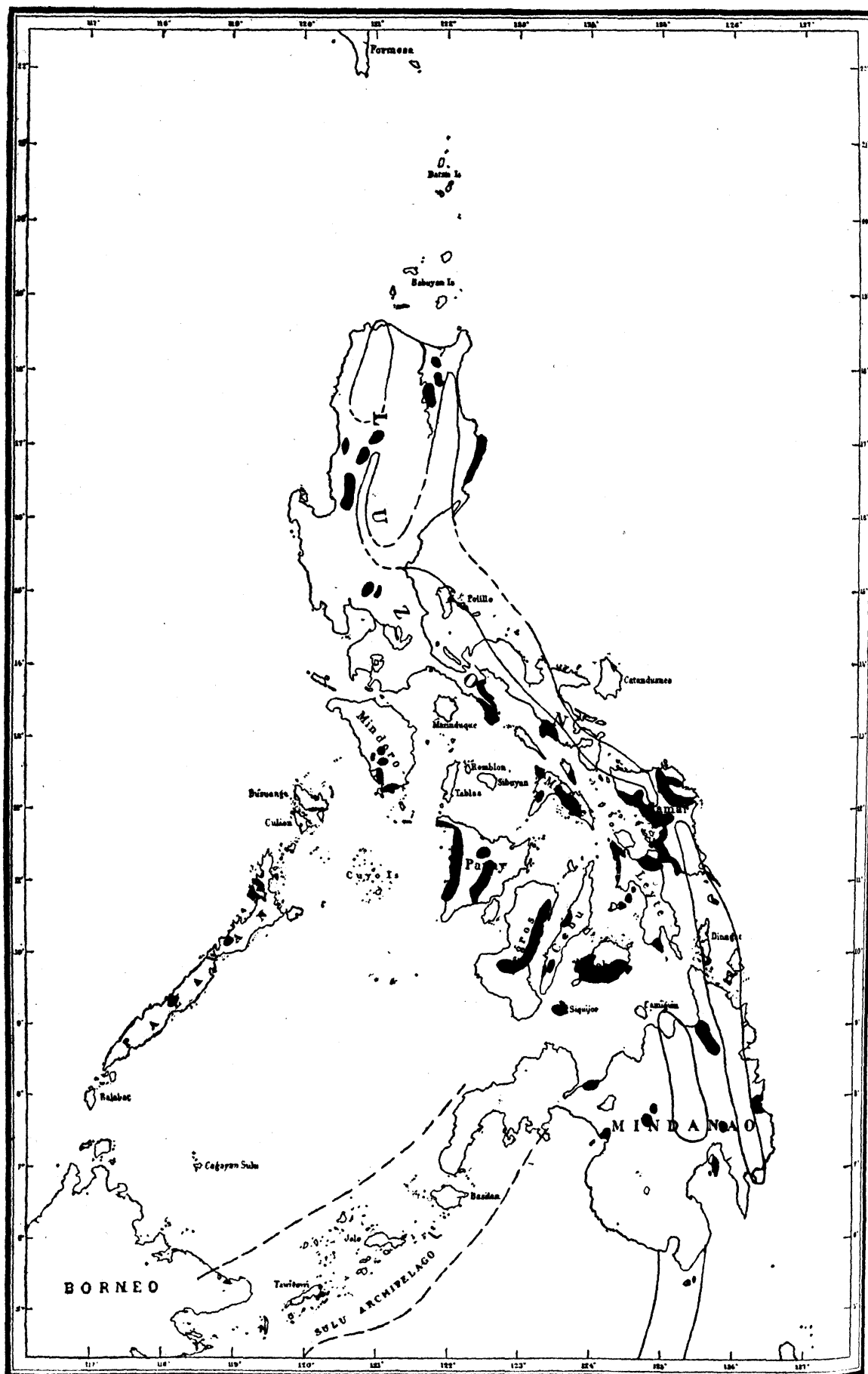


FIG. 18. Some probable Pliocene islands of the Philippines. Black areas represent marine Pliocene rocks.

condition. The possibility that Mindanao was connected by the Sulu bridge with Borneo during the Pliocene is suggested by the reported discovery in northern Mindanao of *Stegodon*, a genus of elephants, which was exceedingly common in the Pliocene of India and other portions of Asia. However, there is some doubt concerning the authenticity of this occurrence in Mindanao, and we are unable to assert with positiveness that the Sulu bridge was a stable structure during this time. The wide extend of shallow-water deposits of Pliocene age in the Philippines indicates that in all probability the submarine topography of that period was different from the complicated topography of the ocean bottom of the present day.

There are other, broader considerations, discussed in connection with the subject of hydrography, which indicate that much of the present sea-bottom topography of the Philippines has been formed since the Pliocene.

PLEISTOCENE PHILIPPINE ISLANDS

Much of interest to the biologist will be found in the consideration of the distribution of Pleistocene sediments in the Philippines, though our knowledge of the Pleistocene is very fragmentary (fig. 20). Moody, who has made an excellent reconnaissance of Mindanao, outlined some of the complexities that occurred during that period. His statement in a letter concerning Pleistocene conditions is as follows:

Along the north coast of Mindanao between Iligan and Cagayan, there are seven wave-cut terraces in the hills to an estimated elevation of 1,200 feet. The north edge of Camiguin Island shows excellent benches. There are well-marked wave-cut benches in the hills south of Cotabato to an estimated elevation of 1,000 feet. Musuan Volcano, south of Mailag, Bukidnon, has a terrace practically around it at an elevation of about 400 meters. The hills west of Malaybalay, Bukidnon, exhibit terraces at elevations well over 600 meters, but these may be due to successive flows of lava producing a bench effect. Malitabug River Valley at Banisilan, Cotabato, has five distinct stream terraces on each side; Banisilan is located on the oldest terrace at about 375 meters elevation, while the present elevation of the river is about 200 meters. [Plate 1, fig. 1.]

A coralline limestone containing many species of coral referable to Recent species, and lying horizontally or only slightly inclined, is widely distributed throughout certain parts of Mindanao, and where in determinable relation with other rocks, it always overlies them. This limestone is found on islands in Davao Gulf; in Saug River, Davao Province; at an elevation of about 210 meters on the ridge between Saug and Agusan Rivers; at elevations of 150 meters in tributaries to Agusan River;

throughout the floor of Cotabato Valley; and in the hills south of Cotabato at estimated elevation of 300 meters. This limestone is probably Pleistocene in age.

The data noted above suggest that Mindanao was divided into five smaller islands in the early Pleistocene. There were probably water connections as follows: Butuan Bay to Davao Gulf; Macajalar Bay at Cagayan de Misamis through Bukidnon Province to Illana Bay at Cotabato with probably a connection to Sarangani Bay; and from Panguil Bay to Illana Bay. [Fig. 19.] Pulangi River rises in the northeasterly part

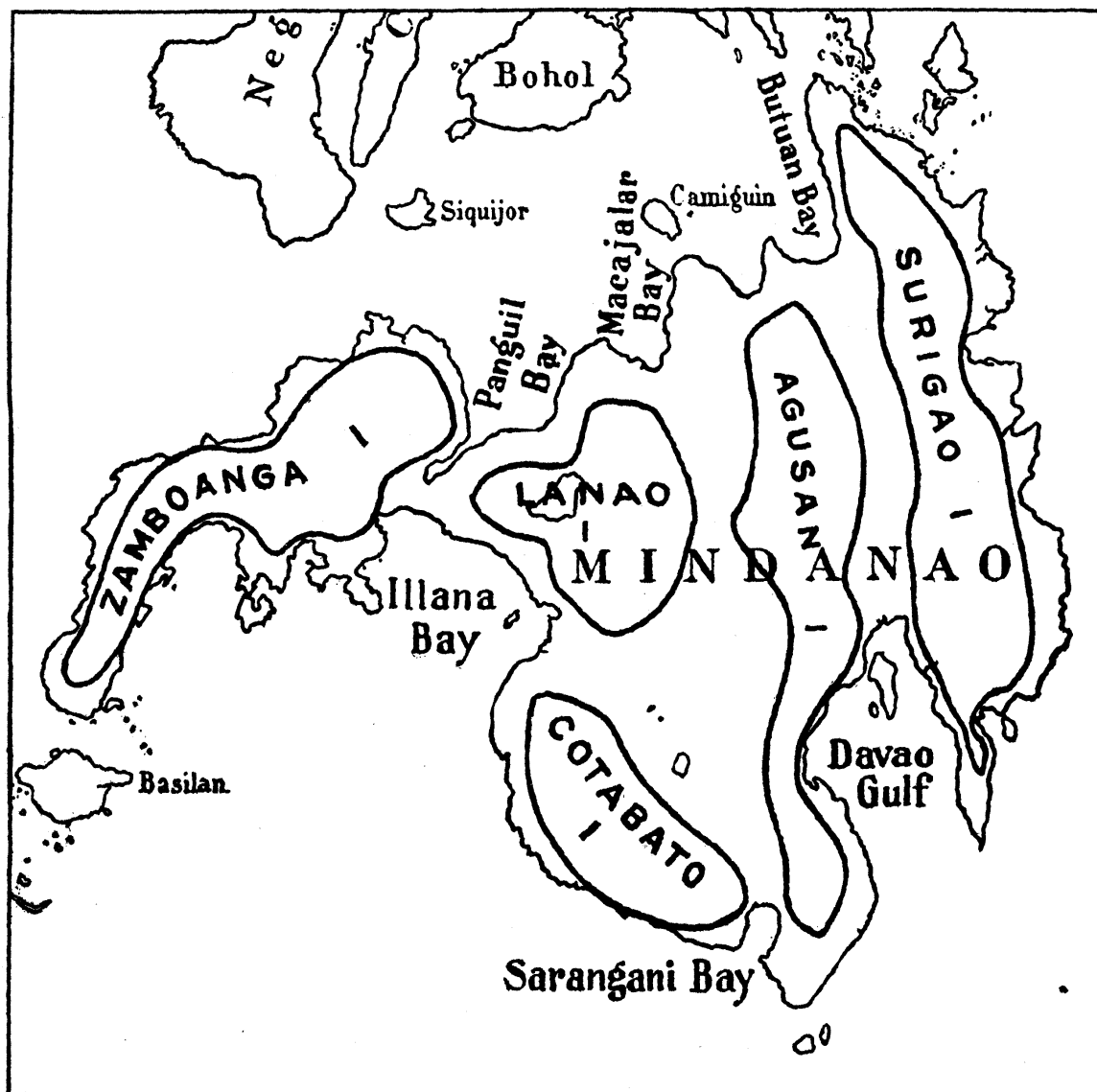


FIG. 19. Some probable Pleistocene islands in Mindanao.

of Bukidnon Province, flows south through the mountains for about 45 miles, than turns abruptly west and debouches upon the Bukidnon Plain to flow south again for about 45 miles to Kabakan, Cotabato Province, at which point it becomes the Cotabato River and meanders west through Cotabato Valley to Illana Bay. The course of Pulangi River indicates, as first suggested by Doctor Dickerson, that this river emptied into the Cotabato-Cagayan Strait at about Lumbayo, Bukidnon, in early Pleistocene time. The gulf floor was then elevated to form the Bukidnon

Plateau and the Pulangi River then intrenched itself in a southern course, emptying into Cotabato Gulf of later Pleistocene time somewhere near Kabakan. The floor of Cotabato Gulf then slowly emerged to form Cotabato Valley, and the Pulangi River found its way west to Illana Bay through Cotabato Valley. The other northern tributaries of Cotabato River—Libungan, Malitabug, and Maridagao Rivers—exhibit analogous drainage histories. Some of the chief tributaries of Agusan River north of Talacogon flow in a southern direction until they meet Agusan River, when the direction of flow turns north. This suggests that these rivers formed their channels and flowed into the Davao-Butuan Strait in early Pleistocene time and that they still indicate their original drainage although subsequent uplift caused the chief drainage to be to the north. The Post-Pliocene uplift of Mindanao seems to have taken place in about seven well-marked stages and the total elevation has been at least 360 meters.

The accompanying map shows the approximate outlines of the five major Pleistocene islands of Mindanao which are for convenience given names. [Fig. 19.] Although this map does not demonstrate clearly the fact, these Pleistocene Mindanao islands coincide closely with the present topographic high places of Mindanao; the present low places correspond to the early-Pleistocene seas and straits. This division of Mindanao into five major early-Pleistocene islands is based upon the distribution of the Pleistocene coralline limestone and wave-cut terraces and is a tentative separation. Further investigation will probably show that the Pleistocene-Mindanao islands of Zamboanga, Surigao and Agusan were really two islands each; but present evidence is not sufficiently definite to subdivide them. Cotabato Island was undoubtedly not a single island, but a group of small islands. It will be noted that the five major Pleistocene-Mindanao islands form an insular group not much dissimilar to the present Visayan group.

As the Pleistocene period was not simple, but was complicated by an alternation of warm and cold stages, it is probable that complications, even greater than Moody's discussion indicates, were present.

Terraces about 120 or 150 meters in elevation, in Bohol, Leyte, and Samar, are described by several observers. The abundance of coralline limestone and marl and a well-marked marine terrace over the southern half of Bohol indicate that but little of Bohol was above sea level during the Pleistocene (Plate 1, fig. 2). Likewise, there are notable terraces in the northwestern peninsula of Leyte, which have been studied with some care.

Similar history with similar complications has been reported by Schenck,* on the eastern side of Samar in the vicinity of Taft and Dolores. Schenck's observations apparently indicate that the last movement on the eastern shore of Samar was that of depression (or rise of the sea, according to Daly's glacial

* Philip. Journ. Sci. 20 (1922) 231-271.



hypothesis). However, previous to this time evidences of the high terraces that cross the middle portion of Samar are indicated by Schenck.

Seemingly, the terracing on Samar, Leyte, and Bohol and the local depressions described indicate that the combined mass was controlled by about the same set of forces during the Pleistocene. In all probability, Leyte was a series of small islands during this time; most of Bohol was covered during early Pleistocene by the shallow water of a sea (Plate 1, fig. 2); and large portions of Samar were in all probability likewise covered. Since the succession of uplifts in the middle or late Pleistocene these three islands began to assume their present form, and the Pleistocene Leyte archipelago supplied the late Pleistocene land masses with their present floras and faunas.

On Cebu, 65 to 80 kilometers west, a vastly different condition exists. The Pleistocene history of Cebu is highly complicated in detail, and on this account only the broad outlines can be sketched. Cebu city is built upon two marine terraces; one is about 3 meters, and the other from about 9 to 18 meters above the present sea level. These two terraces extend north and south of the city giving a narrow but good means of travel along this coastal stretch. According to Smith, higher terraces, the uppermost of which is 300 meters above the sea are well developed in the hills near the city. Similar terraces resting unconformably on Malumbang limestone were noticed on the west coast south of Barili at approximately the same elevations. About 4 kilometers up the steep slopes from Alegria on the west coast is a plateau of remarkable evenness the elevation of which is approximately 600 meters. It is cut across the truncate edges of the Malumbang sandstone, which has a prevailing dip of 30° . As indicated in a previous chapter, Cebu Island is probably an upthrust block and Tañon Strait is the corresponding depression block in a well-marked northeast-and-southwest fault system. Cebu, in the early Pleistocene, was a string of coralline-topped islets, which in later Pleistocene were united to form the present island.

Recent explorations in Negros by Smith and Beckwith disclosed extensive terracing. A wide marine terrace occurs on the west side and narrowly skirts the east coast to the vicinity of San Carlos and beyond. According to Smith, this uplift is further indicated by incised meanders in the lower part of the volcanic plain which borders the marine plain.

Negros was intimately connected with Guimaras, Panay, Masbate, and Ticao during the Pleistocene. This fact is brought out by tracing the 30-fathom line and the 100-fathom line on Coast and Geodetic Survey chart 4718, of Panay, Negros, Cebu, and Masbate. Negros and Panay are closely connected to the northwest with Masbate by a sea that is everywhere less than 30 fathoms (55 meters) in depth. An extensive series of marine terraces is reported by Abella, and later by Beckwith, in the area west of Lucena in central Panay. Five kilometers south of Ulian River, near Curoton, just north of Abangay River, about 40 kilometers north of Iloilo city in the central portion of Panay, marine gravel terraces of Pleistocene age rest unconformably upon a loose, fossiliferous sandstone of Malumbang age. These marine terraces indicate that during one stage of the Pleistocene Panay was divided into at least two large islands. Some of these terraces reach an elevation of about 30 meters.

Guimaras is likewise terraced. Following the formation of terraces in Negros, Panay, Guimaras, and Masbate, apparently the general region was uplifted without any marked faulting during the Pleistocene and a land mass of considerable extent in middle Pleistocene connected these large islands with Masbate. Between the present sites of Panay, Negros, and Masbate a broad low plain was developed. Ferguson first definitely announced this interesting relationship,* and he published further notes in a later paper.†

As Worcester ‡ pointed out Negros, Panay, Guimaras, and Masbate are a zoölogical unit. McGregor notes that "the birds of Ticao show that this island belongs to the Masbate-Panay complex." The relationship of the indicated islands is shown on the relief and hydrographic map, Plate 5. Becker's clever interpretation and Ferguson's support and strengthening of his peneplain hypothesis are excellent pieces of geologic reasoning. As is indicated in a preceding discussion, without uplift, this broad, low-lying plain would be covered by the waters restored from glacial ice at the close of the last phase of the Pleistocene and the resultant drowned topography beautifully exhibited in Masbate would be now easily comprehensible. Upon the crest of the small elevations of late Pleistocene time coral polyps

* Philip. Journ. Sci. § A 4 (1909) 1.

† Philip. Journ. Sci. § A 6 (1911) 397.

‡ Proc. U. S. Nat. Mus. 20 (1898) 575-578.

are erecting limestone platforms in the shallow area between Masbate and Negros.

The startling conception of the Penck-Daly hypothesis surely aids greatly in interpreting this particular area. Apparently this interpretation is further substantiated when the seaward extension of Cebu Island is studied.

Little is known concerning the Pleistocene of Palawan. There is a low, well-marked marine terrace at Puerto Princesa, according to photographs taken by Dr. Paul C. Freer, first director of the Bureau of Science (Plate 1, fig. 3). The embayments, such as Malampaya Sound, indicate the drowned river valleys of a former cycle, during which the island was at a much greater elevation than at present (Plate 2). The marine terrace of Puerto Princesa on the east coast and Table Point terrace on the west probably indicate a still earlier cycle, during which submergence was greater than in the Recent (Plate 1, fig. 3). At present the shore line indicates drowning of such an order that a rise of the sea of 60 fathoms (the estimate of Daly) would be more than sufficient to flood the stream valleys of the second cycle. The 60-meter curve of the Coast and Geodetic Survey chart illustrates this condition beautifully.

Zoölogically and botanically, the Calamianes and Palawan are, in broad terms, a unit with a dominantly Bornean flora and fauna. Mindoro is less strictly Bornean with more endemic species, both plant and animal, than Palawan possesses. The unique timarau *Bubalus mindorensis* Heude, a dwarf water buffalo, is a distinct Asian type, and judging by its resemblance to the common water buffalo it developed in the late Pleistocene from an early Pleistocene or Pliocene ancestor. Such endemism, which is probably the result of isolation, indicates that Mindoro was separated from Palawan previous to Palawan's separation from Borneo. The present fragmentary knowledge of the Pleistocene geology of Mindoro leads to the same conclusion.

Moody reports coralline limestone from Mindoro from Hospital Hill, which is about 300 meters in elevation, on the side of Lumintao River about 2.5 kilometers from this stream ($121^{\circ} 6'$ east longitude, $12^{\circ} 35'$ north latitude). Previous to the cutting of the 300-meter terrace Mindoro, in all probability, was more emergent than at present and was connected with Palawan.

Tablas probably emerged during the late Pleistocene as an upthrust block between two well-marked faults. It is so recent geologically that its biologic story is in all probability a short

one. However, a biologic study of such an island would give much interesting information. This island would contrast strongly with its faunistically and floristically richer neighbors.*

Luzon has had an exceedingly complicated Pleistocene history and, since but little attention has been paid to the study of marine terraces, there are great gaps in our knowledge of this interesting, irregularly formed island. In its western portion considerable study has been made of Bondoc Peninsula which lies within the longer and more irregular Camarines Peninsula. On the west side of Bondoc Peninsula, about 2 kilometers east of Pinamuntangan Point, at an elevation of 80 to 90 meters, a well-preserved Pleistocene fauna containing gastropods and pelecypods, in addition to reef corals, establishes a definite Pleistocene horizon at this place. As Moody found in Mindoro, this occurrence is a mere residual, as the soft underlying shales and sandstone of the Vigo group have been easily eroded by the torrential rains. There is a still higher terrace, about 160 meters in elevation, east of Mulanay. In this vicinity there are several excellent residuals which mark this much-eroded marine terrace.

In the low divide between Calauag Bay and Ragay Gulf, an excellent 9-meter terrace, marked by coralline limestone which is found resting unconformably upon the truncate edges of Vigo shales, clearly indicates a stage during which a Pleistocene Camarines island existed. The study of the terraces on the southern end of Bondoc Peninsula suggests that at a still earlier stage of the Pleistocene a wide channel existed, which connected the greater Limon Bay with the southern Sibuyan Sea. Smith reports the Paracale district, Camarines Peninsula, as being drowned. The general broken character of this region is in accord with his specially studied case, and here again drowning is probably the episode that closed the Pleistocene.

One of the most striking bits of coastal scenery is on the southern coast of Batangas Province at Cape Santiago. A beautiful succession of fairly broad-stepped terraces rises gradually to an uppermost tread of about 180 meters. Smith noted

* McGregor, in litt., says that "Tablas has several endemic bird species—four, I think. Two of these, *Chibia managei* Bourns and Worcester and *Iole cinereiceps* Bourns and Worcester, differ much from their nearest relatives, suggesting isolation of unusual length or change of unusual rapidity." Taylor notes: "My recent studies brought to light no new species or endemic subspecies of snakes, lizards, or frogs, so the supposed *Sphenomorphus moellendorffi* is probably widely distributed."

well-marked evidences of a marine Pleistocene terrace in the vicinity of Bamban, Tarlac Province, in the central valley of Luzon. So recently has this great valley become land that within historic times canoes have been enabled to pass during flood seasons from Manila Bay to Lingayen Gulf; only within the Recent or the late Pleistocene, through a double process of uplift and filling the Pleistocene Zambales island has been firmly tied to Luzon. Further evidence of this condition is found in the peninsula that forms the western side of Lingayen Gulf. On the westward, or seaward, side there is a well-developed system of marine terraces upon which Fanning * reported numerous residuals of coralline limestone. Cabarruyan Island in Lingayen Gulf also shows evidences of uplift; it has but recently been disconnected from the mainland. On this island, near Anda, a small tooth of a young individual of *Elephas* species is reported to have been collected.

Along the western coast of Ilocos Norte, Ilocos Sur, and a portion of La Union there are well-marked marine terraces of two or three different stages. These terraces extend to an elevation of 75 to 90 meters in the coastal region south of Vigan. In the vicinity of the last-mentioned town, Abra River breaks through a 600-meter range of diorite but 4 kilometers from its mouth in the China Sea. The abrupt western face of this diorite range extends northeast and southwest for many kilometers, and it is sharply set off from the marine terraces, the elevations of which approximate 30 to 45 meters. Evidently this range has been recently thrust up along a well-marked rift, the general trend of which is north 15° east. This region of faulting is in all probability not wholly simple, but consists of several parallel, or approximately parallel, faults, as the marked feature of recent rifting known as kernbutts occurs between these parallel faults. Kernbutts, which are typically described by Lawson, in the valley of Kern River, California, are due to differential displacements between parallel faults (Plate 9). In addition to this well-marked feature, the water gap of the Abra near Vigan is inexplicable on any other basis than that of antecedency, as there is a far easier course across the softer Tertiary rocks a short distance south of Sulvec Point (Plate 9). By movement along the Abra fault in the late Pleistocene this range of diorite was upthrust against the down-cutting Abra. In that particular region faulting undoubtedly has complicated the Pleis-

* Paul R. Fanning, metallurgist in the Bureau of Science from 1910 to 1914.

tocene problem greatly, and in even late Pleistocene time great movements have occurred along many of these fault lines. This fact becomes quite evident when the region around Baguio and Trinidad, Mountain Province, is studied.

The City of Baguio and Trinidad Valley are located on a high upland plateau with an elevation of from 1,200 to 1,500 meters. The Tertiary and Quaternary history of this plateau has been worked out in some detail by Dickerson, whose conclusions are that this plateau is a peneplain, developed near sea level during early or middle Pleistocene and hoisted by faulting on a great scale during late Pleistocene. Because of the torrential tropical rains much of its surface has, even during late geologic and Recent times, been removed entirely from large areas. Only such residuals as the Baguio Plateau, Haight's Plateau, and Mount Dana Plateau remain as evidence of this once extensive upland. Farther east and north of this plateau higher mountains, attaining elevations of from 1,200 or 1,500 meters, probably existed during the Pleistocene, and upon these higher and colder peaks the representatives of the early Formosa-Himalayan flora were preserved.

Cagayan River in Cagayan Valley, northern Luzon, passes through low hills even a few kilometers south of Aparri, and according to certain contour maps this stream is entrenched in a series of low hills from which it has cut narrow shallow valleys. No definite information is available, but it seems entirely probable that Cagayan Valley was occupied by the sea during the late Pleistocene.

The Babuyan Islands, north of Luzon, are in part limestone, in part volcanics. Fuga and Calayan Islands are, according to McGregor, composed of limestone, which is cut by a series of terraces. Fuga is composed entirely of limestone, whereas Calayan exposes columnar lava. The channel separating Fuga from the mainland is shallow. According to Ferguson, Camiguin is built up of various lava flows interbedded with volcanic agglomerate and is apparently a rather recent product of volcanism; Babuyan Claro, the island north of Camiguin, is volcanic. The Babuyanes and the Batanes are separated by Balintang Channel, which has considerable depth. Ferguson reports a marine terrace at 270 meters on Batan Island and at 210 meters on Sabtan. The connection of the Batanes with the Babuyanes and, in turn, with Luzon during the Pleistocene seems rather unlikely. Taylor notes that "the complete



FIG. 21. Some possible Pleistocene Philippine islands.

absence of Amphibia from the Batanes is significant." The Babuyan Islands, on the other hand, may have been directly connected with Luzon during a high-standing period of this land mass in early Pleistocene. (Plate 7 and fig. 21.) It is noteworthy that representatives of five genera of Dipterocarpaceæ occur in Camiguin, but none has been found north of this island.

Such then are mere sketch lines of the intricate Pleistocene design; although the gaps in the information are very great, certain of the larger features of the Pleistocene Philippine Archipelago are clear in broad outline.

HYDROGRAPHY OF THE PHILIPPINES

THE RELATION BETWEEN HYDROGRAPHY AND BIOLOGY

Pleistocene palæogeography as based upon known geologic and physiographic data in the Philippines is incomplete and at times indefinite. Fortunately, another line of attack is furnished by hydrography, the phase of oceanography which has to do with a study of undersea topography. The meaning of a diversified submarine topography such as exists in the Philippines is clearly set forth by Molengraaff,* who says:

Submarine topography all over the world is much simpler than the topography of the subaerial portion of the globe. This is, at least near the continental borders, evidently the consequence of the covering or blanketing influence of continuous sedimentation on the relief of the sea-bottoms contrasting with the carving and sculpturing influence of never-ceasing erosion on the land surfaces. Wherever this rule does not hold good the submarine topography, not yet being obliterated by sedimentation, must be of recent date. A bold relief of the sea-bottom is, therefore, at least near the continents, apt to indicate portions of the Earth's crust which either have been warped in recent geological time or still continue to be orogenetically active, and thus continually rejuvenate and remould the sculpture of their surface.

This excellent statement is directly applicable to the Philippines, for the island group has been warped and faulted in recent geologic time and still continues to be orogenetically active. Practically all students of distributional problems agree that the shallow zone between the shore line of the ocean and the 100-fathom isobath, the usual limit of the continental shelf, is alternately dry land connected with the mainland and a flooded area. This edge of the continental platform has a great significance in connection with distributional problems. Earle and Wallace recognized its importance, and Matthew † said that—

* * * in all those islands which are separated by deep ocean from the mainland, we find that just that evidence is lacking which would afford convincing proof of former union with the mainland. Their faunae are widely different from those of the adjoining mainland, they lack just those animals which could not possibly have reached there except by land bridges, they point often to long periods of independent evolution and expansion, and the primary elements of the faunae of every one of them

* Geog. Journ. 57 (1921) 95. † Ann. N. Y. Acad. Sci. 24 (1925) 202, 203.

are such as might possibly at least have reached the island without continental union, whether by accidental transportation, by swimming or by other means.

Take for example the mammals of Sumatra, Java and Borneo. We cannot reasonably suppose that rhinoceroses, tapirs, deer, wild dogs, felids and numerous other large animals common to them and the adjoining continents reached these islands except by land. They are too large for transportation on "rafts" of vegetation such as occasionally drift to sea from the mouths of tropical rivers. They are dry-land animals not given to swimming long distances. And we would not invoke the agency of man to account for a whole fauna. But most important is the fact that all the animals that we might fairly expect to find there in view of a former land connection are really present.

The great advances made during the last thirty years in sounding the depths of the East Indian Sea have added much to our understanding of the nature of the changes in this interesting region. Many preconceived ideas have been greatly modified by the startling contrast among parts of the Australasian Region. The Philippines are merely the northernmost portion of this terrane. On this account the East Indian Archipelago and Australia must be considered broadly. Molengraaff's * paper is the principal source of the following discussion upon this general region.

The Australasian mediterranean sea is divided into three distinct parts, two of which exhibit a submarine topography of exceeding simplicity and lack of diversity, in marked contrast with a great intermediate zone of diversified form. The Philippines, for the most part, belong to this area of great ocean depths and contrastingly great heights of neighboring land, which will be called Wallacea. The Asian, or Sunda shelf; Wallacea; and the Australian, or Sahul, shelf are the three well-defined divisions of the Australasian mediterranean sea (Plate 40 and fig. 4).

ASIAN, OR SUNDA, SHELF

The Sunda shelf has an area of 1,850,000 square kilometers, the greatest in the world, and is notable for its remarkable evenness and its shallow-sea covering of 30 fathoms average depth. According to Molengraaff, this shelf is geologically notable for its great stability at least since the "beginning of the Neogene Age."† Probably during the Miocene and Pliocene, at

* Geog. Journ. 57 (1921) 95-118.

† Seismologically this shelf has also remarkable stability as shown by Doctor Visser, of Batavia; seismic centers are all located on the southern borders. The eastern border between Borneo and Celebes also seems to be unstable, but much less so than the southern.—M. SADERRA MASÓ.

times Asia included within its continental borders Java, Sumatra, Borneo, and the area between these land masses of the present, Sundaland of Molengraaff (Plate 40 and fig. 4).

Sundaland was a very extensive worn-down plain, bordered on the south by the volcanic cones and nonvolcanic mountains of Sumatra and Java and limited on the east and northeast by the granite bosses and high sandstone plateaus of western

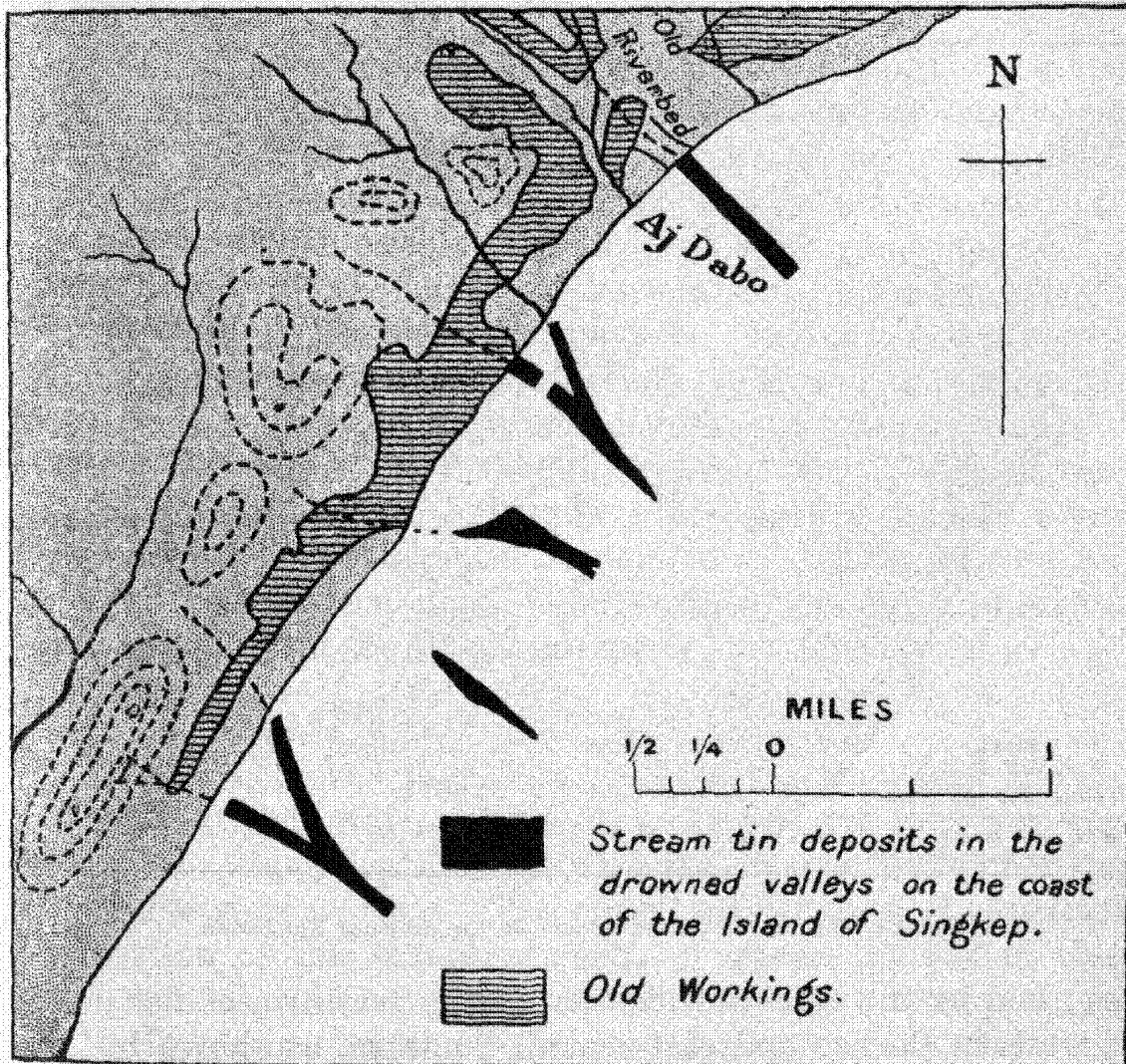


FIG. 22. Showing where stream tin occurs in drowned valleys off Singkep Island, Sunda Sea, east coast of Sumatra, south of Singapore.

Borneo. The low mountains of Malaysia formed a distinct barrier on the west. The seaward extension of many of the streams of the Malay Peninsula, as shown by stream-tin dredging operations and by the low, gently countoured, Malay Peninsula mountains, prove the existence of such a barrier (fig. 22).

The principal drainage of this peneplain of upper Pliocene or lower Pleistocene age was to the north, with a low divide located between the present sites of southern Borneo and Java and

marked by the now drowned monadnocks Banka, Billiton, and the islands of the Karimata group. From this low divide an eastward-flowing stream wended its tortuous way to the Celebes Sea. This picture is clearly shown by the isobathic contouring of the now submerged Sundaland (fig. 23); by the character of the topography of northern Sumatra and Java, where much-eroded mountains gently merge into an extensive plain, which in turn gradually dips beneath the waters of the shallow Sunda

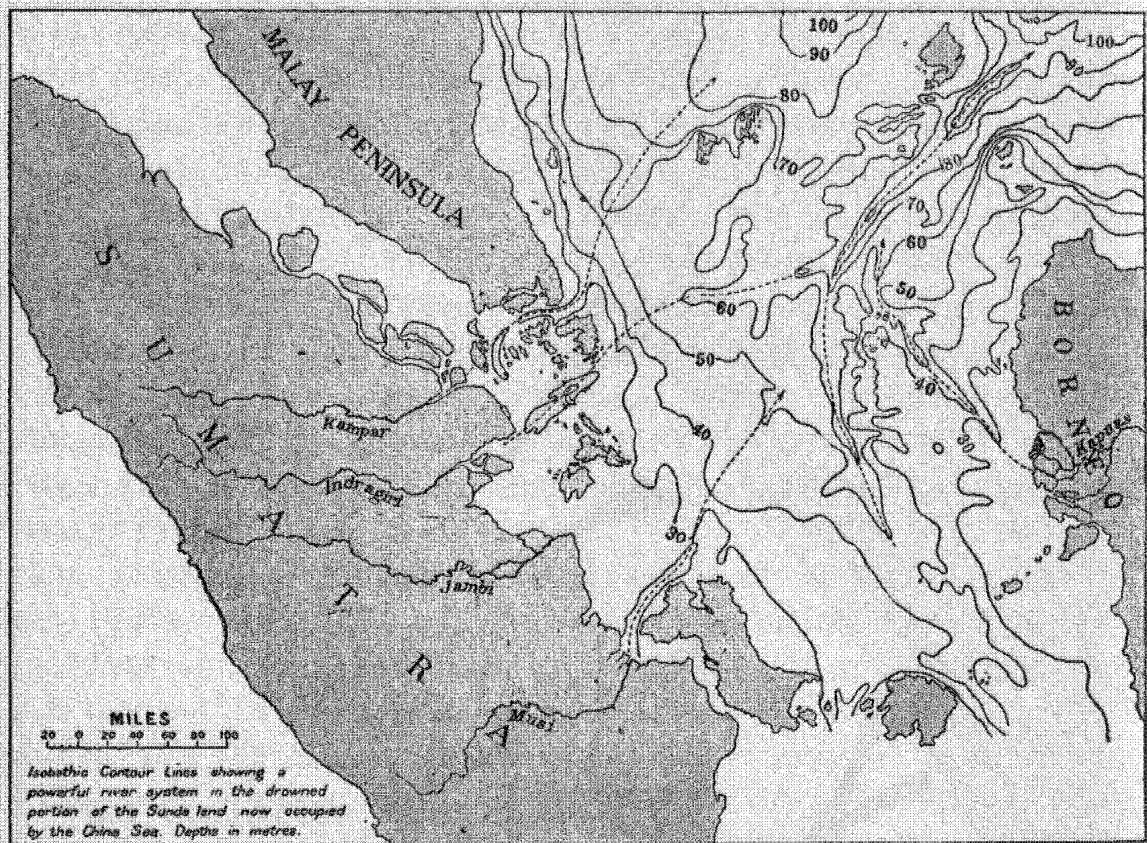


FIG. 23. The ancient river system of the drowned Sundaland.

Sea; and by the essential identity of the fresh-water fish fauna of western Borneo and east-central Sumatra, as shown by Max Weber. Molengraaff says that—

The various rivers of Sumatra and Borneo now discharging into the Sunda-shelf sea are the dismembered side branches of these large main streams. Thus, the Musi, one of the largest rivers of Sumatra, and the Kapuas, the largest river of West Borneo, both were confluent of the northern main stream and consequently belong to the same river system.

The general absence of uplifted marine plains on the borders of the Sunda Sea indicates that diastrophism has not been active during late Neocene time; hence, the flooding of Sundaland during the warm phases of the Pleistocene and during the Recent must have been due to the liquidation of waters pre-

viously withdrawn during the cold phases of the Pleistocene; that is, tied up in the glacial ice of higher latitudes. If this explanation be true, then the fringing coral reefs that bordered the low, outer, eastern edge of Asia must now be represented by offshore barrier reefs. That this condition exists is clearly demonstrated by Molengraaff. Proof of such immersion is given by the magnificent Sunda barrier reef, which is admirably shown on the map adapted from Molengraaff (fig. 24). The depth of the lagoon inclosed by this reef is nearly uniform, averaging about 45 meters with a maximum of but 75 meters. The contours (fig. 24) show that the slope from the edge of this barrier reef into Macassar Straits is very abrupt; it drops rapidly to 200 meters, thence in a short distance to 2,385 meters.

Molengraaff does not recognize a similar condition on the northern coast of Sundaland in the southern China Sea between Indo-China and Borneo and suggests that the absence of a barrier reef is due to the unfavorable condition of the bottom, which here consists of sandy and muddy sediments.

Along Palawan at the 200-meter isobath, recent investigations indicate the presence of a barrier reef, which is in larger part now drowned. The apparent absence of a northern barrier reef marking the northern edge of the Sunda shelf will be discussed in connection with the Palawan trough.

SAHUL, OR AUSTRALIAN, SHELF

Wallace recognized that New Guinea was connected to Australia beneath the waters of the Arafura Sea and that here also, around this island continent, is a fringe of now submerged land of late Pleistocene time. The great barrier reef of Australia is a portion of this extensive shelf. Features similar to those of the Sunda shelf have been described by E. C. Andrews and W. M. Davis incidental to the consideration of barrier reefs. So apparent is the direct connection of New Guinea with tropical northern Australia that it is not deemed necessary to describe this notable shelf in further detail.

WALLACEA

Between the two last-described shelves lies Wallacea (new geographic name). The topography of this elongate narrow area, which extends from Timor through Celebes, through the major portion of the Philippines, and to the Batanes, is highly complex and diversified. The present form of Wallacea has been largely attained during Pleistocene and Recent times. The

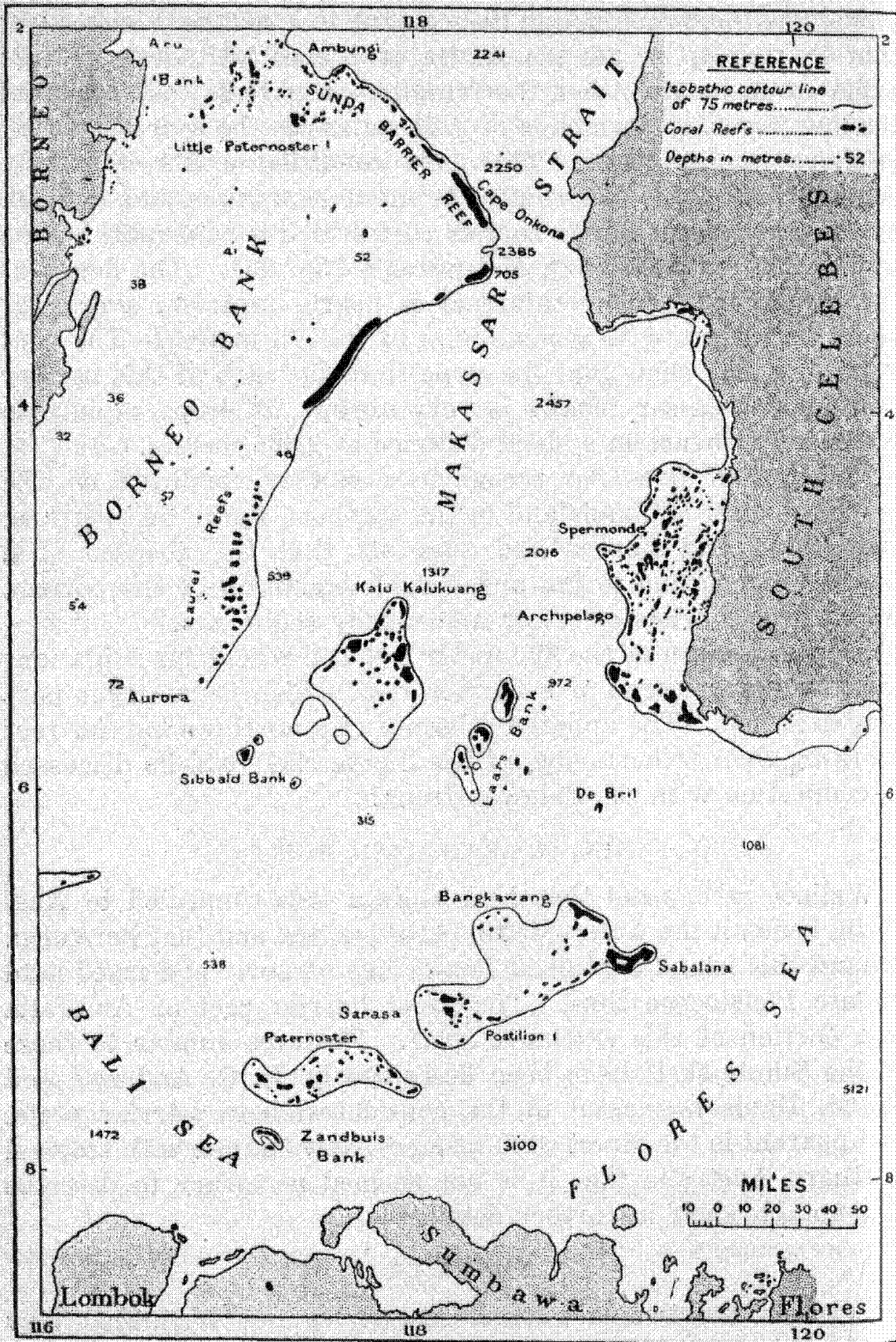


FIG. 24. The great Sunda barrier reef and atolls.

sudden changes from the depths of ocean to the narrow shelf seas, the unnumbered marine step terraces veneered at times with coral-reef material, the general lack of barrier reefs and

atolls, and the numerous deeps bordered by steep-sided mountain islands are the principal features that contrast strongly with those of the Sahul and Sunda shelves. Again Science must acknowledge a great debt to the indefatigable workers—Verbeek, Fennema, and Martin—who laid the foundations of East Indian geology and to the later eminent workers in this field who at present are building the splendid superstructure—Brouwer, Molengraaff, the Sarasins, and Abendanon.

The southern portion of Wallacea (fig. 4) is well described by Molengraaff as follows:

Although the topography both of the land and the sea-bottom is very complicated, a few main features stand out well, and cannot fail to attract attention. These features are the well-marked trough-shape of the majority of the deep-sea basins, the elongation being in the same direction as that of the troughs; the arrangement of both the basins and the islands in curved rows; and the conspicuous signs of elevation in modern times exhibited by those islands.

It is reasonable to surmise that a genetic connection must exist between the subsidence of the trough-shaped deep-sea basins and the elevation of the adjoining elongated islands; indeed, the common origin of these antagonistic movements, according to my opinion, has to be sought in one and the same crustal movement, viz. in a process of folding at a certain depth. If the question were raised as to what might be seen at the Earth's surface if an area were folded by crustal movement at a certain depth, I should be inclined to reply that its appearance would be similar to what obtains at present in the eastern portion of the Indian archipelago.

Molengraaff supports this conception with interesting data. In this connection, he makes an ingenious use of the Dana-Darwin coral theory to explain the distribution of fringing reefs in one group of islands of the Tukang Besi Archipelago as being due to uplift along the curve of an anticlinal axis and corresponding and flanking groups, which but a few kilometers away exhibit striking barrier reef and atoll conditions. The latter two groups he regards as being due to submergence while two synclines were forming, the upward growth of corals in these two cases keeping pace with the down-folding.

The uplifted coral reefs of Pleistocene age in Timor at elevations of 1,300 meters above sea level, the step terraces cut upon Kissar, Kambing with thirteen terraces, and Dawara with sixteen are cited by Molengraaff as well. These terraces are interpreted by him as indicating the upfolded portion of anticlines. W. H. Hobbs has suggested that rapid movements characterize the formation of fault blocks and that the slower movements, such as Molengraaff has described in his discussion of the

Tukang Besi Archipelago, are indicative of folding. Faulting, as suggested by Hobbs's statement, explains the conditions for Timor and its neighboring deeps better than does the anticlinal theory of Molengraaff.

A particularly interesting case of sudden, downward, diastrophic movement, so rapid that reef-building corals could not maintain themselves by upward growth, was discovered by the Siboga Expedition in 1900, in the deeper portion of the Ceram Sea deep. The Siboga Expedition found an area of sea bottom not less than 3 kilometers in length, at depths varying from 1,304 to 1,633 meters, that was covered by great quantities of reef-building corals specifically identical with living reef-building corals now flourishing near the surface at 42 kilometers from the dredging site. These manganese-oxide-covered corals very evidently could not have grown at such depths but were carried there during the Pleistocene by some great and sudden movement. This evidence is most important in that it gives us, in this particular case at least, a picture of a shallow Pleistocene sea which is now covered by the notable Ceram Sea deep. Indirect evidence obtained through a study by Weber of fresh-water fishes indicates that Timor and its neighboring deeps were likewise formed during the Pleistocene. According to Weber, the present fresh-water fish fauna of Timor was undoubtedly derived from marine fishes inhabiting shallow shelf seas. Some of the species are not now found in the extremely narrow shelf sea that surrounds Timor. Hence, it is reasonable to conclude that the present high mountain tops of Timor were surrounded by shallow seas at the time the marine ancestors of the fresh-water fishes migrated from the sea into the streams of Timor. Since the 1,300-meter terrace on Timor is Pleistocene, it is highly probable that the deepening of Timor Sea took place in middle or late Pleistocene.

Such, in part, is Molengraaff's interesting discussion of the region south of the Philippines.

DEEP-SEA TROUGHS AND SHELVES OF THE PHILIPPINES

FAULTING

Faulting, rather than folding, seems to be the dominant process in the Philippines. The coincidence of several seismic areas, the presence of many straight-line elements, the landward extensions of some of these straight-line elements which limit certain troughs, well-marked precipitous scarps of great height sharply

set off from the gentle slopes adjoining the presence of locally uplifted blocks, and locally depressed troughs within the sunken area are the essential criteria for recognition of undersea faults. Taber,* in a discussion of the great fault troughs of the Antilles, states that—

The last-mentioned features develop within fault zones as a result of the differential displacement of long narrow blocks or wedges formed by the branching and intersection of nearly parallel faults. The formation of these subordinate troughs and horsts is a common accompaniment of normal faulting on a large scale and especially of trough faulting. On land these minor topographic effects of faulting are soon obliterated by erosion and by the accumulation of rock-waste in the troughs; therefore the significance of these criteria in the recognition and interpretation of faulting has been generally overlooked. Because of their short life these topographic features are seldom found on land except in arid regions and where very recent displacements have occurred along old fault zones. Beautiful examples of this type of fault topography on a small scale have developed along the Wasatch fault zone in Utah as a result of post-Pleistocene displacements. Similar topographic effects were produced in California by the faulting that accompanied the Owens Valley earthquake of 1872; and there are many examples along the line of the San Andres fault zone of California.

In the following discussion the recognition of faults will depend, in part, upon the usual topographic criteria; in part, upon seismic areas; and, finally, upon the landward extensions of the tectonic lines associated with these unstable areas.

PHILIPPINE TROUGH

The landward extension of tectonic lines is well illustrated by the most-notable deep of the Philippines, the Philippine trough, which extends northward beyond northern Samar and has a general depth of 9,000 meters with a maximum of 9,788 meters, according to the *Planet* soundings. This remarkable feature (fig. 25) is nearly rectilinear in outline, but is not wholly simple. When the land-sea slopes are considered, the very sudden descent is the most-notable feature of this deep. The east-and-west sections (figs. 26 and 27) show clearly "extremely precipitous slopes" and "abrupt changes in slopes at top and bottom."

That this trough is a graben, or dropped block, is also indicated by seismology. Saderra Masó has described the seismic conditions.†

* Journ. Geol. 30 (1922) 90-91.

† Philip. Journ. Sci. 20 (1922) 253.

In an earlier publication, the first discussion of the seismic conditions in the Philippines in relation to the dominant tectonic lines, Saderra Masó and Smith refer to this deep as follows:*

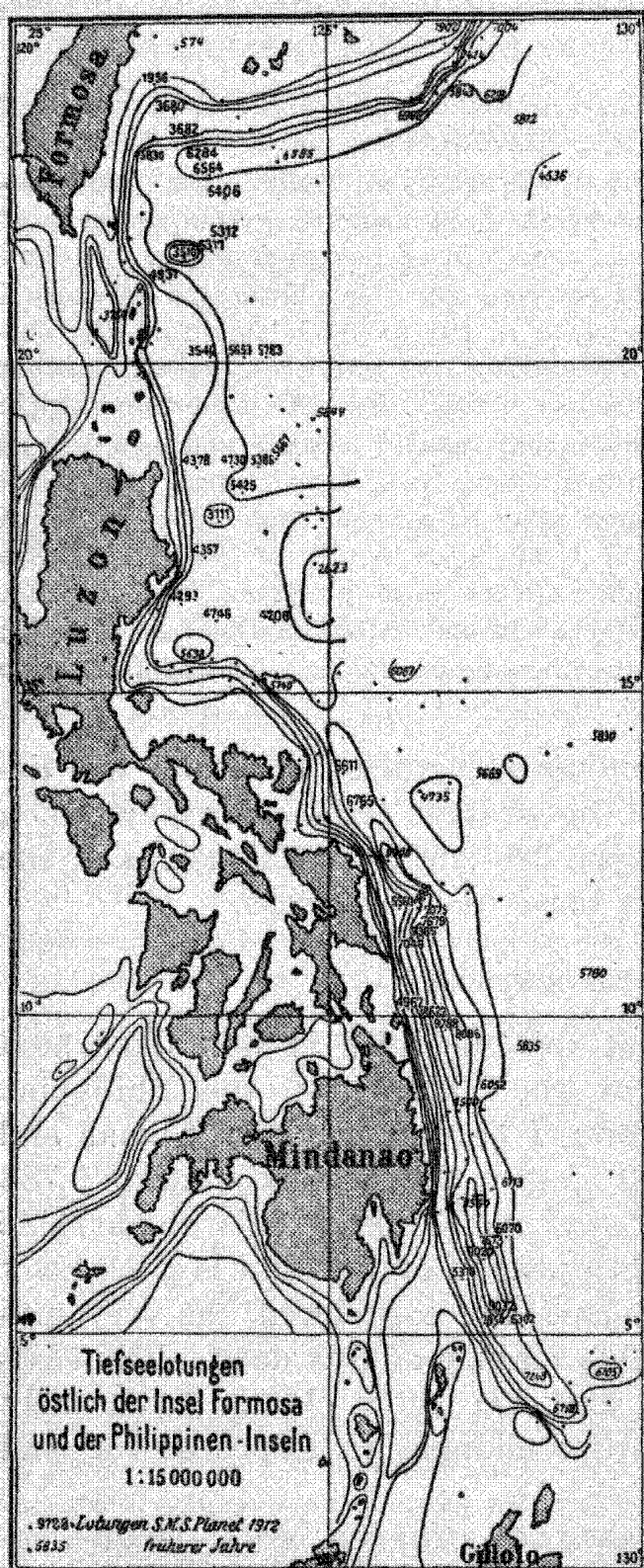


FIG. 25. Deep-sea soundings taken by the *Planet* east of Formosa and the Philippines.

The region which has suffered the most from violent earthquakes during the past fifty years is without doubt eastern Mindanao and particularly the Agusan Valley. We have no seismic data of this region from a period more remote than 1889, but this is doubtless owing to the undeveloped state of that part of the Archipelago and to the consequent lack of communication with the outside world. The great deep-sea trough which exists along the east coast of this part of the island indicates that many earthquakes must have occurred there since it first began to form. The same may be said of the coasts of Samar which also are exposed to the influence of the same "deep," and hence that they also are as unstable as the eastern coast of Mindanao. The principal epicenter of Samar is near the northwest coast.

However, the Philippine trough is beyond much doubt directly connected with another graben, the Agusan Valley of Mindanao. Concerning this region the same authors state:†

"We call this line the 'Line of the Agusan River Valley' because the portion of it which lies within the

* Philip. Journ. Sci. § A 8 (1913) 217.

† Op. cit. 223.

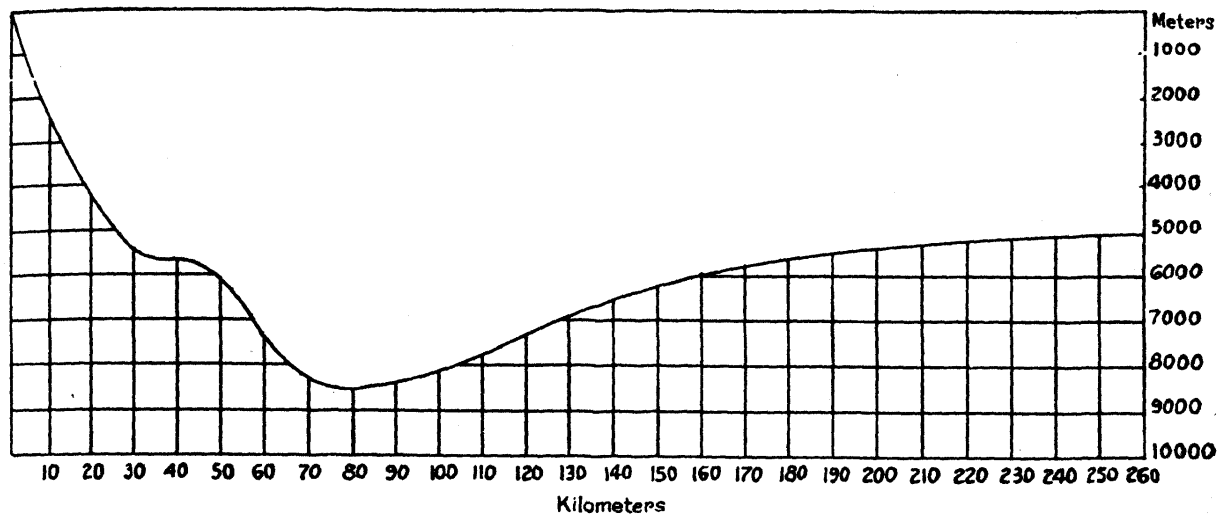


FIG. 26. Diagram profile of the Philippine deep at the southern end of Mindanao.

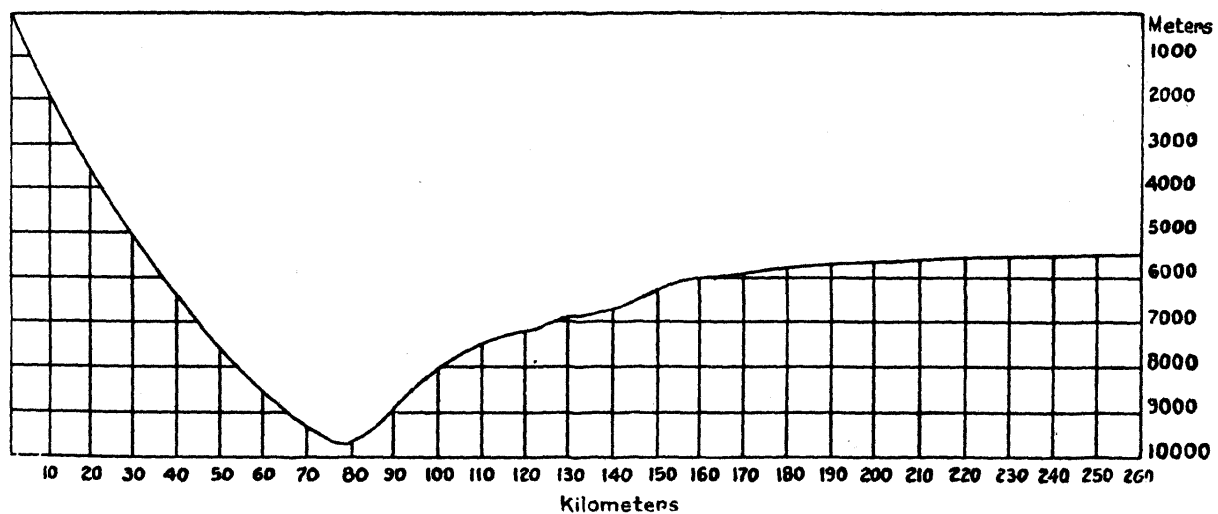


FIG. 27. Diagram profile of the Philippine deep at the northern end of Mindanao.

said valley has been the seat of the greatest number of violent earthquakes which occurred during the last fifty years. The first seismic district of importance of this line comprises the large Gulf of Davao, which is 120 kilometers long and 50 to 70 kilometers wide. The average depth of this basin is 800 meters, increasing, however, toward the southeast in such manner as to exceed 1,650 meters west of Cape San Agustin. * * *. To the west of the gulf rise the gigantic Apo Volcano, Matutum, and several other cones of less importance, which constitute the northern boundary of the volcanic zone extending, as it seems, from Mount Apo as far as Celebes, * * *. [See Plate 3.]

"The extensive valley of the Agusan River runs from south-southeast to north-northwest, almost parallel to the east coast of Mindanao, * * *. The entire bottom of the Agusan Valley consists of marine sediments containing an abundance of recent shells: only at the mouths of the water courses, which descend from the mountains bounding it east and west, is found gravel containing well-worn pebbles of andesite and other igneous rocks."

Centeno,* in 1879, investigated the very severe earthquakes in the vicinity of Surigao, northern Mindanao, and described many

* Temblores de tierra ocurridos en Julio de 1880 en la Isla de Luzon. Madrid (1885).

fissures and subsidences along the ridges of the mountains of Surigao Peninsula, especially near Point Bilaa. He also reported that the depth of the water in Surigao Harbor had actually changed.

Evidently a system of parallel faulting exists, as these movements are distinct from those of the very dominant faults of Agusan Valley. According to Moody, the west coast of Surigao ridge in Davao Province, east of the Hagimitan is a fault scarp which indicates a maximum upheaval of 450 meters (1,500 feet). Mount Mayapay on the western side of Agusan Valley, a few kilometers southwest of Butuan, is a notable block mountain. Other parallel faults were noted by this geologist.

All the evidence indicates that Agusan Valley is essentially a graben; Surigao, a horst; and the Mindanao trough, a graben (Plates 3 and 8).*

In striking contrast to the Philippine trough and the northern seaward extension of the Agusan graben into the elongate Sogod Bay in southern Leyte and the 700-fathom deep of Surigao Channel is the shallow sea which connects eastern Leyte and southern Samar through Dinagat and Surigao Islands to Mindanao. Beyond much doubt this area was an important portal during the varying phases of the Pleistocene, an open gateway for the movement of plants and animals during the glacial phase (the time of withdrawal of tropical sea waters) and a closed passage during interglacials (Plate 3).

SULU MEDITERRANEAN SEA

The Sulu Sea deep, which has a northeast trend and an arclike form, is apparently related to the Sulu Archipelago and Zamboanga Peninsula as the corresponding uplifted feature. Whether folding or faulting has given rise to this deep is not known; but in all probability this true mediterranean sea, which has the exceptionally high bottom temperature of 10.2° C., was cut off during the Pleistocene from the colder, deep, oceanic waters whose prevailing temperature is 3.3° C. The northerly extension of this deep has the same trend as central Panay,

* I am convinced that in the Agusan Valley there must exist a faulting system which complicates its nature. There is a great difference between the northern part and the central basin. It seems that the northern part from Butuan to Talacogon is rather aseismic, relatively to the central. On the other hand, some great earthquakes which very presumably originated near 8° north latitude had a mesoseismic area from east to west as they were felt eastward as far as Pelew Islands.—M. SADERRA MASÓ.

which is, in general, geosynclinal. This relation suggests folding, rather than faulting, as the dominant process in the formation of Sulu Sea.* Northwest of this deep is a series of coral atolls such as Tubbataha and the Cagayan Islands. Soundings only 2 miles off Tubbataha reached depths of 1,000 fathoms, indicating a rapid descent from the coral strand with a slope of about 30° , which is approximately that of volcanic cinder cones like Mount Mayon. The Cagayan Islands are reported as being composed of andesitic lava. Possibly these islands as well as Zamboanga Peninsula and Sulu Islands are genetically connected with the Sulu Sea deep.

Molengraaff,† in a recent publication, discusses the Celebes deep, Sulu Sea, and Sulu Archipelago. The following is a translation by Mr. A. v. H. Hartendorp of Molengraaff's statement:

The most noteworthy basins of the Sulu Sea and the Celebes Sea appear to be no other than modified basins of synclinal strips which lie alternate with the anticlinal axis which from the Philippines goes outward in two directions. From the tectonic sketch of Dr. W. D. Smith, one must suppose that a folding with southwest and northeast direction is noticeable with—

1. The basinlike trough in the southeastern part of the China Sea, Palawan basin, geosynclinal.
2. The row of islands, of which Palawan is the principal island, from northwestern Borneo to Mindoro Island, geoanticlinal.
3. The northwestern part of the Sulu Sea, geosynclinal.
4. The row of islands which connects north Borneo with Panay Island and divides the Sulu Sea in two parts, geoanticlinal.
5. The troughlike basin which is the deepest, southeastern part of the Sulu Sea, geosynclinal.
6. The row of islands known as the Sulu Archipelago which forms the bridge between the northeast point of North Borneo to the most western point of Mindanao, geoanticlinal.
7. The Celebes Sea, geosynclinal.

The very broad basin of the Celebes Sea is the only deep sea basin of the East-Indian Archipelago which is not lengthened in one troughlike direction. It lies as a broad cuplike region between volcanoes with southwest and northeast direction which connect North Borneo with the Philippines and for some distance press themselves in the island without anywhere reaching the coast of the Pacific Ocean and it falls in with a north and south or a northwest and southeast direction, which on all the islands of the Philippines are met with along the Pacific Ocean coast. On Mindanao the two tectonic lines push together as can be seen from Smith's chart. In the western part of Mindanao the southwest and northeast

* Modern earthquakes have originated generally in the southeastern part of Panay.—M. SADERRA MASÓ.

† *De Geologie der Zeeën van Nederlandsch Oost-Indie*. E. J. Brill, Leiden (1921) 301–303.

direction rules, which through the Sulu Archipelago has a ridge which goes southwestward, in the eastern part preponderates the north and south direction, which can be followed through Sangir Island as a geoanticlinal ridge southward. The separation of these two geoanticlinals gives room for the broad synclinal Celebes basin. To the south the Celebes basin is again narrowed where in north Celebes against the geoanticlinal fold which connects Mindanao with Celebes and with a northeast and southwest direction runs through the Minahassa and connects with the nonvolcanic fold ridge of the north coast of Celebes with an east and west direction. As a small deep depression, the Celebes basin continues to Macassar Strait southward and from the Celebes basin follows the succeeding tectonic element.

BORNEAN SHELF

Molengraaff's general map of the East Indian Archipelago shows clearly that Palawan Island and the dependent Calamianes are united with Borneo beneath the waters of the shallow sea by the 200-meter isobathic curve.* Much interesting detail is brought out when the 60-meter isobath and the 200-meter isobath are drawn upon the United States Coast and Geodetic Survey chart of Palawan. Particularly notable is the series of shoals, for the most part submerged, which occurs on the western side of this elongate island near the 200-meter isobathic curve. The general direction of this isobathic curve is northeast and southwest, parallel to the elongate narrow deep that separates the Palawan-Borneo shelf from the comparatively shallow area in the South China Sea farther west.

PALAWAN TROUGH

The elongate character of the Palawan trough and the bordering Palawan shelf have a striking significance when studied in connection with the known faults in the Philippines (Plates 4 and 5). The Palawan deep is in direct line with the faulted area northeast of Lake Taal which Pratt † has described in careful detail in a paper upon Taal Volcano and its eruption of 1911.‡ He says:

* Calamianes and Palawan seem to be as aseismic as Borneo. Historians of the seventeenth century remarked such a fact and those of subsequent ages did not deny it.—M. SADERRA MASÓ. In Cuyo Island I experienced several rather severe earthquakes in 1918–1919.—A. v. H. HARTENDORP.

† Philip. Journ. Sci. § A 6 (1911) 74–76.

‡ I tried to extend such a line to the Pacific, founded on seismological data (Month. Philip. Weather Bulletin, Nov. 1911). All the region northeast of Taal, including Laguna de Bay and the mountains to Dingalan Bay, presents great irregularities, both orographic and hydrographic.—M. SADERRA MASÓ.

The trend of the recent fissuring indicates a line of weakness passing through Taal Volcano and bearing about N. 30° E. This trend extended beyond the limits of the system and runs closely parallel to the east coast of Luzon and the length of Palawan, passing through Laguna de Bay and Balayan Bay. * * * The earthquakes were strongest in Taal and Talisay, along this line. The alignment of the craters on Volcano Island conforms well with such a trend as do also the outline features of both island and lake. No recent fissure could be traced across the island itself, a fact scarcely explained by the greater fall of ash. If the fissures noted owe their trend entirely to movement radial from the crater their location is still significant, since careful search discovered no other radial fissures around the lake.

* * * * *

If this system of fissures is along a plane of extensive former faulting, as has been suggested, then earthquakes which affect southwestern Luzon, independent of volcanic action, as well as those due directly to eruptions from Taal, probably would be most violent along its trend. It would mark both a volcano-tectonic and a seismo-tectonic line. The towns of Lemery and Taal, situated as they are on this line, would especially be menaced by earthquakes.*

The recognition of a dominant fault system on Luzon with a general direction of north 30° to 35° east is particularly impressive when studied in connection with certain coast lines and trends. The general isobathic curve of 200 meters on the general hydrographic chart of the Philippines brings out the fact that the Palawan deep, the recent faulting northeast of Lake Taal, and the northeast-and-southwest trend of the Luzon eastern shelf fall in the same system of trend lines. In addition to such features, Casiguran Sound on the east coast of northern Luzon and Dilasac Bay, with the elongate peninsulas between Cape San Ildefonso and Tarigtig Point, indicate another feature of this dominant rift.

What is the age during which the Palawan deep was generated? Apparently, if the interpretation given above is correct, this deep is a late Pleistocene and Recent feature. The chart of Palawan shows certain notable features on the southeastern coast. Recent soundings in the vicinity of Wakefield and Circe Shoals, near the southwest edge of this chart, indicate many submerged shoals that rise abruptly from 400 meters. Following the 60-meter isobath and the 200-meter isobath in a

* Seismic history shows that the part of the line most affected by earthquakes is the northern, from Laguna de Bay to Baler Bay and Casiguran. Historians of former eruptions remark that in the eruption of 1719 fissures opened toward northeast of Bombon, some reaching as far as Calamba on the Laguna de Bay. They destroyed the town and lands of old Tanauan located toward the present Talisay.—M. SADERRA MASÓ.

northeasterly direction to a point south of the narrow central portion of this peninsula a striking change is seen. The two curves suddenly turn from their northeasterly direction and take a course approximately north 5° west. East of these curves the shelf descends abruptly to depths varying from 50 to 1,000 fathoms. South of Puerto Princesa, they take an easterly course. When this feature is studied in connection with the known topography of Puerto Princesa, Honda, and Ulugan Bays, a very suggestive relationship is discovered; and here again, apparently, the north-and-south fault system is recognized cutting across the narrowest portion of Palawan and delimiting Ulugan Bay, the western limits of Honda Bay, and the north-and-south shelf of southwestern Palawan. This feature must be considered in connection with the barrier reefs that rise abruptly from the 400-meter depths, such as the Wakefield and Circe Shoals. Apparently the southwestern portion of Palawan has undergone movements that are probably not the same as those in the northeastern half of this island. It seems highly probable that this southwestern portion has been uplifted along the hypothetical Puerto Princesa fault and tilted or warped to the southeast, plunging the former submerged barrier reefs so slowly that some of the corals on them have grown upward against this submergence (Plates 5 and 6). Cagayan Sulu rises above the northeastern Borneo shelf, and there are biologic data that indicate a land connection with Borneo during the Pleistocene. This island is clearly a monadnock that rose above the general level of a worn-down plain. The San Miguel Islands, north of Cagayan Sulu, rise above the general shelf in a similar manner. Possibly this peneplain extended northward to the shoals of Palawan, which would there be interpreted as monadnocks also. These two hypotheses need more study and more detailed hydrographic information before one or the other, or both, may be asserted with confidence.

Is it not possible that the South China Sea deep and the Palawan trough are very late Pleistocene and Recent features and that in earlier Pleistocene time the Sunda shelf stretched broadly to the north to about 18° north latitude, and that the comparatively shallow area between Indo-China and Palawan in reality represents a relatively submerged portion of this Asian Sundaland, and that a submerged barrier reef about 18° north latitude should be sought? Herre's studies of the distribution of fresh-water fishes indicate an affirmative answer to this question.

TICAO TROUGH

Another interesting relation exists between Ticao and Masbate (Plate 6). Ferguson calls attention to this in his discussion of earthquakes. He says:*

The Atlas de Filipinas divides the island between "rather frequent" and "rare" earthquake areas, the "rather frequent" zone lying, as would be expected, along the very deep Ticao strait between Masbate and Point Bugui.† In a recent catalogue of destructive earthquakes, six earthquakes above VI of the Rossi-Forel scale are stated to have been felt in the years 1869, 1874, 1893, (two) 1897, 1900.

Recent work by Krysh-tafovich upon Ticao indicates that Ferguson's ideas of faulting are nearly correct. In addition, Krysh-tafovich recognizes Ticao as a fault-block island with marked escarpment on the west and with gentle slopes toward the east. The mountain system of Ticao is apparently a very simple one. A moderately elevated, northwesterly trending ridge of this island with extreme altitudes of 322.5 to 348 meters parallels Ticao Strait and runs close to its western shore in marked contrast to that of Masbate; the principal mountain range is situated closer to the eastern coast of the larger island. The eastern shore of Ticao is low, abounding in deep bays fringed with mangrove swamps, in marked contrast to the steep and, in some places, even abrupt western slopes. This orogenic condition is also reflected by the stream drainage, since all the important streams flow from the west to the eastern coast. Ticao is connected at its southern extremity, beneath the shallow waters of the sea, with Masbate. Evidently the faulting that produced the separation of Ticao from Masbate was a comparatively late Pleistocene event, as coralline limestone of probable Pleistocene age has been given an easterly inclination by the tipping of the block. Since Ticao Strait is even now decidedly a seismic area, movements along this fault line are probably continuing to-day; and the last movement recognized by Ferguson, the low terraces in the vicinity of Point Colorado, probably represent an exceedingly late Pleistocene or Recent uplift of the Masbate block.

* Philip. Journ. Sci. § A 6 (1911) 401.

† This map was made by me years ago, and published for the first time in 1895; but even in recent years I was not able to locate accurately the seismic centers affecting Masbate, due to lack of data from southern Masbate and from Burias and Ticao! It seems as if there would be two centers, one in the north close to the coast and a second to the northwest toward the deep south of Bondoc but not so far from Masbate.—M. SADERRA MASÓ.

The stream drainage patterns between Dinasalang and Cataingan and their fiordlike elongate bays are strikingly like the topography along the San Andres rift, between Bolinas and Tomales Bays in the region north of San Francisco, California. A parallel feature is seen at Uson Bay; the straight coast line between Gorda Point and this bay is suggestive of recent faulting along it (Plate 6). Ticao Strait is interpreted as a graben between two parallel faults of the Ticao rift zone. Southeast of Masbate, the Ticao rift probably extends into Biliran Strait and Leyte Bay and beyond. The straight eastern coast of the northwestern Leyte peninsula also indicates this possibility. The alignment of Leyte River Valley may mark the landward extension of this great rift. Only through detailed geologic work will it be possible to determine these extensions or to decide whether or not the Ticao rift and the Surigao rift are identical.

Apparently this rift zone extends northerly in Burias Pass, as the isobaths bend sharply. The bending is particularly well marked by the crowding of these lines upon the southeastern coast of Burias (Plate 6).

The relations of the Visayan shelf, Masbate, Panay, and Negros are discussed in the chapter on Palæogeography. The 200- and 400-meter isobaths around Sibuyan and Romblon indicate the possibility of a former connection with Masbate.

SAN BERNARDINO BRIDGE

Although San Bernardino Strait, between Luzon and Samar, is a notable passage for ocean-going vessels, during certain stages of the Pleistocene a direct land connection probably existed, since even now the greatest depth in the center of the main channel is only 89 fathoms (about 163 meters).

SHELVES AND TROUGHS OF SOUTHEASTERN LUZON

When the hydrography of southeastern Luzon is studied, two distinct tectonic systems appear to be present: the one with general east-and-west direction, the other about north 50° west to north 60° west. The east-and-west system is clearly shown on Plate 5, immediately north of Polillo, and is distinctly marked by the 200-meter isobath and the precipitous descent north of this curve. The edge of this shelf makes an acute angle of 60° with the shelf of eastern Luzon near Polillo. As indicated in the discussion of the Palawan trough and the Taal rift, the

latter shelf is probably due to faulting. A similar condition probably explains the abruptness of the Polillo shelf.

Between Bondoc Peninsula and Sibuyan there is a deep of 1,800 meters. This deep is somewhat rectangular, with its longer sides extending in an east-and-west direction. The eastward extension of the southern side cuts Burias south of Mount Engañoso at a point of sudden narrowing in the island mass. West and south of Mount Engañoso the 400- and 600-meter isobaths reflect a similar condition. Eastern extension of the trend line strikes Sorsogon Bay. According to Saderra Masó and Smith, the isoseismal lines of the Sorsogon earthquake are drawn out in an east-and-west direction. Possibly all of this is mere coincidence, but it is noted here for future workers.

The crowded isobaths along the straight eastern coast of Ragay Gulf near Pasacao and the corresponding elongate 600-meter deep close to the eastern shore suggest a fault zone running north 60° west which, when extended northward, cuts Tayabas Peninsula and apparently forms the eastern shore of Calauag Bay. Possibly the straight eastern shore of Alabat also marks this possible tectonic line.

Saderra Masó, from a study of seismic data, recognizes a notable seismic area along the northern mountain boundary of the central plain of Luzon. A glance at the topographic map of northern and central Luzon reveals at once the character of this dominant Recent line of movement (Plates 7 and 9). The abrupt scarp that limits the northeastern side of the central valley of Luzon and the stream drainage near Agria Point in Dingalan Bay indicate very clearly the direction of this prominent fault. So recent have the movements been along this line that Mr. C. G. Wrentmore, a former director of the Bureau of Public Works, reports, from his surveying data, that there is no indication of an alluvial fan at the point where Agno River debouches upon the central plain of Luzon. The lack of any alluvial cone at this point indicates that the northern Luzon block has been upthrust and the central plain of Luzon dropped so recently that the Agno has not had time to build a new cone.

Dingalan Bay apparently, then, is a vertex of several intersecting faults. Another fault probably bounds the western side of Polillo Strait, and by its north 15° west trend determines in large part the stretch of coast that borders the strait (Plates 7 and 9). Such are some of the structural complications in northern and central Luzon.

Smith, who made an intensive study of Batan Island and vicinity, describes, in litt., Albay Bay and environs as follows:

Extending from the southeastern peninsula of Luzon in an east-and-west direction on the north side of Albay Gulf is a string of six islands which is the superstructure upon a very distinct platform, as indicated by the hydrographic charts of that region. These islands are in order of size, Cagraray, Batan, Rapurapu, San Miguel, and two much smaller ones. The bathymetric contours on the south side of the three larger islands strongly suggest a fault, trending slightly south of east. [Plate 5.]

A geologic reconnaissance of the three larger islands and a detailed study of Batan Island made by me in 1905 enforce the above suggestion and clearly point to faulting.

On the north side of this group there is the suggestion of another fault, trending about north 50° west. On Batan Island is a long stream, the Caracaran, which is oriented about in the same direction as the above.

Saderra Masó suggests another fault parallel to the Batan faults described by Smith. This probable fault passes "through the ancient strait formerly separating the peninsula of Caramoan from Camarines which later was filled up by volcanic ejecta" and is reflected in the submarine contours of Lagonoy Gulf.

The depths north of Marinduque Island are only from 30 to 40 fathoms and thus indicate that this land mass was probably tied to Luzon during the glacial phases of the Pleistocene.

FORMOSAN RIFT SYSTEM

The detailed Coast and Geodetic Survey charts of the central portion of the Philippine Archipelago are not yet available for northern Luzon and its surrounding deeps. One of these charts, Manila Bay to Taiwan, No. 4705, gives excellent shore detail, but many of the deeps only a few kilometers offshore are still unfathomed. The Babuyan Islands clearly rise above the shelf sea of northern Luzon, as the 200-meter isobath encircles them (Plate 7). The known depths of Balintang Channel are 473, 332, and 1,106 fathoms. Such depths separating island groups of Wallacea are not uncommon; although Balintang Channel is at present a definite barrier for plant and animal migration, during early Pleistocene it may not have been so well developed. Faulting along a north 30° east line in Pleistocene and Recent times has probably brought about the present separation of these island groups. On the other hand, the Bashi Channel depths are considerably greater; namely, 1,287, 1,009, and 2,009 fathoms. The waters between this channel and off Cape Bojeador, the

northwestern point of northern Luzon, along a zone about north 20° west to north 25° west, vary from 1,009 fathoms in the straits to 2,964 fathoms at a station north 60° west of Cape Bojeador.

Bashi Channel has the same trend as the Formosan rift which delimits eastern Formosa. Great movements have taken place along this rift in Formosa and consequently the eastern scarp of the Formosa cordillera is exceedingly abrupt. Recent rift features are common along this trend line, and many earthquakes are due to movements along it. Likewise, in northern Luzon, the well-marked Abra rift has the same orientation. This feature is not a simple one, but consists of parallel faults between which small blocks have differentially dropped, producing the characteristic hill called the kernbut (Plates 7 and 9). Isobaths between the town of Vigan and Lingayen Gulf indicate, by their inward bending, the seaward extension of this zone. The peninsular range of Pangasinan may be also limited upon the east by the southward extension of this line. Two epicenters of notable earthquakes are starred on the earthquake map of Saderra Masó and Smith* as being present in the vicinity of Lingayen Gulf along this line and two more, farther north, upon land also near the Abra rift.

On the same map the area off the coast of Ilocos Norte is marked by a row of four stars. These stars are on a line the extension of which passes through the Bashi Channel and strongly suggests a rift at sea which delimits the west side of northern Luzon and the western edge of the shelf sea upon which the Babuyan and Batanes sit. In other words, there is a broad zone of rifting between Formosa and northern Luzon along which movements are still taking place. Recent soundings by the *Stewart* by means of the sonic depth finder substantiate this conclusion. Palæogeographic studies indicate that the Formosan rift system is an old one—at least middle Miocene in age—and movements along it have prevented any direct land connection between Formosa and Luzon.

ZAMBALES RIFT SYSTEM

The closely spaced isobaths along the Zambales coast, with a trend of north 10° west, indicate a very well-marked scarp; and, in addition, this zone is the locus of fault movements that have

* Philip. Journ. Sci. § A 8 (1913) 199.

given rise to several earthquakes during recent years. The same rift is paralleled by faults along the western border of the great central valley of Luzon, according to Smith, and it is probable that a rift system similar to the Mindanao rift system exists here. The Pleistocene Zambales island, which is described in the chapter on Palæogeography, beyond much doubt was an upthrust block with its corresponding graben to the east (Plates 7 and 9).

MINDORO DEEP AND ITS ORIGIN

One of the most striking features shown upon the contoured Coast and Geodetic Survey map of southwestern Luzon and Mindanao is found in the region west of Mindoro. In this area the submarine contours are bent inward in a manner which upon land marks a well-developed stream valley. At first sight, the explanation of a former, well-developed valley, now drowned, is immediately suggested; but upon further consideration of the consequences this hypothesis does not appear tenable. The outermost reëntrant isobath, the 5,500-meter line, would represent possibly a contour near the former sea level, and a bold relief with mountains of 5,500 meters and more would be a necessary result as well. No such enormous heights during the Pleistocene are indicated from a study of Mindoro and its surroundings; nor are there any evidences of later pronounced drowning. In the discussion of the Sulu Sea deep the conclusion was reached that this deep represented the seaward extension of the Panay geosyncline. A similar explanation for this Mindoro deep must be entertained, with an alternative rifting hypothesis. No extensive geosyncline upon the Mindoro land has been recognized by the few geologic workers in this field. The closely spaced isobaths southwest of the Lubang Islands, with north 60° west and south 85° east trends, parallel corresponding sets of isobaths of the Mindoro deep. A well-recognized east-and-west fault passes through the Verde trough. These sets of isobaths, marking very abrupt slope changes, indicate faulting. An east-and-west fault * probably bounds the Mindoro deep on the south and is complicated by faulting along north 60° west lines in addition. Of the two structural hypotheses, extensive rifting

* It is noteworthy that the seismic centers southwest of Luzon are chiefly placed along the Mindoro Strait. South of the trough, that is, the region of Calamianes, south of Mindoro as far as Cuyo and Palawan, seems to be aseismic. In a recent note, I joined this region to aseismic Palawan and this to aseismic Borneo.—M. SADERRA MASÓ.

appears to be the more reasonable explanation for the Mindoro deep.

CELEBES SEA DEEP

The great deep between Mindanao and Celebes may represent a geosyncline, a feature corresponding to the Sulu Sea deep with an intervening geanticline, the Sulu Archipelago between. Complicated faults along axes about north 30° east probably exist. One of these, which probably passes through Panguil Bay and the west side of Illana Bay, is a notable feature since seismic disturbances have repeatedly taken place along it (Plate 3).*

The northeastern arm of Celebes, when prolonged beneath the sea, clearly suggests a former connection between Celebes and Sarangani Peninsula, Mindanao.† The east side of this connection is, however, definitely limited by a seaward extension of the Agusan graben through Davao Gulf and beyond. Geologic evidence in Agusan Valley indicates that this graben has been present since Pliocene time in as much as sediments of that age occur in Agusan Valley.

CONCLUSIONS RELATIVE TO HYDROGRAPHY

Within the Philippine Archipelago the evidence of hydrography is, on the whole, remarkably definite. The shallow shelf sea, around Palawan and its dependent island groups which are now cut off on the north by Mindoro Strait, unites the Calamian and Cuyo groups with this elongate island. That Mindoro was connected with Palawan in geologic time is demonstrated by palæogeographic history. Eastern Mindanao is connected to Leyte and Samar beneath the shallow seas of Leyte Gulf. Bohol is a member of the same shelf group, but the considerable Bohol deep in the Mindanao Sea separates that island from central Mindanao. Likewise, hydrography clearly shows the connection of Panay, Negros, Masbate, and Ticao; and a very late Pleistocene fusion into one island mass, Visaya, is highly probable. The great deep of the Romblon Sea is due to long-

* Undoubtedly the Celebes deep and the deep around Camiguin formerly joined through the Panguil pass or isthmus. This strait was probably filled up by volcanic material coming east and west.—M. SADERRA MASÓ.

† This region, including the group of Sangi and Talaur, is at the present time one of the most active of the eastern regions; the seismic activities extend southward to the Moluccas, and pass west of Gilolo. I expressed this opinion many times and recently Doctor Visser corroborated it, locating centers of tectonic earthquakes which occurred in 1909 and 1919.—M. SADERRA MASÓ.

continued faulting and, hence, the time during which Sibuyan, Tablas, and Romblon were probably joined to this Pleistocene Visaya, was probably early Pleistocene. Palæogeographic and hydrographic studies, however, indicate that Cebu has also had a different history from that of Visaya during the Pleistocene, and that that island is in reality a fusion of several small islands, which took place in middle Pleistocene time. Camarines Peninsula of southeastern Luzon was probably connected at times with Samar during the Pleistocene, as the relatively shallow San Bernardino Strait shows. Camarines Peninsula has been in all likelihood at times an archipelago, as it is traversed by several well-marked rifts which have been active during Pleistocene and Recent times. Its junction with Tayabas Peninsula was a late Pleistocene event. Tayabas and Bondoc Peninsulas were probably much larger during late Pleistocene time, since both Marinduque and Burias are connected with them by shallow seas whose waters were probably withdrawn during the glacial phases of the Pleistocene. Tayabas Peninsula was probably strongly connected with eastern and northern Luzon during the entire Pleistocene.

The Pleistocene Zambales island has been but recently tied to Luzon, and this elongate horst probably had a separate existence during most of the Pleistocene. Northern Luzon during early Pleistocene may have been connected with the Batanes, and it was surely connected with the Babuyanes during the glacial phases.

Broadly, the Philippine Archipelago has four well-marked former land connections, according to the results obtained through a study of the present hydrography aided by historical geology and palæogeography. Of these, the most ancient is the land bridge between Formosa and northern Luzon which, according to palæogeographic studies, has not been a firm structure since Oligocene or Miocene time. The great zone of faulting, whose general direction is 20° to 25° east, lies between Formosa and the Batanes, the Babuyanes and northern Luzon. This zone has been the locus of many earth movements, at least since middle Miocene time, which have caused a separation into definite island masses. Palawan and its dependent isles, the Calamianes and the Cuyos, are tied to Borneo by the northerly extension of the Sunda shelf sea, as indicated by the 200-meter isobath (Plate 4). Palæogeographic studies place the date of the present separation of Palawan from Borneo at very late Pleistocene. The Sibutu Islands of the Sulu Archipelago are upon the Bornean

shelf and are separated from Tawitawi by the relatively deep Sibutu Passage, which has probably been a definite strait since early Pleistocene. During most of Pleistocene time the Sulu connection between Borneo and Mindanao appears to have been a stepping-stone bridge. The tectonic Sangi line of Suess marks the connections between Celebes and Sarangani Peninsula of southern Mindanao. The northern sigmoid arm of Celebes has been very evidently connected with this peninsula. From a study of the Agusan rift system it appears probable that Sarangani Peninsula, a part of the western upthrust block or horst, was once extended to make a definite land bridge with Celebes during Neocene time. Orogenic movements along the Agusan rift have been very complicated, and great persistence of this connection is not to be expected. The tectonic line of Ternate of Suess indicates another possible southern connection with Halmahera and, in turn, with New Guinea. This line, however, is far more tenuous than any of the other connections, as seas of considerable depth intervene. The southerly extension of the Mindanao trough suggests that persistent faulting has kept this bridge in a nearly useless condition during Neocene, Pleistocene, and Recent times.

The unified characteristics of Wallacea are very notable and in sharp contrast with those of the Sunda and Sahul shelves. The great diversity in submarine and land topography, the numerous marine step terraces and drowned coasts in close proximity indicating great diversity of orogenic movements, the recency of the faulting and folding which have affected not only the land but also the sea bottom, and the general absence of coral atolls and barrier reefs are the dominant characters of this terrane. As Molengraaff and others have shown, the Sunda shelf is limited on the east by the Borneo barrier reef, and the narrow but deep Macassar Strait is a definite boundary which separates Celebes from Borneo. Southward this line extends between Bali and Lombok, and the results of the investigations described above indicate that in a northerly direction the boundary between the Sunda shelf and Wallacea passes through the narrow Sibutu Passage, skirts the north Bornean shelf sea, passes through Cuyo East Pass and Mindoro Strait, passes near the west coasts of Mindoro and of central and northern Luzon, and turns northeastward through Bashi Channel. This boundary line is merely the revised physical base line for that notable biologic limit, Wallace's Line. The

dredging of reef corals from the deeps of Ceram Sea by the Siboga Expedition and their specific identity with recent species demonstrate a late Pliocene or early Pleistocene age for the formation of the Ceram Sea deep. Molengraaff gives other data which indicate a Pleistocene age for the formation of the deeps and islands in their present forms in the southern part of Wallacea, and shows that orogenic movements still continue. Philippine results are in general accord with the conclusions of Molengraaff. Palæogeographic studies show that such features as the Mindanao rift system probably started in the Neocene, have been rejuvenated from time to time, and are still being modified. In other words, in the Philippines the deeps and their corresponding land masses differ somewhat in time of formation; for example, the Ticao rift is a very modern feature and the dependent block, Ticao, was broken away from Visaya during late Pleistocene and Recent times. The Formosa rift system, like the Mindanao, has been a marked feature since at least early Neocene time. Certain indications on the other hand point to a very late movement along the Taal rift which broke western Palawan away from the northern extension of Sundaland. Similar movement may have resulted in the foundering of portions of this northern Sundaland west of Palawan and the development of great separating deeps such as the South China Sea in late Pleistocene and Recent times.

These studies in the historical geology, palæography, and hydrography of the Philippines relate the geologic history of the past and gradually merge into the Recent through the deep-sea researches just described. They have dealt largely with the inorganic, and this foundation is necessary for an intelligible knowledge of organic life and its development.

CHARACTERISTIC PHILIPPINE HABITATS

Within the Philippines a well-recognized lowland flora and an associated fauna prevail throughout the Archipelago with essential unity. The forests of this lowland region are divided rather sharply into mangrove, beach, dipterocarp, and molave types. Above the lowland forests, which reach an altitude of 800 meters, is the pine forest in Luzon and Mindoro, and still higher is the mossy forest which reaches to the uppermost heights in the Philippines. As many forms of animal life are associated with these forest types, a brief description is pertinent before the various plants and animals are considered in detail.

MANGROVE TYPE OF FOREST

The mangrove type is literally a forest in the sea. Where conditions are favorable it occupies beaches washed by the tides (Plate 10, figs. 1 and 2). It is especially well developed on mud flats at the mouths of rivers that enter the sea at the heads of protected bays. Wherever wave action allows a fairly stable shore line, trees of this type are present. They occur on the quieter portions of bars and may be the only indication of shallow water. In such cases what appear at a distance to be forested islands are found to have no land exposed except perhaps at the lowest tides. Most of the trees in mangrove forests belong to the family Rhizophoraceæ and include the following species:

Rhizophora mucronata Lamarck.
Rhizophora candelaria de Candolle.
Bruguiera conjugata Merrill.
Bruguiera sexangula Poiret.

Bruguiera cylindrica (Linnæus) Blume.
Bruguiera parviflora (Roxburgh) Wight and Arnott.
Ceriops tagal C. B. Robinson.

Species of other families that are characteristic of the mangrove type of vegetation include—

Sonneratia caseolaris Engler.
Avicennia marina Vierhover.
Lumnitzera littorea (Jack) Voigt.

Xylocarpus moluccensis (Lamarck) M. Roemer.
Excoecaria agallocha Linnæus.
Heritiera littoralis Dryander.

Although this type of forest, from the nature of its habitat, is free from undergrowth, it is difficult to make one's way through a typical stand because of the complex and tangled system of stilt roots of the species of *Rhizophora*, the dominant species in these swamps, and also because of the soft mud forming the substratum (Plate 11, fig. 1). At the inner limits of the mangrove there may be a fringe of the nipa palm, *Nipa fruticans* Wurmb, and this palm is inclined to form extensive thickets on low land along streams where the water is only slightly brackish (Plate 12).

BEACH TYPE OF FOREST

Sandy beaches above the limits of high tide usually have been cleared and are occupied by towns or are planted to cocos. Where this has not occurred there is a distinct type of forest in which the following trees are found:

Terminalia catappa Linnæus.

Erythrina indica Lamarck.

Barringtonia asiatica Kurz.

Hibiscus tiliaceus Linnæus.

Pongamia pinnata Merrill.

Thespesia populnea Correa.

Heritiera littoralis Dryander.

Colophyllum inophyllum Linnæus.

Casuarina equisetifolia Linnæus.

Pemphis acidula Forster.

Some of these species—for example, *Casuarina*—may occur in more or less extensive, pure stands as a result of favorable soil and other conditions, while some of the valuable timber trees of other types, such as ipil, narra, and bansalaguin, may be mixed in the beach type.

DIPTEROCARP TYPE OF FOREST

The dipterocarps are the most important trees of the Philippine forests. They comprise fifty species in nine genera; and, while some of the species are scattered and hence negligible for commercial purposes, trees of many of the species are numerous enough to be very important. The genera are *Isoptera*, *Balanocarpus*, *Dipterocarpus*, *Anisoptera*, *Parashorea*, *Pentacme*, *Shorea*, *Hopea*, and *Vatica*. The lumber from different species is adapted to different uses and is marketed under many trade names (Plates 13 and 14).

Whitford divides the dipterocarp forests into five types, each of which is characterized by certain dominant dipterocarps and by species of other families. It is not necessary to consider each of these types here. The dipterocarp types cover 75 per cent of the virgin forest of the Philippine Islands, or about 30,000

square miles, and contain 95 per cent of the commercial timber. They are found on all kinds of topography, from immediately behind the beach type to from 600 to 1,000 meters altitude on the slopes of the largest mountains.

Dipterocarp forests are best developed on well-watered plains or on the lower slopes of large mountains. Here the soil is usually a deep loamy clay of volcanic origin; passing to drier soils of calcareous origin the dipterocarp species give way and the forest becomes more open, usually dominated by such species as molave, *Vitex parviflora* Jussieu. As higher elevations are reached, the trees become smaller and the dipterocarps less numerous. At 800 meters or less this type gives way to one in which miscellaneous trees—*Quercus* and other genera—are more prominent.

MOLAVE TYPE OF FOREST

Molave, *Vitex parviflora* Jussieu, is fairly well distributed throughout the forest that is designated the molave type. It is found typically on low limestone hills, which are usually composed of crystalline coral limestone with a honeycomb structure and the rocks are generally covered by shallow or scanty soil. The habitat is very dry, since ground water readily flows away through solution caverns in the limestone. A large part of the molave type has been destroyed by man. In its virgin state it is open, its large trees few and far apart; the intervening spaces are filled with small trees or by a jungle of sprawling, climbing, and small erect bamboos. In some expressions of this type the dominant trees include—

<i>Vitex parviflora</i> Jussieu.	<i>Albizzia acle</i> Merrill.
<i>Tarrietia sylvatica</i> Merrill.	<i>Wallaceodendron celebicum</i>
<i>Sindora supa</i> Merrill.	Koorders.
<i>Kingiodendron alternifolium</i>	<i>Zizyphus talanai</i> Blanco.
Merrill.	<i>Pterocarpus vidalianus</i> Rolfe.
<i>Intsia bijuga</i> O. Kuntze.	<i>Aglaia clarkii</i> Merrill.

Among the smaller species there may be—

<i>Maba buxifolia</i> Persoon.	<i>Cassia javanica</i> Linnæus.
<i>Diospyros discolor</i> Willdenow.	<i>Pterospermum</i> sp.
<i>Taxotrophis ilicifolia</i> Vidal.	<i>Mallotus</i> spp.

PINE TYPE OF FOREST

The pine type is distinctly characterized by open stands of *Pinus insularis* Endlicher in north-central Luzon, of *Pinus merkusii* Junghuhn and De Vriese in Mindoro, and of both species in Zambales Province, Luzon. The pine type is found in a

mountainous habitat at elevations of from 500 to 1,500 meters, with straggling individual pines up to 2,700 meters. No other tree of importance is found in this type of forest (Plate 15).

MOSSY TYPE OF FOREST

The summits and the sides of many high and rough mountains are covered with a thick growth of more or less dwarfed trees, which are characteristically decorated with a luxuriant growth of mosses, liverworts, foliaceous lichens, orchids, and ferns. The strong winds of these regions cause the stunted growth of the trees, while the high humidity favors the development of the fantastic epiphytic plant species that are characteristic of the mossy forest. Among the characteristic tree species of the mossy forest are *Podocarpus imbricatus* Blume, *Drimys piperita* Hooker f., *Dacrydium elatum* Wallich, and species of *Vaccinium*, *Rhododendron*, and *Quercus*. High-altitude species of *Eurya*, *Symplocos*, *Eugenia*, and many other genera that are also represented in the lowland forests are noteworthy.

To the casual observer the most obvious botanic feature of the mossy forest is the great quantity of epiphytic lichens, mosses, liverworts, ferns, orchids, and epiphytic flowering plants of certain families, which grow in such profusion on every shrub and tree that their stems and branches are entirely hidden. The tree species are fewer than those of the lower and more-level forests. The trees of the mossy forest are small; for the most part their trunks and branches are slender and are so twisted and distorted as to be useless for commercial timber (Plate 16). Many of the individual trees are so covered with moss that the branches and the smaller trunks appear to be two or three times their actual diameter. The forest is so crowded with inclined and twisted trunks, which are hidden beneath a dense growth of ferns and herbaceous plants, that walking is difficult. On the steeper slopes progress is slow and laborious and, in places, dangerous if not nearly impossible. All of this vegetation is almost continuously saturated with moisture.

On the higher ridges and the summits of many peaks the vegetation is much dwarfed, and tree species are reduced to mere shrubs. Mount Pulog is an exception to this rule, for above the mossy forest its summit protrudes entirely free of shrubs and trees, the only vegetation here being a thick carpet of small grasses, sedges, and herbs (Plate 17).

The discontinuous distribution of many bird species is directly connected with the irregularity in distribution of these forest types. The discontinuity is in part caused by man, and since his advent another type of habitat, the grassland, has developed. The earliest inhabitants—presumably the Negritos—were not skilled in any kind of agriculture and were not numerous enough to have been an important factor in the extermination of the coastal and other lowland forest. With the increase in population by the advent of the peoples that are now the Christian Filipinos, the cultivation of rice was introduced or, at any rate, much extended in the lowlands. This necessitated the clearing of large areas of level or nearly level land (Plate 18). If the population of an island increased, the area of cleared land was increased, until in some of the islands there was no more level land that could be brought under wet-rice cultivation. In such cases some of the surplus population migrated to other islands or pushed into the hills and raised upland rice which matures without irrigation and, therefore, can be grown on steep slopes. Even rice that requires much irrigation can be grown on steep mountain sides where level areas are made by means of retaining walls, as in many parts of Mountain Province, Luzon (Plate 19). This method of cultivation is not practiced in the lowlands. Clearing means the destruction of forest, and other uses for wood, such as cooking and house and boat construction, play their part in thinning the forest near large towns.

It is practically certain that before the advent of man in the Philippines the entire country was covered with unbroken forest of one kind or another, from sea-level to the tops of the highest mountains except, perhaps, where the vegetation had been temporarily destroyed by natural causes, such as volcanic eruptions. Such types of vegetation as the extensive grass-covered hills, mountain sides, and plains, and the open cultivated areas, now very prominent features in the landscape, did not originally exist, so that the whole aspect of many localities must have been quite different from what it is to-day or has been within historic times (Plates 20 and 21). When one considers that about two-thirds of the entire land surface of the Archipelago consist of cultivated areas, open grassland, thickets, and second-growth forests, all due directly or indirectly to the presence and activities of man, some idea can be obtained of the profound changes that have been wrought in the vegetation of the country in past centuries.

CAIÑGIN SYSTEM OF AGRICULTURE

A method of agriculture common to various tropical countries is practiced also in the Philippines, where it is known as the caiñgin system. The caiñgin is merely a clearing in the forest, and if the cleared land were continuously cultivated no harm would result. The caiñgin is seldom thoroughly cleared; the smaller trees are cut and when dry are burned. Nearly all the large trees in the field are killed in this process (Plates 22 and 23). Corn, rice, sweet potatoes, or yams are then planted. For a few seasons good crops can be taken off a caiñgin without much labor, but grass soon becomes so well established that the farmer finds it easier to make a new caiñgin than to struggle with the grass. Among such Mindanao peoples as the Manobos, Bagobos, Bilans, and Tagabilis, the caiñgin is used but one season, except under very unusual conditions. Around their barrios, which are moved at short intervals, grass quickly becomes well established and, upon the abandonment of the caiñgin, holds the area for a short time and then is supplanted by second-growth forest.

In the part of the Archipelago having distinct wet and dry seasons (that is, the western half), grass areas tend to remain in grass. The grass is frequently burned during the dry season, either by accident or by intention; and thus any forest-tree seedlings that have entered the grass are killed, while the deep-seated perennial rhizomes of the grasses are uninjured. After the first rain the grass soon produces a luxuriant growth (Plate 21). On the eastern side of the Islands there is a nearly continuous wet season. Here the more uniformly moist condition prevents grass fires and the grassland is soon invaded by tree species and gradually returns to forest, first by the establishment of characteristic second-growth species, usually quick-growing forms, and eventually, if undisturbed for a long time, by the establishment of primary-forest species.

If the population of a thickly inhabited island decreases, which has undoubtedly happened as the result of war or epidemic disease, some of the rice fields are abandoned. These, even when bordering forest, do not grow up to the old forest species of trees, but are first covered with a rank grass and later with species of shrubs and second-growth trees or by gregarious bamboo forests (Plate 24). If the region be one of marked wet and dry seasons, it will be very difficult for the forest species to regain a foothold in an area from which they have been removed.

SPECIFIC AND GENERIC BIOLOGIC AREAS

In a study of the present distribution of species, the types of habitat of species must be considered, as certain species flourish only under peculiar conditions. Scott,* in speaking of the distribution of mammals, says that—

Though with fluctuating boundaries and subject to slow secular changes, a mammalian species is limited to a fairly definite area, which may be of immense or very restricted extent, and throughout which it may be found in greater or less abundance. Many species however are not distributed continuously over the areas which they inhabit, but occur only in suitable stations adapted to their habits and mode of life. Thus, some will be found only where there are trees, others in the neighborhood of water, others only on open places, etc. A specific area is then the whole extent of country within which the species may be found, while the stations are the limited districts contained in the area which are exactly suited to the habits of the species in question; these stations may be hundreds of miles apart, as in the case of mountain tops, or they may be close together. A marsh living species, for example, will occur in all the marshes throughout its area, whether these be many or few, near together or widely scattered; for such a species marshes are its stations.

In the study of distribution of life in the Philippines, the recognition of specific, generic, and family areas is highly important, as one of the principal objects of this work is to offer an explanation for at least some of these zoölogically and botanically restricted regions, to correlate them with one another, and to relate them to the neighboring regions.

* A History of Land Mammals in the Western Hemisphere (1913) 136-137.

FLORA OF THE PHILIPPINES *

SEED DISPERSAL WITH REFERENCE TO PHILIPPINE SPECIES

The general problem of the dissemination of seeds in the Philippines is the same as elsewhere in the world. The actual means by which seeds may be disseminated are relatively few, yet adaptations are numerous. Seeds are distributed by wind, water, mammals, birds, insects, mechanical means, and man. No single agency and no combination of agencies is entirely satisfactory to explain all anomalies in plant distribution without postulating land connections over which plants could march unimpeded at some time or other in geologic history, although such land connections may now no longer be evident.

Each means of dissemination enumerated has its strict limitations. Seeds, to be disseminated by wind, must be light and, usually, small; unless they be minute and dustlike, they must be provided with wings, hairs, or other special organs to secure buoyancy. Seeds, to be disseminated by water, must be lighter than water, must be impervious to water, and must possess the faculty of retaining their germinating power for an indefinite period when immersed in water. Such seeds or fruits usually are provided with an impervious testa or pericarp and are not infrequently supplied with air chambers of one type or another. Seeds adapted for dissemination by animals are of two types; namely, those with special adaptations for adhering to the fur of mammals, and those, usually from fleshy fruits, which pass in an undigested condition through the alimentary canal of animals. Manifestly, any seed adapted for dissemination by mammals can be distributed only over the range of the animal; bats naturally fall in the category with birds. Seeds that are disseminated by birds may be transported in the alimentary tract by frugiverous birds, although it is exceedingly doubtful that any seed is distributed over great distances through this agency, as recent observations,† accompanied by an examination of the intestinal contents of migratory birds, show that they always

* See also E. D. Merrill, *An Enumeration of Philippine Flowering Plants* 4 (1926) 7-154.

† Ostenfeld, C. H., *Botany of the Faroës* 1 (1901) 117.

travel with the stomach and the crop empty.‡ Seeds with special adaptations for adhering to the feathers of birds may, of course, be distributed over great distances, although the number of species having seeds so adapted is comparatively small. The seeds of minute-seeded types of plants characteristic of fresh-water lakes, marshes, and rice paddies are present in immense quantities in the mud of the marshy portions of such localities. Minute seeds are distributed in the mud attached to the feet and the feathers of migratory marsh and shore birds. Apparently this is one of the most-efficient methods of distribution. Insects as disseminators of seeds are relatively unimportant, and seeds adapted to such dispersal are subject to the same limitations as those adapted for transportation by birds or mammals or to greater ones. Man, during the many thousands of years of his development and migrations, has been an important agent in the dissemination of seeds, and he is now able to carry practically any living plant from any part of the world to any other part of it.

DISPERSAL OF SEEDS BY WIND .

Seeds, and even fruits, have many special adaptations for dissemination by means of wind, yet that many species have been naturally carried across wide stretches of water by means of wind is rather doubtful. The minute, dustlike seeds of the Orchidaceæ, each fruit capsule of which produces millions of individual seeds, are apparently admirably adapted to dissemination by wind; yet, among all of the families of flowering plants, probably no group is characterized by a higher percentage of local endemism than is the Orchidaceæ. No genus of this entire family, except *Habenaria*, is pantropic. All the other genera of this family in the Tropics of the Old World are different from those in the Tropics of the New World. *Habenaria* is well developed in the temperate zones. Considering only the Philippine species, of which approximately nine hundred are known, the percentage of endemism in the family is as high as or higher than in any other plant family that has numerous representatives in the Archipelago. Comparatively few of the orchids found in the Philippines extend to other countries, although the Philippine genera are mostly Indo-Malaysian; but the percentage of species confined to single islands or to parts of single islands is high, although the genera may be widely distrib-

‡ Bobolinks with undigested rice in their crops have been shot in New York or Pennsylvania.—A. W. HERRE.

uted both within and without the Archipelago. Local endemism is highly developed. One limitation on dissemination of the Orchidaceæ through the medium of wind is the fact that the minute seeds do not retain their germinating power when subjected to long drying, but the most important factor is unquestionably the symbiotic feature of the group. It is claimed that the seed will not develop beyond the embryonic stage in the absence of the mycorrhizal fungus characteristically found in the roots of orchids.

As is well known, in most species of the family Compositæ, by far the largest family of flowering plants, the fruits are supplied with a tuft of hairs known as the pappus, while in the Apocynaceæ and Asclepiadaceæ the seeds are supplied with similar but morphologically entirely different appendages known as the coma; the object of the pappus and the coma is the dissemination of seeds through the medium of wind. It is perfectly evident that most of the local representatives of the Apocynaceæ and the Asclepiadaceæ, as well as a relatively high percentage of the indigenous species of Compositæ, reached the Archipelago through natural means; that is, through the medium of wind-blown seeds. It is, however, well known that at least one of the commonest asclepiadaceous plants (*Asclepias curassavica* Linnæus) and many of the commonest Philippine weeds belonging in the Compositæ were originally introduced into the Archipelago through the agency of man; when once introduced, they spread very rapidly from one end of the Archipelago to the other through natural means. Cases can be cited where species of Mexican origin, that were introduced into the Archipelago two hundred or more years ago and had become dominant weeds throughout the Archipelago, have extended through natural means northward to Formosa and southeastern China and southward into Borneo, but are unknown in any other part of the Old World. In various other families of plants the seeds or fruits of some genera present special adaptations for dissemination through the medium of wind, usually in the form of wings or hairs attached to the seeds or the fruits. Among the Philippine families so provided are the following:

Pinaceæ.
Typhaceæ.
Gramineæ.
Dioscoreaceæ.
Salicaceæ.
Juglandaceæ.

Aristolochiaceæ.
Ranunculaceæ.
Hernandiaceæ
Nepenthaceæ.
Leguminosæ.
Simarubaceæ.

Meliaceæ.
Malpighiaceæ.
Anacardiaceæ.
Hippocrateaceæ.
Burseraceæ.
Tiliaceæ.

Sterculiaceæ.
Theaceæ.
Guttiferæ.
Dipterocarpaceæ.
Begoniaceæ.

Combretaceæ.
Convolvulaceæ.
Verbenaceæ.
Gesneriaceæ.

Bignoniaceæ.
Rubiaceæ.
Cucurbitaceæ.
Compositæ.

Some of these adaptations are exceedingly efficient; others are relatively inefficient. In no case, except under the most exceptional circumstances, would they serve to distribute a seed or a fruit over very wide expanses of sea, although it is conceivable that under favorable conditions some of the seeds or fruits might be transported several hundred kilometers.

The family Dipterocarpaceæ illustrates the relative inefficiency of winged fruits for wind dissemination. With the exception of one or two genera, all representatives of this characteristic family are supplied with distinctly winged fruits. The form and the arrangement of the wings give the fruit a gyratory motion in falling rather than buoyancy. It is improbable that the fruits are carried more than a few hundred meters, even in a very heavy wind. The family is distributed from Ceylon and British India to Indo-China, southward to Java, eastward throughout the Philippines, and to a lesser degree southward through Celebes, the Moluccas, and New Guinea. Practically wherever the family occurs in the primary forests of the entire Indo-Malaysian region, outside of southeastern Malaysia, the dipterocarp trees are dominant. In spite of the fact that the fruits are winged and are thus adapted to a certain degree for dissemination by wind, land connections must be postulated to account for the present distribution of this family of plants. The seeds of the Dipterocarpaceæ retain their vitality for a very short period of time and apparently will not withstand drying. It will be found that the distribution of the various winged seeds or fruits, for the most part, is strictly limited by their weight or by other characters. In most of the families of large size this winged fruit or seed habit is found in only a few genera within the family and is generally a constant generic character. There are many more families without species adapted for wind distribution than there are families with species that are so adapted.

Small,* before a meeting of the Linnean Society of London, demonstrated an apparatus to determine the wind velocity required to blow seeds of Compositæ a sufficient distance to secure

* Journ. Bot. 55 (1917) 30.

their proper dispersal. He experimented with types of *Compositæ* common in England, and secured the results recorded in Table 7.

TABLE 7.—*Velocity at which the seeds of various species of Compositæ may be transported by wind, as determined by Small.*

Species.	Mi'es per hour.	Type of wind.
<i>Senecio vulgaris</i>	1.6	Light air.
<i>Ursinea speciosa</i>	2.6-4.6	Light to gentle breeze.
<i>Taraxacum vulgare</i>	1.5	Light air.
<i>Tussilago farfarea</i>	0.6-0.65	Less than a light air.
<i>Centaurea imperialis</i>	7.7	Moderate breeze.
<i>Leontopodium alpinum</i>	4.78	A gentle breeze.

It will be noted that, at least for certain species of *Compositæ*, the fruits can be disseminated by a very slight movement of the air; that is, on dry days. In the Philippines great wind velocities occur at times, especially during the typhoon season. The highest recorded wind velocity in the Philippines is 121 miles per hour, the recording apparatus breaking when this speed was registered. The highest recorded wind velocity in this part of the world is 152 miles per hour, off the east coast of Formosa in 1920. It should be noted, however, that the periods of high wind velocity in this part of the world coincide with the period of very heavy rainfall, strong cyclonic winds being always accompanied by great precipitation. Any great amount of humidity inhibits or prevents the dissemination of most seeds and fruits that have adaptation for distribution through the medium of wind, this being especially true of seeds or fruits that are supplied with hairs, such as those of the *Asclepiadaceæ*, the *Apocynaceæ*, and the *Compositæ*.

DISPERSAL OF SEEDS BY WATER

Plants adapted for dissemination by water may be considered under two heads; namely, those adapted for dissemination by fresh water and those adapted for dissemination by salt water. The limitations on species adapted for dissemination by fresh water are so self-evident that it is scarcely necessary to discuss the subject further; they are of course limited to water distribution in single continents or islands.

Examination of the constituent species that make up the flora of any island in the Philippines or any island having a considerable degree of altitude in Polynesia or in any other part of the world will bring out one striking fact; namely, that

practically all species growing on or near the immediate vicinity of the strand have definite adaptations for dissemination of fruits or seeds through the medium of ocean currents, whereas practically none of the species growing in the interior have such adaptations. As indicated above, a seed or fruit, to be efficiently disseminated by ocean currents, must present a peculiar combination of characters; namely, the testa or the pericarp must be impervious to salt water, the seed or fruit must be able to float for long periods of time, and the seed must retain its germinating power for equally long periods of time. On the basis of actual experimentation, especially that carried on by Guppy,* it is found that practically all of the seeds or fruits of inland species sink at once or within a few days after they have been placed in salt water. This character eliminates such species from the category of those that may possibly be disseminated by ocean currents. In all countries the species that make up the great bulk of the flora have, as a rule, seeds or fruits that present little or no buoyancy. On the other hand, seeds or fruits of coastal plants will, as a rule, be found to float for weeks and even months. Again, a considerable number of these strand plants, which are manifestly native in the Orient, are also indigenous in tropical America and tropical Africa, and a fair percentage of the species and even a larger percentage of the genera of the strand plants are identical in the Tropics of both hemispheres. Therefore, the facts that Guppy brought out are emphasized; namely, that plants with buoyant seeds or seed vessels have been for the most part located near the coast, and that, in the genera comprising both coast and inland species, only coast species possess buoyant seeds or seed vessels. Sometimes, of course, seeds may be distributed on floating branches, or even in crevices in floating tree trunks; but such occurrences, at least their successful consummation, must be very rare.

Species of the genera *Rhizophora*, *Bruguiera*, and *Ceriops*, in the family Rhizophoraceæ, are characteristic of and constitute most of the vegetation of the mangrove swamps. In these species germination takes place on the tree, the seedling itself being adapted to floating. In addition to the mangrove species proper, representatives of the following genera inhabit the strand: *Xylocarpus*, *Lumnitzera*, *Nipa*, *Excoecaria*, *Heritiera*, *Sonneratia*, *Aegiceras*, *Cerbera*, *Avicennia*, *Acanthus*, *Derris*, and *Sophora*. Representatives of these genera are found in or ad-

* Observations of a Naturalist in the Pacific 2 (1906), Seed Dispersal.

joining most or all mangrove swamps in the Old World Tropics and their seeds or seed vessels have special adaptations for dissemination by ocean currents. On the strand, but seldom in the mangrove swamps, are species of the following genera:

<i>Terminalia.</i>	<i>Gyrocarpus.</i>	<i>Mucuna.</i>
<i>Barringtonia.</i>	<i>Dodonaea.</i>	<i>Pongamia.</i>
<i>Suriana.</i>	<i>Scaevola.</i>	<i>Cocos.</i>
<i>Casuarina.</i>	<i>Cassytha.</i>	<i>Intsia.</i>
<i>Hernandia.</i>	<i>Guettarda.</i>	<i>Pemphis.</i>
<i>Colubrina.</i>	<i>Entada.</i>	<i>Tournefortia.</i>
<i>Pandanus.</i>	<i>Ipomoea.</i>	<i>Erythrina.</i>
<i>Caesalpinia.</i>	<i>Sophora.</i>	<i>Premna.</i>
<i>Canavalia.</i>	<i>Ximenia.</i>	<i>Calophyllum.</i>
<i>Vigna.</i>	<i>Cordia.</i>	<i>Crinum.</i>
<i>Mallotus.</i>	<i>Hibiscus.</i>	<i>Vitex.</i>
<i>Morinda.</i>	<i>Thespesia.</i>	<i>Dolichandrone.</i>
<i>Wedelia.</i>		

All of these strand plants, like those of the true mangrove-swamp types, have buoyant seeds or seed vessels and are thus adapted to dissemination through the medium of ocean currents. The genera are found throughout the Tropics of the Old World, and some of them occur in the Tropics of the New World, where they are represented either by identical or by closely allied species.

DISPERSAL OF SEEDS BY MAMMALS

Seeds may be disseminated through the medium of animals by either of two means; namely, by hard seeds passing through the alimentary tract in an undigested state and by seeds or fruits adhering to the hair or the fur of mammals. However, no seed or fruit could be transmitted from one region to another by this means unless the animals themselves were able to migrate. Therefore, the presence of comparatively few species in insular floras can be credited to this method of dissemination.

DISPERSAL OF SEEDS BY BIRDS

The adaptations by which seeds are disseminated by birds are exactly the same as those by which seeds are disseminated by mammals. However, many birds are migratory and pass from one region to another, even when there are wide intervening stretches of sea. Just how efficient birds are in disseminating seeds of plants that have fleshy fruits, at least over long distances, remains to be proved. It has been very generally assumed that many species of plants have attained their present geographic distribution largely through the agency of migratory

birds, which transmitted the seeds in their crops or stomachs; but recent investigations of migratory birds seem to show definitely that they usually travel on an empty stomach.* Moreover, under normal conditions, digestive processes are rapid in birds, and seeds would under normal conditions remain in the alimentary tract not more than a few hours. Ernst † quotes as short a period as a half hour, and states that the interval between ingestion and ejection in most birds is from one and one-half to three hours. Many frugiverous birds are not migratory. It is admitted that this is a very efficient method of seed distribution within short distances and within any geographic entity such as a continental mass that has more or less uniform climatic conditions, and within the limits of individual islands generally. However, it is exceedingly doubtful that many species have been transmitted to distant islands through this means.

It seems highly probable that migratory birds have been, and still are, efficient agents in the dissemination of many species of plants that are characterized by the production of an infinite number of minute seeds, such as marsh plants in general, fresh-water aquatics, and most of the so-called rice-paddy weeds. It is a noteworthy fact that aquatic, semiaquatic, and fresh-water marsh plants are mostly of very wide geographic distribution, and furthermore that a high percentage of fresh-water aquatics present identical species in practically all parts of the world, including temperate and tropical regions. The same is true of a high percentage of the rice-paddy weeds found in the Philippines. It is highly probable that most of the Philippine marsh plants, fresh-water aquatics, and rice-paddy weeds have been introduced in mud attached to the feet or the feathers of migratory birds. Darwin's classical experiment has shown that pond mud is charged with an infinite number of the minute, viable seeds of aquatic, semiaquatic, and marsh plants. In 6.75 ounces (dry) of pond mud he succeeded in raising five hundred thirty-seven seedlings from viable seeds present naturally in the mud; yet all this mud was contained within a teacup. Mud is, of course, not transmitted by migratory birds in any great quantities and many migratory birds transmit no mud at all, either on their feet or on their feathers; yet, in the history of the migration of plants, the introduction of one or two species in a thousand years

* Ostenfeld, C. H., *Botany of the Faroës* 1 (1901) 117.

† *The New Flora of the Volcanic Island of Krakatau* (1908) 59.

in such a country as the Philippines would be ample to account for the presence of several hundred species in the Archipelago to-day, even though there were no other means by which such species might be introduced. It is highly probable that the Mediterranean *Erythraea* introduced into Formosa when that island was colonized by the Portuguese has reached the Batan group between Luzon and Formosa by this means. Without postulating this method of dissemination it is impossible to explain the universally wide distribution of aquatic, semiaquatic, and marsh plants.

There are a few species of plants that have fairly large fruits adapted for dissemination through the medium of migratory birds by the glutinous character of their pericarps. *Pisonia* is a noteworthy example of this. *Pisonia aculeata* Linnæus is pan-tropic and is certainly of "natural" distribution. *Pisonia excelsa* Blume is distributed from the Malaysian region throughout Polynesia. In the Philippine Archipelago this species is known from one locality only, Bancoran Island in the Sulu Sea, where the numerous vast trees of this species entirely cover the island to the exclusion of all other arborescent vegetation. The island is frequented by thousands of boobies (*Sula*) for breeding purposes. The *Pisonia* is scattered on the smaller islands of the Pacific throughout Polynesia where the booby ranges, at least as far east as the Palmyra Islands south of Hawaii, and the species has been unquestionably transported from island to island through its glutinous fruits adhering to the feathers of this particular bird. On Bancoran Island the booby nests on the *Pisonia* trees and thus frequently comes in direct contact with the fruits. The fruits in the herbarium retain their adhesive qualities indefinitely.

Generally speaking, however, it is only plants with minute seeds that are transmitted by migratory birds over great distances, and none of these minute seeds has any special definite adaptation for dissemination; yet, species presenting these are everywhere very successful migrants. In the Philippine flora, there are not only many Asiatic species of wide distribution throughout the entire Indo-Malaysian region in the rice paddies, fresh-water swamps, and fresh-water lakes, but also in the rice paddies a few very characteristic Australian rice-paddy weeds identical with species occurring in northeastern Australia, but otherwise scarcely known outside of Australia; these could have reached the Philippines only through the medium of migratory birds and will unquestionably be found in intermediate areas

between Mindanao and northeastern Australia when the intervening islands shall have been more thoroughly explored. Outstanding examples are *Stylidium alsinoides* R. Brown, a characteristic Australian type, for many years known only from Luzon and Australia, but recently discovered in New Guinea; and *Calogyne pilosa* R. Brown, the species of a monotypic genus, all the allies of which are Australian. The latter species is known from Amoy, China; from Luzon, where it is in places a common plant in fallow rice paddies; and from Australia. In both cases the Australian-Luzon distribution is undoubtedly due to the minute seeds being transmitted by migratory birds. The occurrence of *Calogyne* at Amoy may be through the accidental transmission of its seeds in rice or in packing material from Manila, as most of the large Chinese colony in the Philippines came from Amoy and there is and has been for several hundred years very much intercourse between the two ports; with northeastern Australia, on the other hand, there has been no commercial connection.

DISPERSAL OF SEEDS BY INSECTS

Insects, like birds, may transmit minute seeds under certain conditions. This method of dissemination, however, is relatively unimportant.

DISPERSAL OF SEEDS BY MECHANICAL MEANS

Certain fruits have adaptations for the dissemination of seeds through mechanical means. The dehiscent pericarp of such fruits acts more or less in the nature of a spring, thus scattering the seeds short distances when the fruits dehisce; the common balsams and several genera of the Euphorbiaceæ are examples. This method of disseminating seeds is, of course, effective only for very short distances. The so-called squirting cucumber (*Ecballium*) is another illustration of adaptation for dissemination through mechanical means. The fully mature fruit is distended with juice and automatically opens at the end and the seeds are squirted out a short distance together with the juice.

DISPERSAL OF SEEDS BY MAN

Man has always been one of the most efficient agents in the distribution of plants. Economic plants generally have been widely disseminated, first by primitive man in the many centuries occupied by him in his migrations, and later by civilized man as various parts of the world have been visited and de-

veloped. In addition to purposely distributing many economic plants, man has inadvertently transmitted numerous weeds of cultivation.

Through a study of the local names or absence of local names of the dominant Philippine weeds, it is possible to approximate the time at which many of them were introduced. Most of the species introduced in the prehistoric period have definite local names of Malay origin; those introduced from tropical America, after the occupation of the Archipelago by the Spaniards, have either Spanish, modified Spanish, or modified Aztec names, the last having been brought from Mexico with the plants themselves. Camanchili, cacauate, camote, tomate, calachuchi, alpazotes, chico, cacao, achuete, and sapote are examples of common plants with Aztec or modified Aztec names. The name acapulco, or capurco, derived from the town of Acapulco whence the galleons sailed from Mexico to Manila, is found in the Philippines as the local name for *Cassia alata* Linnæus. Plants introduced from Europe and from various parts of the Indo-Malaysian region after the advent of the Spaniards usually have Spanish names or modified names of Spanish origin; many common and dominant weeds, manifestly of comparatively recent introduction have no definite vernacular names. Early introductions from India by way of Malaysia in the period of dominance of the Buddhist and Brahman empires in Sumatra and Java frequently have definite Sanskrit names; such as, sulasi, lasona, malisa, kachumba, malunggai, kastuli, patola, champaca, dansuli, lagundi, and daua. Early introductions by the Chinese are represented by batau, sitau, kuchai, pechai, and ungsoi.

Taking for illustrative purposes the flora of the vicinity of Manila, there are represented approximately 1,000 species, of which about 550 are indigenous; that is, true natives of the Archipelago that have reached the Islands through natural agencies. About 450, or nearly 50 per cent, have been purposely or inadvertently introduced by man; about half of these are spontaneous and half are rarely met with outside of cultivation. Tropical America has produced at least 178 of the introduced species, and these have been introduced into the Islands since the Archipelago was discovered by the Spaniards in 1521.

With the exception of the abacá plant, the numerous forest trees yielding valuable timbers, a few palms, some bamboos, the rattans, and a few others, practically all of the species of plants now found in the Philippines that are of the greatest importance from an economic standpoint, whether for food, for

condiments, for clothing, for dyes, for medicines, or for ornamental purposes, have originated outside of the Archipelago and have been purposely introduced into the Philippines by man. Not a single important food plant or fruit tree has originated in the Archipelago; all have been introduced.

It is perfectly evident that man has been a most efficient agent in introducing both economic and useless plants into the Philippines. As an illustration of the influence of trade routes on the flora of a region like the Philippines, it is interesting to note the many plants that were purposely or accidentally introduced into the Philippines from Mexico through the medium of the Acapulco-Manila galleons. Up to the time that Mexico gained her independence in 1821, the Philippines was governed as a dependency of Mexico, and practically all communication between Spain and the Philippines was via Vera Cruz and Acapulco. From the latter part of the sixteenth century a single galleon was dispatched each year from Acapulco to Manila and one from Manila to Acapulco, yet up to the time the galleons were discontinued, 1811-1815—say, during a period of two hundred fifty years—more than two hundred species of American origin had been introduced into the Archipelago. As such introduction occurred within a comparatively short period of time, we can readily realize that a very large number of species may have been introduced into the Archipelago from different parts of Malaysia and Asia through trading vessels; for it is well known that commercial relations existed between the Philippines and surrounding countries for at least fifteen hundred years before the Islands were discovered by the Spaniards. We have also to consider in this connection the considerable period of time in which the Archipelago was being populated, for it may safely be admitted that most or all incoming peoples brought with them various economic species and, unquestionably, at the same time certain of the common weeds.

The isolated island Guam, in the Marianne Islands, affords another very excellent example of the activities of man in the dissemination of plants.* Of the 550 known species, 9 per cent are endemic; 280, or about 51 per cent, are pantropic, and 113 of these are definitely of American origin, mostly introduced from Acapulco via the Acapulco-Guam-Manila galleon route, and 112 are definitely of Asiatic origin. Of the 280 pantropic species, about 50 are of "natural" distribution, 156 purposely dis-

* See E. D. Merrill, *Philip. Journ. Sci.* § C 9 (1914) 17-155.

tributed by man, and 74 inadvertently distributed by him. Of the total 550 species known from Guam, 314 owe their presence there directly or indirectly to man; 36 families and 193 genera are represented in Guam by introduced species only.

VIABILITY OF SEEDS

It is hardly necessary to discuss in detail certain very evident limiting factors in reference to the establishment of a species in a new region to which the seeds may have been distributed by any of the means indicated above. Manifestly, the seeds of any species adapted to growth in the open will fail to establish the species in a new region when the seeds are deposited in a densely forested area. Also, most seeds of forest trees, at least of those characteristic of the primary forests in the Tropics, will fail to establish a species when such seeds are deposited in grasslands, cultivated areas, etc. Again, it is a thoroughly established fact that many species occur in nature only on acid soils, and seeds of such species, when they fall on neutral or alkaline soils, must of necessity fail to establish the species; likewise, many species adapted to neutral or alkaline soils will fail to grow in acid soils. Other limiting factors are altitude, temperature, humidity, and seasonal distribution of rainfall; no discussion of these points is necessary in detail, as the limiting factors are evident. Viable fruits or seeds of many species transmitted by ocean currents frequently fail to establish an individual species in a new locality, owing to the fact that the region back of the strand is occupied to its fullest extent by other plants, so that the new arrival has no chance whatever to gain a footing, even when the seeds germinate. Recently I had an opportunity to examine in detail the strand of Culebra Island, a small uninhabited islet near Maricaban in the Verde Island Passage between Luzon and Mindoro. Without making a minute search, I found there viable seeds of fifteen species, but less than 20 per cent of the species represented by these seeds were established on the island, owing to the fact that the plants already growing there covered all available space, thus preventing the establishment of any additional species. In one or two cases the special habitats for certain species represented by viable seeds on the strand were not present, but with these exceptions the habitat as such was favorable to the growth of all the other species on this small island. This condition might readily be duplicated on any one of several hundred small islets

in the Philippines. Briefly, for a species to become established it is essential that conditions and circumstances be favorable.

REVEGETATION OF KRAKATAU AND TAAL

Ernst,* in summarizing the means by which the various species found on Krakatau became established there, concluded that approximately 39 per cent of the flowering plants reached the island through the medium of ocean currents. If certain typical strand plants were included that may possibly have been distributed by birds, as well as strand species of Compositæ, Gramineæ, and Cyperaceæ which may have been introduced by ocean currents as well as by wind and birds, the percentage would be approximately 72.

The number of plants brought to the island by birds cannot be exactly estimated. Nine inland species, or 10 per cent, certainly reached there through that medium; including nine species in the list of strand plants possibly introduced by this means, the total would be 19 per cent. This number does not take into account the possible part played by marsh and water birds in the dispersal of grasses and sedges.

The number of species distributed by wind is as difficult to estimate closely as is that of bird-distributed forms. At least 16 per cent were introduced by wind or, including all of the Compositæ and four species of Cyperaceæ, 30 per cent of the total.

Ernst concludes that of the flowering plants, according to the method of reckoning adopted, 39 to 72 per cent have been introduced by ocean currents; 10 to 19 per cent, by birds; and 16 to 30 per cent, by air currents. In addition to the phanerogams that occur in Krakatau, the presence of a large number of ferns and other cryptogams can be explained only on the assumption that their spores were transmitted to the island through the medium of wind. Ocean currents have been the most important factor in the revegetation of Krakatau since the total destruction of its vegetation by the great volcanic eruptions of 1883.

In the revegetation of Taal † birds appear to have been the most important agency for dispersal, 54 per cent of the plant species being thus accounted for, but this percentage includes the plants with numerous minute seeds that may be transmitted

* The New Flora of the Volcanic Island of Krakatau (1908) 66.

† Brown, W. H., E. D. Merrill, and H. S. Yates, Philip. Journ. Sci. § C 12 (1917) 177-248, pls. 4-16.

in mud; 21 per cent are apparently distributed by wind, and only 9 per cent by water. Krakatau, however, is not close to neighboring islands and is surrounded by salt water, while Taal is an island in a fresh-water lake, separated from the mainland by only a short distance. The contrast between the revegetation of Krakatau and that of Taal shows conclusively that birds are the most efficient medium in transmitting seeds over short distances; this conclusion is in harmony with the known fact that food remains in the alimentary tract of birds but a very short time, usually from thirty minutes to three hours.

DISTRIBUTION OF PLANTS AND THE PRIMARY FORESTS

In attempting to determine the actual phytogeographic relationships between the flora of one region and that of another, it is manifest that the methods by which plants may have been disseminated must be given very careful consideration. In drawing conclusions based on the study of existing plants all references to the strand vegetation, to the weeds of cultivation, and generally speaking to most of the species found in the open settled areas at low and medium altitudes as well as many of those found in the secondary forests should be eliminated. As very many of the species that occur in the Philippines have been introduced into the Archipelago from other countries, many by man, others through natural means after man had prepared the proper habitats for such species, it may with reasonable safety be assumed that the original vegetation of the Philippine Islands before man reached the Archipelago was continuous forest of one type or another. With this type of vegetation in a tropical country like the Philippines, the habitats in which most of the species now found in the open country and in the secondary forest would thrive would be absent, and the introduction of seeds of these species into the Archipelago, so long as it was a forested area, would of necessity fail to establish them in the Archipelago. In this connection it is interesting to note the percentages of endemism in the floras of the settled areas and of the primary forests of the Philippines. In the open country and in the secondary forests of the Philippines specific endemism is less than 10 per cent, while in the primary forests it exceeds 80 per cent. This condition merely emphasizes the facts that the primary forest represents the true indigenous flora of the Archipelago; that a high percentage of the species found in the settled areas, open grasslands, and secondary forests represents species of

recent or comparatively recent introduction; and that a high percentage of such species may be accredited to man and his activities, either as the introducing agent or as the chief agent in preparing the proper habitats for the dominant species of the now open country.

GENERAL DESCRIPTION OF THE PHILIPPINE FLORA

The Philippine flora is a very rich one, approximately ten thousand species of flowering plants and ferns being known from the Archipelago. The flora is in general essentially Malaysian, its chief alliances being with that of the Malay Archipelago, but with distinctly continental (Himalayan) elements in the mountains of northern Luzon, and a small but interesting series of Australian types at both low and high altitudes. The flora is further characterized by a comparatively small percentage of endemic genera and a high percentage of endemic species, the specific endemism approximating 75 per cent.

Because of the geographic position the chief floristic alliances of the Archipelago would be sought in western Malaysia on account of the two parallel lines of connecting islands; namely, the northerly Mindoro, Calamianes, Palawan, and Balabac group and the southerly Sulu Archipelago; such is indeed the case, so far as the genera are concerned. There is, however, a very striking series of genera and species indicating special alliances with the islands south and southeast of the Philippines; namely, Celebes, Gilolo, the Moluccas, New Guinea and, to a certain extent, northeastern Australia and New Caledonia.

In general, the dominant species along the seashore, in the settled areas at low altitudes, in the vast areas of open grassland, and in the secondary forests are identical with widely distributed Indo-Malaysian species that occur in similar habitats over the vast Indo-Malaysian region. In the primary forests, however, the dominant species are, for the most part, endemic. The percentage of endemism is very low in the settled areas at low altitudes, in the open grasslands, and in the secondary forests, a condition which indicates destruction of the original primary forests and replacement of endemic by introduced species. In drawing conclusions as to the origin of the Philippine flora the vegetation of the coastal regions, the settled areas, the open grasslands, and the secondary forests should be largely ignored.

The settled areas, except for the cultivated plants, are characterized by a predominance of introduced weeds, mostly of

pantropic distribution, and various introduced trees and shrubs with comparatively few endemic species. The vast areas of open grassland are characterized by the dominance of lalang, or cogon, grass (*Imperata*), talahib (*Saccharum*), *Themeda*, and other coarse grasses, probably due to the activities of man. The forest was destroyed in preparing the land for agricultural purposes, and the primitive agriculturist was later forced to abandon the cleared areas because he was unable, under primitive agricultural conditions, to compete with the coarse gregarious grasses with which such cleared areas usually were quickly covered. The vegetation of the coastal areas, including the mangrove swamps, is practically identical with that of similar areas throughout the Malay Archipelago and, for that matter, throughout the Tropics of the Old World.

The primary forests at low altitudes are characterized by many tree species; between twenty-five hundred and three thousand are known from the Archipelago. Many of these attain a large size; especially the dominant Dipterocarpaceæ, from which are obtained such commercial timbers as lauan, apitong, mayapis, yacal, tangile, and others. Gregarious forests (that is, forests composed chiefly or entirely of a single species) do not exist in the Philippines, except in the pine regions of Luzon and Mindoro—and there chiefly in the mountains at medium and higher altitudes—and in the mangrove swamps about mouths of tidal streams. The average primary forest in the Philippines more closely approximates the mixed deciduous forests of temperate countries, but is vastly more complex than are such forests.

At higher altitudes in the Philippines the character of the forest changes radically; the species dominant at lower altitudes disappear and are replaced by representatives of other genera. On the mountains are found numerous representatives of groups more or less characteristic of the North Temperate Zone, such as oaks, rhododendrons, huckleberries, and other temperate types. The mossy forest, which characterizes the higher mountains of the Philippines, usually commencing at an altitude of about 800 meters but sometimes not below 1,500 to 1,800 meters, is composed of many species of trees and shrubs, the trunks and branches of which are covered with a highly developed moss flora, accompanied by numerous ferns, liverworts, lichens, epiphytic orchids, and some herbaceous plants.

In the number of known species the family Orchidaceæ is by far the largest in the Philippines; nearly nine hundred species of this group are now known. The next largest group is

the Polypodiaceæ, a family of ferns; but the entire group of ferns and fern allies includes more known species in the Philippines than does the family Orchidaceæ. Among the families of flowering plants other than the Orchidaceæ the most highly developed ones in number of species are, in approximately the order named, the Rubiaceæ, the Euphorbiaceæ, the Myrtaceæ, the Moraceæ, the Leguminosæ, and the Gramineæ. Other large families are the Palmæ, the Urticaceæ, the Anonaceæ, the Lauraceæ, the Meliaceæ, the Sapindaceæ, the Guttiferæ, the Dipterocarpaceæ, the Melastomataceæ, the Sapotaceæ, the Apocynaceæ, the Gesneriaceæ, and the Verbenaceæ.

GENERIC DISTRIBUTION OF FLOWERING PLANTS IN MALAYSIA

A critical examination of all available botanic literature of a systematic nature appertaining to the Malaysian region brings out a rather important fact in generic distribution. In eastern Malaysia (that is, Celebes, the Moluccas, and New Guinea, or the islands east of Wallace's Line) there are approximately one hundred ninety-one genera that do not extend to the islands west of Wallace's Line, or the Sunda group proper; fifty-one, or approximately 26 per cent, of these genera have representatives in the Philippines.

Contrasted to this, in western Malaysia (that is, the Malay Peninsula, Sumatra, Java, and Borneo, or the islands west of Wallace's Line) there are three hundred sixteen genera that do not extend to the islands east of Wallace's Line, except in the Philippines where one hundred ninety-eight, or approximately 62 per cent, of the genera from western Malaysia are represented.

In addition to the thirty-nine genera that are confined to the Philippines (that is, endemic genera), there are also in the Archipelago representatives of fifty-three genera, chiefly Asiatic types, that have no representatives in the Malay Archipelago outside of the Philippines. Most of these Asiatic genera occur in the Philippines in the mountains of northern Luzon, although in several cases representatives are widely distributed at low altitudes in the Philippines.

This generic distribution conforms with the distribution of the very characteristic Malaysian family, the Dipterocarpaceæ. It seems to indicate that the geographic connections between the Philippines and western Malaysia through Borneo have been much stronger and longer continued than have similar geographic connections between the Philippines and the islands south and southeast. Although the bulk of the Philippine flora

has originated in western Malaysia, it would seem that there were at times very definite connections with the islands south and southeast of the Archipelago, thus allowing certain migrations from that region into the Philippines and in all probability certain migrations from the Philippines in the opposite direction. Yet these geographic connections existed after the geographic connections between the Philippines and Borneo were broken. Later there were apparently other connections between Borneo, Palawan, and the Calamian group, which did not extend to Mindoro and the Philippine Archipelago proper and, through the Sulu Archipelago, with the Zamboanga Peninsula of Mindanao, allowing a later migration to these regions of a limited number of Bornean types; such as, *Hallieracantha*, *Philbornea*, *Cowiea*, *Clemensia*, *Baphia*, *Eusideroxylon*, *Myrmeconauclea*, *Koompassia*, *Merope*, *Anplectrum*, *Artocarpus superba* Beccari, *Hydnocarpus hutchinsonii* Merrill, *Mallotus miquelii* Boerlage, *Fagraea fragrans* Roxburgh, and others. It is interesting to note that these genera and species, mostly of limited Bornean-Philippine distribution, do not extend into the Philippines farther than the Palawan-Calamian group to the north (two species extend to Mindoro) and the Zamboanga Peninsula to the south. From geologic evidence, the Zamboanga Peninsula (probably at the time the last connections with Borneo existed) was separated from the rest of what is now Mindanao; in fact, what is now Mindanao was then five separate islands. It is interesting to note that this peculiar mingling in the Philippines of genera from eastern and western Malaysia confirms the opinion that Wallace's Line, extending through Macassar Strait between Borneo and Celebes, and south through the passage between Bali and Lombok, represents a relatively ancient and persistent geologic boundary of great importance.

It must be remembered that the flora of western Malaysia and the Philippines as a whole is infinitely better known than is that of eastern Malaysia; future exploration of the latter region may bring to light representatives of a fairly large number of genera now known only from western Malaysia, or from western Malaysia and the Philippines. On the other hand, judging from recently published works on the flora of eastern Malaysia, numerous totally new genera are to be expected from that region. With the few endemic Philippine genera it is not reasonable to suppose that many additions to the generic list of eastern Malaysia can be expected from this source. It is, therefore, rather confidently expected that future botanic explorations

and studies on the entire Malaysian flora will not materially affect the percentages of Philippine-eastern Malaysian genera and Philippine-western Malaysian genera.

GEOGRAPHIC DISTRIBUTION OF THE DIPTEROCARPACEÆ

The geographic distribution of the Dipterocarpaceæ in Malaysia strikingly confirms the conclusions that may be drawn from the study of the range of all Malaysian genera given above. This characteristic family is essentially Indo-Malaysian in distribution, and has only a few representatives in tropical Africa and Madagascar and one in the Seychelles. It is not represented in tropical America, nor in tropical Australia. As at present understood, the family comprises sixteen genera and about three hundred seventy species, for the most part confined to India, Ceylon, the Eastern Peninsula (Burma, Indo-China, Siam, and the Malay Peninsula), Sumatra, Borneo, Java, and the Philippines; and has a few representatives in the Moluccas, Celebes, and New Guinea. Borneo, with thirteen genera and slightly over one hundred known species, is apparently the center of distribution for the family. The Eastern Peninsula is the next richest area, and the Philippines is third, although it is probable that, when the flora of Sumatra is better known, more species of Dipterocarpaceæ will be found in Sumatra than in the Philippines. The dipterocarp flora of Java is comparatively poor, undoubtedly owing largely to the fact that the primary forests of Java below an altitude of 1,200 meters have been practically destroyed, and destruction of the primary forests means the extermination of the dipterocarps (Plates 13, 14, 21, and 22).

One species only is known from China (Kwangtung Province) and another in Hainan Island, while none is known from Formosa, although representatives of five genera extend through the Philippines into the Babuyan Islands between Luzon and Formosa. In the Philippines the family is represented by nine genera and about fifty species.

The family is richly represented in the Eastern Peninsula, Sumatra, Java, Borneo, and the Philippines, and in these regions representatives of the family are dominant in the primary forests at low and medium altitudes; however, it is very poorly represented in the islands south and southeast of the Philippines, including Celebes, Gilolo, the Moluccas, and New Guinea, although everywhere in those regions the climatic conditions are favorable to the development of the dipterocarps, which may possibly not be true of Formosa.

The genus *Anisoptera* is represented by about twenty-one species spread over the entire range of the family except Africa, and four species are known from New Guinea. The genus *Hopea*, which has the same geographic distribution as *Anisoptera* and has about fifty-six known species, is represented in New Guinea by three species, one of which also occurs in Celebes. *Shorea*, which has the same geographic distribution as the preceding two genera and is represented by over one hundred known species, presents one species in Amboina, one in New Guinea, and one in Celebes. *Vatica*, with about fifty known species, having the same geographic distribution as the genera mentioned above, presents one species in Celebes and two in New Guinea. Thus, in the entire area extending from Celebes through the Moluccas to New Guinea, this family of trees so dominant in the Western Peninsula, the Sunda Islands, and the Philippines, is represented by but thirteen species in four genera.

It would seem probable, in view of the geographic distribution of the group, that Celebes, the Moluccas, and New Guinea have been separated in part or in whole from the Sunda group for a long time; we may assume this period to be approximately the time in which the Dipterocarpaceæ, as a family, took its rise and developed its geographic distribution, during early or middle Tertiary. On the other hand, it seems probable that northerly land connections between Borneo and the Philippines by way of Palawan and Mindoro and southerly through the Sulu Archipelago existed after such connections had been broken between Borneo and the islands to the south and southeast of the Philippines, thus allowing a general migration of representatives of this family into the Philippines, at the same time inhibiting their migration into the islands to the south and southeast. That representatives of at least five genera reached the Babuyan group but not Formosa would seem to indicate that Formosa has been separated from the Philippines from a very early time, a contention that is fully supported by the distribution of species in other groups of plants and animals. The Formosan flora presents no single genus and comparatively few species that are common and confined to Formosa and the Philippines.

The Dipterocarpaceæ, so far as its Philippine representation goes, presents an overwhelming relationship with western Malaysia, with nine genera and fifty species in the Philippines and but four genera and about fourteen species in eastern Malaysia.

The family reaches its greatest development in the Malay Peninsula, Sumatra, and Borneo.

In contrast to this we find that the Philippine myrtaceous flora is overwhelmingly Papuan, presenting a striking series of genera and species in common with the islands south and south-east of the Philippines and with Australia, but with practically no special alliances with western Malaysia.

Mooria (*Cloezia*) presents one species in Mindanao, and six in New Caledonia; the genus is unknown from any other region.

Eucalyptus deglupta Blume (*E. naudiniana* F. Mueller) is abundant and dominant in some parts of Mindanao; it occurs also in Celebes, the Moluccas, New Guinea, and the Bismarck Archipelago, but not in Australia. It is, however, one of the very few species of this large genus known from outside of Australia.

Mearnsia, originally described from the Philippines, there represented by a single species in Mindoro and in Mindanao, has one additional species in New Guinea and another in New Caledonia.

Osbornia is a monotypic genus, originally described from Australia, but now known to occur from central Luzon to Mindanao, and also in British North Borneo. It grows along tidal streams associated with the mangrove, and doubtless occurs in Celebes, the Moluccas, and New Guinea, although it is not as yet recorded from those islands.

Xanthostemon presents about a dozen species in New Caledonia, three in Australia, two in New Guinea, one in Celebes, and three in the Philippines; no representative is known from western Malaysia.

There are thus found in the Philippines representatives of five genera in the Myrtaceæ that are otherwise Australian and eastern Malaysian, which have no known representatives in western Malaysia (except *Osbornia octodonta* F. Mueller, which occurs on the eastern coast of Borneo but which is probably water-distributed).

Leptospermum and *Tristania* are well-developed genera in Australia and New Caledonia, but both are represented in western Malaysia and in the Philippines, the former by one or two species, probably not distinct from Australian forms, the latter by perhaps fifteen species five of which are Philippine. Both genera are probably to be considered as Australian types.

In western Malaysia, however, we find one Australian type that is absent from the Philippines; namely, *Baeckea frutescens* Linnæus, which extends from southeastern China to the Malay Peninsula, Borneo, and Sumatra; the genus with somewhat more than fifty known species is otherwise largely Australian, with some species in New Caledonia.

Melaleuca, also largely an Australian genus, is represented throughout Malaysia by the cultivated species *M. leucadendron* Linnæus, which does not occur in the Philippines. It is in all probability an introduced plant in western Malaysia and in India, and should therefore be ignored.

The Myrtaceæ, a world-wide tropical group, highly developed in Asia, Africa, and America, attained its distribution as a group while New Guinea and Australia were a part of the Asiatic continent; that is, in Cretaceous time. The family is just as well developed—perhaps more so in genera, certainly in species—in Sundaland and Wallacea as it is in Papualand. A secondary center of development and distribution of Myrtaceæ was in or near New Guinea, and from this center Papualand types extended to the Philippines but failed to reach Sundaland.

As shown above, the Dipterocarpaceæ, whose probable center was Sundaland, is but slightly represented in Papualand. From the palæontologic viewpoint these facts may be explained by assuming that the Myrtaceæ developed earlier than the Dipterocarpaceæ. Thus, for example, the Myrtaceæ apparently spread throughout the Indo-Malaysian and Australian regions during the early Cretaceous, and at a later time in geologic history Australian and Papuan myrtaceous types migrated northward into the Philippines; while the spread of the Dipterocarpaceæ did not occur until just before the beginning of the Eocene, thus permitting a few species to enter Papualand at that time. A few forms may have entered later via the Philippines and Celebes.

The dipterocarps, representing a strong Malaysian element, indicate distinct affinities of the entire Philippines with Borneo and in turn with the Malay Peninsula and the Sunda Islands during early or mid-Tertiary time, as will be shown when the special high-altitude flora of northern Luzon is discussed. In this connection the reader will recall that this characteristic family was shown to be present in the Philippines during the Pliocene.

DISTRIBUTION OF THE ORCHIDACEÆ

When the largest family of the Philippine flora, the Orchidaceæ, is studied, the floristic connections of the Philippines with Celebes, the Moluccas, and New Guinea are distinctly shown, although Schlechter was not impressed with this alliance. He has given the results of his investigations of the Celebesian orchid flora, and in this connection he discussed Philippine affinities as follows:*

There are probably few regions not difficult of access in the Tropics concerning the flora of which we are still so completely in the dark as the Island of Celebes. This fact is the more astonishing when we consider that its geographical location, between two floral regions, proclaims it as especially interesting botanically.

Certain interesting forms which I have known from Celebes, and the location of the island itself, convinced me that its flora should be considered as transitional between the phytogeographical regions of the Philippines and of Papuasia. I therefore decided, on leaving New Guinea, to devote a few months before my return to Europe to botanical exploration of the northern point of the Island of Celebes lying nearest to the Philippines.

The results in Orchidaceæ are truly astounding, for the greater part of the species collected showed a remarkable affinity to typical Papuan species. Certain relations to Philippine species were also unmistakable, but so scattered that the character of the flora as a whole led to the belief that this part of the Island should in a wider sense be included in the Papuasian region, as a separation of Papuasia from the Moluccas is, in my opinion, neither fixed nor possible. Unfortunately, I was unable to explore the southern part of the Island and therefore cannot state whether the Moluccan-Papuasian types are as prominent there as in the northern part.

Closer study of the Orchidaceæ of the northern part, especially Minahassa, shows, as might be expected, that there is a certain intermixture of west Malayan types; largely, however, those that have invaded the Papuan flora; I mention here *Gastrodia*, *Galeola* (§ *Cystosia*), *Epipogon*, *Aphyllorchis*, *Goodyera*, *Corymbis*, *Pholidota imbricata* Ldl., several species of *Dendrobium* and *Bulbophyllum*, *Cymbidium*, *Grammangis*, *Aeriopsis javanica* Reinwardt, and several others.

On the other hand, there are several genera which I should consider typically Moluccan-Papuan, such as *Glossorrhyncha*, *Epiblastus*, and *Mediocalcar*. (Of the genus *Microtatorchis* one species is known from the Philippines.) In addition, in the larger genera are found representatives of sections which have hitherto been known only from Papuasia; namely, in *Dendrobium* sections *Diplocaulobium* [also in the Philippine Islands] and *Oxyglossum*; in *Bulbophyllum*, sections *Codonosepalum*, *Polyblepharon*, and *Thyridiosepalum*. Only one hitherto purely west Malaya genus greets us, namely *Sarcostoma*. *Doritis* was known from Ceylon, western Malaya,

* Fedde Repert. 10 (1911) 1, 2.

and the Philippines. Other than these two, none are found in the sixty-four genera here treated that were not already known to me from New Guinea. We must, however, take into consideration that Papuasias has not yet been thoroughly explored, whereas western Malaysia has been comparatively well explored, at least in the important regions. In the remaining genera the single species are mostly related to Moluccan-Papuan species, rarely to Philippine.

However, when the entire Philippine flora is taken into consideration, the special alliances between the floras of the Philippines and of Celebes are found to be so striking that it is evident that land connections must have existed to account for extensive intermigration. The data brought out below indicate the fallacy of attempting to draw conclusions on the basis of the geographic distribution of the plants in any one family, as Schlechter did in the case of the Orchidaceæ.

CELEBESIAN AND PHILIPPINE FLORAL ALLIANCES

For a number of years it has been evident that the floras of Celebes and the Philippines are closely allied. In spite of the fact that the flora of Celebes is little known, as compared with that of the Philippines, or of Java, or of the Malay Peninsula, sufficient is known regarding the vegetation of the island to warrant drawing some general conclusions in regard to the apparent floristic relationships between the Philippines and Celebes. At the present time the following species are known from Celebes and the Philippines:

Podocarpus pilgeri Foxworthy.

Pandanus linnaei Gaudichaud. Also in Kei and Aru Islands.

Calamus symphysis Martius. Of thirty-six species of *Calamus* occurring in the Philippines, all are endemic except *C. symphysis* Martius, *C. dimorphacanthus* Beccari, and *C. ornatus* Blume; the latter two occur in Sumatra, the Malay Peninsula, and Borneo, and the last in Java; both are represented by varieties in the Philippines.

Aglaonema haenkei Schott.

Alocasia heterophylla Merrill.

Pothodium lobbianum Schott, a monotypic genus, also in Ternate.

Scindapsus falcifolius Engler.

Spathiphyllum commutatum Schott, also in Amboina; the genus otherwise entirely American.

Pleomele multiflora Merrill.

Quercus celebica Miquel, also in Buru.

Quercus minahassae Koorders.

Ficus heteropoda Miquel, also in Gilolo.

Ficus luzonensis Merrill.

Ficus rudis Miquel.

- Pycnarrhena celebica* Diels.
Litsea perrottetii F.-Villar, also in the Moluccas.
Spiraeopsis celebica Miquel, the genus otherwise known only from New Guinea.
Dalbergia mimosella Prain.
Gleditsia rolfei Vidal.
Pithecolobium subacutum Benthham.
Pueraria pulcherrima Merrill.
Wallaceodendron celebicum Koorders, a monotypic genus.
Aglaia macrobotrys Turczaninow.
Aglaia luzoniensis Merrill and Rolfe, also in Borneo and New Guinea.
Reinwardtiadendron celebicum Koorders, a monotypic genus.
Ryssopterys dealbata Jussieu.
Neotrewia cumingiana Pax and Hoffman, a monotypic genus.
Strophoblachia fimbriicalyx Boerlage, a monotypic genus, also in Indo-China.
Dracontomelum dao Merrill and Rolfe.
Koordersiodendron pinnatum Merrill, a monotypic genus, also in Borneo.
Cubilia blancoi Blume, a monotypic genus, also in the Moluccas.
Euphoranthus obtusatus Radlkofer, a genus with one other known species in the Moluccas, New Guinea, and New Caledonia.
Ampelocissus ochracea Merrill.
Elaeocarpus cumingii Turczaninow.
Elaeocarpus multiflorus F.-Villar.
Sterculia oblongata Robert Brown.
Dillenia ochreatea Teysmann and Binnendyk.
Cratoxylon celebicum Blume.
Osmelia celebica Koorders.
Begonia pseudolateralis Warburg.
Terminalia comintana Merrill, also in Borneo.
Eucalyptus deglupta Blume, also in the Moluccas, New Guinea, and the Bismarck Archipelago.
Astronia cumingiana Vidal.
Medinella myrtiformis Triana.
Acanthophora scandens Merrill, a monotypic genus.
Medinella cumingii Naudin.
Anompanax, with three species in the Philippines, one in Celebes, and one or two in New Guinea.
Tetraplasandra, one species in Palawan, one in Celebes, the others in Hawaii.
Clethra canescens Reinwardt.
Vaccinium myrtoides Miquel, also in the Moluccas.
Palaquium celebicum Burck.
Couthovia celebica Koorders.
Fagraea plumeriaefolia A. de Candolle.
Tabernaemontana mucronata Merrill.
Hoya gracilis Schlechter.
Hoya imbricata Decaisne and *H. pseudomaxima* Koorders, with one other species in Celebes forming a subgenus confined to Celebes and the Philippines.
Clerodendron minahassae Teysmann and Binnendyk.

Premna cumingiana Schauer.

Nycticalos cuspidatum Miquel, also in the Moluccas.

Hemigraphis cumingiana F.-Villar.

Ixora macrophylla Bartling.

Ixora philippinensis Merrill, also in Borneo.

Scaevola minahassae Koorders.

There are also many genera and species that are known only from the Philippine Islands, various parts of the Moluccas, New Guinea, the Solomon Islands, etc. Among these are the following:

Gnetum gnemonoides Brongniart, Moluccas and New Guinea.

Sararanga, a very strong genus of the Pandanaceæ with one species in the Solomon Islands and one in the Philippines.

Mapania macrocephala K. Schumaun, Moluccas and the Bismarck Archipelago.

Thoracostachyum lucbanense Kükenthal, Amboina.

Heterospathe elata Scheffer, Moluccas; the remaining three species of the genus are confined to the Philippines.

Pothos rumphii Schott, Celebes, Moluccas, New Guinea.

Alpinia pulchella K. Schumann, New Guinea.

Costus glabra Merrill, the Moluccas.

Monophrynium, a genus with three species, all confined to the Philippines except one, which occurs also in Gilolo.

Casuarina rumphiana Miquel, Celebes and the Moluccas.

Piper decumanum Linnæus, Moluccas.

Piper fragile Benthams, New Guinea.

Pseudotrophis, with one species in the southern Philippines and one in the Kei Islands.

Pisonia longirostris Teysmann and Binnendyk, Buru and New Guinea.

Drimys piperata Hooker f., Borneo to New Guinea, the genus otherwise Australian.

Papualthia, with eight species in the Philippines and about twelve in New Guinea.

Quintinia, one species in Mindanao, fifteen in New Guinea, New Caledonia, Australia, and New Zealand.

Clianthus binnendickianus Kurz, Celebes and Ceram; the genus otherwise Australian.

Dalbergia densa Benthams, Moluccas and New Guinea, with a variety in Australia.

Macropsychanthus, with one species in New Guinea and two in the Philippines.

Rynchosia calosperma Warburg, New Guinea, Kei Islands, and the Bismarck Archipelago.

Macaranga hispida Mueller, Ceram and Amboina.

Mallotus papuanus Pax and Hoffmann, New Guinea.

Distyoneura sphaerocarpa Radlkofer, New Guinea.

Guioa glauca Radlkofer, New Caledonia.

Lepidopetalum perrottetii Blume, Kei Islands and Timor Laut.

Schuurmansia elegans Blume, Moluccas; this small genus with one other species in the Philippines, all the others confined to the Moluccas.

Osmelia philippina F.-Villar, New Guinea.

Mooria (*Cloezia*), one species in the Philippines, all the others (five or six) confined to New Caledonia.

Xanthostemon, three species in the Philippines, one in Celebes, the remainder confined to New Caledonia and Australia.

Medinella venosa Blume, Moluccas.

Otanthera crenata Naudin, Aru Islands.

Dimorphanthera, twenty-seven species in New Guinea, one in Amboina, two in the Philippines.

Vaccinium micropylum Blume, Moluccas.

Myxopyrum macrolobum Hill, Amboina and New Guinea.

Lepiniopsis ternatensis Valetton, a monotypic genus, Philippines, Ternate, and Amboina.

Rauwolfia amsonifolia A. de Candolle, Timor Laut, Kei, and Tinimber Islands.

Dischidiopsis, a small genus confined to the Philippines and the Moluccas.

Clerodendron lanuginosum Blume, Bender, Ternate, and Ceram.

Clerodendron macrostegium Schauert, Ceram, Amboina, and Sapuraea.

Vitex parviflora Jussieu, Moluccas and Timor.

Antirrhoea hexasperma Merrill, Moluccas.

Dolicholobium philippinense Trelease, the genus otherwise Polynesian.

Hedyotis buruensis Valetton, Moluccas.

Xanthomyrtus, thirteen species in New Guinea, one in New Caledonia, one in Australia, two in the Philippines, and three in Borneo.

FORMOSAN AFFINITIES OF THE BENGUET-BONTOC FLORA

The flora of the Benguet-Bontoc region, an area essentially characterized by the dominance of a species of pine, *Pinus insularis* Endlicher, is in striking contrast to that of other parts of the Philippines; it presents numerous northern types that do not occur elsewhere in the Archipelago and indicates a derivation, so far as these northern types are concerned, from the central mountain mass of Asia, as many of the same types are found in China, Japan, and the Riu Kiu Islands, and most of them in Formosa. Northern Luzon and Formosa, in numerous cases, present the most southern and eastern extension of the Himalayan flora. Most of the Himalayan types found in northern Luzon occur also in Formosa.

About five hundred species of plants in the higher groups are known in the Philippines only from the Benguet-Bontoc region, indicating a distinctly specialized flora. Approximately three hundred fifty of these, or 70 per cent, are endemic as far as

the Philippines are concerned, while the remaining 30 per cent are found outside of the Archipelago chiefly in India, China, Japan, and Formosa. A very few extend south of Mountain Province on the higher mountains; some even occur at higher altitudes, in Mindanao, and a few extend as far south as Celebes and Timor. Six genera are endemic to this region.

If the flora of the Benguet-Bontoc region be examined by larger groups (families), two striking facts are evident. The families that are essentially characteristic of the temperate regions are relatively strongly developed, while those that are highly developed in tropical regions are poorly represented. Thus, such essentially temperate-region families as the following are well represented in the Benguet-Bontoc region:

Pinaceæ (one species of <i>Pinus</i> , but dominant).	Caryophyllaceæ.	Ericaceæ.
Gramineæ.	Ranunculaceæ.	Primulaceæ.
Cyperaceæ.	Berberidaceæ.	Gentianaceæ.
Juncaceæ.	Saxifragaceæ.	Labiataæ.
Liliaceæ.	Rosaceæ.	Scrophulariaceæ.
	Violaceæ.	Compositæ.

In contrast, the families that are in general strongly developed at low and medium altitudes in the Philippines and in other tropical countries are either entirely unrepresented in the Benguet-Bontoc region or are represented by only few species, and of the few species that do occur there practically none is confined to the Benguet-Bontoc region. Perhaps the most striking case is the Dipterocarpaceæ. This family is represented in the Philippines by nine genera and about fifty species, and is dominant in the primary forests of the entire Archipelago at low and medium altitudes. No representative of the family is known from the region under discussion. The tropical families either unrepresented or very poorly represented in the Benguet-Bontoc region are the following:

Pandanaceæ.	Sterculiaceæ.	Combretaceæ.
Palmæ.	Malvaceæ.	Sapotaceæ.
Nyctaginaceæ.	Dipterocarpaceæ.	Ebenaceæ.
Anonaceæ.	Ochnaceæ.	Apocynaceæ.
Myristicaceæ.	Guttiferæ.	Convolvulaceæ.
Capparidaceæ.	Dilleniaceæ.	Verbenaceæ.
Connaraceæ.	Flacourtiaceæ.	Bignoniaceæ.
Meliaceæ.	Lecythidaceæ.	Acanthaceæ.

The two lists of family names on this page show that the plants of the highlands and of the lowlands in Luzon constitute very distinct floras.

The geographic distribution of smaller groups (genera) presents the same condition as does that of families. It is unnecessary to enumerate the many essentially tropical genera that occur elsewhere in the Philippines but are very poorly represented in the Benguet-Bontoc region or are altogether lacking in the region. The following, as Philippine genera, are essentially confined to the Benguet-Bontoc region; three of them are also represented on Mount Banahao, and one has two species in Zambales and one species in Mindoro:

<i>Taxus</i> (also on Mount Bana- hao).	<i>Sagina</i> .	<i>Petalonema</i> .
<i>Pinus</i> (also in Zambales and one species in Mindoro).	<i>Stellaria</i> .	<i>Bothriospermum</i> .
<i>Agrostis</i> .	<i>Anemone</i> .	<i>Calamintha</i> .
<i>Aniselytron</i> .	<i>Ranunculus</i> .	<i>Plectranthus</i> .
<i>Arundinaria</i> .	<i>Thalictrum</i> .	<i>Teucrium</i> .
<i>Brachypodium</i> .	<i>Berberis</i> .	<i>Alectra</i> .
<i>Bromus</i> .	<i>Mahonia</i> .	<i>Bythophytum</i> .
<i>Calamagrostis</i> .	<i>Sedum</i> .	<i>Ellisiophyllum</i> .
<i>Chionachne</i> .	<i>Astilbe</i> .	<i>Hemiphragma</i> .
<i>Deschampsia</i> .	<i>Deutzia</i> .	<i>Veronica</i> .
<i>Microlaena</i> .	<i>Fragaria</i> .	<i>Galium</i> .
<i>Monostachya</i> .	<i>Rosa</i> .	<i>Peracarpa</i> .
<i>Poa</i> .	<i>Dumasia</i> .	<i>Lonicera</i> .
<i>Luzula</i> .	<i>Lespedeza</i> .	<i>Ainslaea</i> (also on Mount Bana- hao).
<i>Aletris</i> .	<i>Shuteria</i> .	<i>Anaphalis</i> .
<i>Asparagus</i> .	<i>Boenninghausenia</i> .	<i>Aster</i> .
<i>Disporum</i> .	<i>Skimmia</i> .	<i>Senecio</i> .
<i>Lilium</i> .	<i>Sarcococca</i> .	<i>Ethulia</i> .
<i>Liriope</i> .	<i>Pistacia</i> .	<i>Carpesium</i> .
<i>Saururus</i> .	<i>Vitis</i> .	<i>Cirsium</i> (also on Mount Bana- hao).
<i>Thesium</i> .	<i>Daphne</i> .	<i>Merrittia</i> .
<i>Arenaria</i> .	<i>Carionia</i> .	<i>Solidago</i> .
<i>Muehlenbergia</i> .	<i>Epilobium</i> .	<i>Pimpinella</i> .
	<i>Acanthopanax</i> .	
	<i>Loheria</i> .	
	<i>Swertia</i> .	
	<i>Potentilla</i> .	

It will be noted that practically all of these genera are characteristic of the North Temperate Zone and poorly represented in tropical regions. Six monotypic genera—*Aniselytron*, *Monostachys*, *Carionia*, *Loheria*, *Petalonema*, and *Merrittia*—are confined to Mountain Province.

In addition to these genera, other essentially temperate or subtemperate groups are much more strongly developed in the Benguet-Lepanto region than in other parts of the Philippines; they are represented there by from one to several species,

elsewhere in the Philippines usually by one or few forms and chiefly at higher altitudes farther south. They are—

<i>Potamogeton.</i>	<i>Vaccinium.</i>	<i>Sopubia.</i>
<i>Carex.</i>	<i>Rhododendron.</i>	<i>Mosa.</i>
<i>Juncus.</i>	<i>Lysimachia.</i>	<i>Lobelia.</i>
<i>Rubus.</i>	<i>Gentiana.</i>	<i>Bidens.</i>
<i>Smithia.</i>	<i>Cynoglossum.</i>	<i>Gnaphalium.</i>
<i>Impatiens.</i>	<i>Ajuga.</i>	<i>Artemisia.</i>
<i>Hypericum.</i>	<i>Salvia.</i>	<i>Eupatorium.</i>
<i>Viola.</i>		

Australian types are poorly represented by two species of *Halorrhagis*, one endemic, the other extending from India to Japan southward to New Zealand; *Uncinia rupestris* Raoul, Luzon, Mindanao, and New Zealand; and *Microlaena stipoides* Labillardière, Luzon, Australia, and Hawaii. *Gaultheria borneensis* Stapf, known from Borneo (Mount Kinabalu), Formosa, and Benguet, is most closely allied to a New Zealand species. The two endemic species of *Ranunculus* confined to the Benguet-Bontoc region find their closest allies in Australia and New Zealand—not on the Asiatic continent.

The Baguio Plateau, in a restrictive sense, is characterized by the dominance of *Pinus insularis* Endlicher. In general, the flora of Baguio and vicinity, including Mount Santo Tomas, is very similar to that of other parts of Mountain Province. However, thirteen genera are not represented there which are found on the higher mountain peaks north of Baguio; namely—

<i>Aniselytron.</i>	<i>Luzula.</i>	<i>Loheria.</i>
<i>Anthoxanthum.</i>	<i>Saururus.</i>	<i>Bythophytum.</i>
<i>Deschampsia.</i>	<i>Ranunculus.</i>	<i>Peracarpa.</i>
<i>Monostachya.</i>	<i>Sarcococca.</i>	<i>Solidago.</i>
<i>Poa.</i>	<i>Potentilla.</i>	

These genera occur at Pauai (Haight's place), on Mount Pulog, and on other high mountains in northern Benguet, in Lepanto, and in Bontoc. Generally speaking, the Baguio flora is characterized by the occurrence of the genera enumerated for the Benguet-Bontoc region as a whole, with the exception of the fourteen genera enumerated above; in most cases these genera are represented in the Philippines by one species only; *Luzula* and *Ranunculus* are represented by two species each. Tropical types—that is, families, genera, and species essentially characteristic of the Malay Archipelago and the low altitudes of the Philippines—are no more prominently represented on the Baguio Plateau than they are in any other part of Mountain Province.

Of the genera essentially confined to the Benguet-Bontoc region, as far as their occurrence in the Philippines is concerned, about seventeen have seeds or fruits adapted for dissemination through the medium of wind, and sixteen contain species that are apparently distributed by their fleshy fruits being eaten by birds. In the remaining thirty-seven cases data are not available as to adaptations for dissemination. It seems highly probable, however, that many species may be distributed through seeds being present in mud that adheres to the feet or feathers of migratory birds, as in numerous species very minute seeds are produced in great abundance. This method of dissemination corresponds in general to that of the large series of rice-paddy weeds that are predominant in the low-country vegetation of the Philippines, whose distribution can scarcely be explained on the basis of any other hypothesis.

It is to be noted that the northern types are for the most part confined to the Benguet-Bontoc region in the Philippines. Many are essentially Himalayan, but others are confined to China and Luzon, or Formosa and Luzon, and a few to Japan and Luzon. Practically all of the Himalayan types found in Luzon occur also in Formosa, indicating that they attained their present distribution at probably the same geologic time. It would seem that this might have been in the Eocene or the Oligocene, when Formosa and Luzon were connected with the Asiatic continent. These types at one time may have extended farther south, but if they did they have been exterminated by changes in climatic conditions. Many of the Formosan-Luzon-Himalayan types are unknown from Sumatra, Java, and Borneo, and could scarcely have reached Luzon and Formosa through these islands. Summarizing, it would seem that from the time these Himalayan types reached the Philippines there have been continued high elevations in some part of the Benguet-Bontoc region which allowed them to persist. Few or none of them can grow under present climatic conditions at altitudes below 1,200 meters, while very many of them cannot grow below an altitude of 2,000 meters; most of them thus characterize a highly specialized flora, the greater part of which inhabits the high-altitude area in northern Luzon.

There seem definitely to have been two routes of migration of Asiatic types into Malaysia; one through the Malay Peninsula and Sumatra to Java and Borneo, and one through Formosa and the Philippines into eastern Malaysia.

GENERAL BOTANIC ALLIANCE BETWEEN THE PHILIPPINES AND
FORMOSA *

Formosa, which lies to the north of the Philippines and within sight of the northernmost island of the Philippine Archipelago, Y'Ami Island, has been included by certain German botanists in the botanical "Subprovinz der Philippinen und Formosa;" but the botanic evidence is that the Formosan flora is radically different from the Philippine and that its alliances are with the continental or Asiatic flora. Incidentally, it is to be noted that Formosa is separated from the northernmost island of the Philippine group by a deep channel; but, on the other hand, it lies on the continental shelf, and the Formosan channel between the island and the Asiatic coast nowhere exceeds 100 fathoms in depth.

Fortunately, for purposes of comparison, the flora of Formosa is remarkably well known, due especially to the efforts of Dr. B. Hayata and other Japanese botanists who have explored the island. Most of the actual botanic work, however, has been done by Hayata.

In 1917 Hayata published his General Index to the Flora of Formosa, which consists of a systematic list of all of the flowering plants and ferns recorded from Formosa up to the publication of his *Icones Plantarum Formosanarum* VI in 1917. Since 1917 four additional volumes of the *Icones* have been issued.† In the General Index, including the ferns and fern allies, 3,446 species were enumerated as indigenous to Formosa. The additions included in the four volumes of the *Icones* issued since 1917 bring the total up to 3,658 species distributed into 1,185 genera and 170 families, following the arrangement of Bentham and Hooker's *Genera Plantarum*. It should be noted that the figures include also the ferns and fern allies.

Examination of Hayata's list shows that certain families which have indigenous representatives in Formosa have no representatives in the Philippines; these are the Valerianaceæ, the Dipsacæ, the Monotropaceæ, the Diapensiaceæ, the Styracæ, the Myoporaceæ, and the Philydraceæ. By way of further contrast, certain families represented in the Philippines by nu-

* See E. D. Merrill, *Engl. Bot. Jahrb.* 58 (1923) 599-604; also A. Engler, *ibid.* 605, 606.

† *Icones* 7 (1918) 1-107, t. 1-14, f. 1-69; 8 (1919) 1-164, t. 1-15, f. 1-88; 9 (1920) 1-155, t. 1-7, f. 1-55; 10 (1921) 1-74, f. 1-48.

merous genera and species are scantily represented in Formosa. Among these families are—

Anonaceæ.	Combretaceæ.	Sapotaceæ.
Meliaceæ.	Myrtaceæ.	Melastomataceæ.
Guttiferæ.	Gesneraceæ.	Begoniaceæ.
Sterculiaceæ.	Bignoniaceæ.	Pandanaceæ.
Burseraceæ.	Piperaceæ.	Palmæ.

On the other hand, families that are infinitely better represented in Formosa than in the Philippines are—

Ranunculaceæ.	Aquifoliaceæ.	Caprifoliaceæ.
Berberidaceæ.	Celastraceæ.	Campanulaceæ.
Cruciferæ.	Rosaceæ.	Gentianaceæ.
Papaveraceæ.	Saxifragaceæ.	Pinaceæ.
Violaceæ.	Crassulaceæ.	Liliaceæ.
Caryophyllaceæ.	Umbelliferæ.	

In this connection, it is to be noted that most of the families enumerated in the first list are largely characteristic of tropical regions, while those in the second list are largely characteristic of temperate regions.

As noted above, several families of plants that have indigenous representatives in Formosa are not represented in the Philippine Archipelago. In contrast to this may be mentioned the following Philippine families which have no representatives in Formosa:

Triruridaceæ.	Dichapetalaceæ.	Datisceæ.
Centrolepidaceæ.	Stackhousiaceæ.	Clethraceæ.
Monimiaceæ.	Gonystylaceæ.	Epacridaceæ.
Nepenthaceæ.	Ochnaceæ.	Salvadoraceæ.
Cunoniaceæ.	Dipterocarpaceæ.	Stylidiaceæ.
Erythroxylaceæ.		

These families, with few exceptions, such as the Centrolepidaceæ, the Stackhousiaceæ, the Epacridaceæ, and the Stylidiaceæ, which must be considered as Australian types, are for the most part characteristically tropical groups. The most striking case is perhaps that represented by the Dipterocarpaceæ.

Of the eleven hundred eighty-five genera that have indigenous representatives in Formosa, no less than two hundred sixty-five are not represented in the Philippines. Among these genera are such characteristic continental and temperate types as—

<i>Abies.</i>	<i>Picea.</i>	<i>Aira.</i>
<i>Chamaecyparis.</i>	<i>Pseudotsuga.</i>	<i>Alopecurus.</i>
<i>Cunninghamia.</i>	<i>Tsuga.</i>	<i>Apios.</i>
<i>Juniperus.</i>	<i>Trillium.</i>	<i>Astragalus.</i>
<i>Libocedrus.</i>	<i>Smilicina.</i>	<i>Lotus.</i>

<i>Vicia.</i>	<i>Cephalanthus.</i>	<i>Dianthus.</i>
<i>Agrimonia.</i>	<i>Patrinia.</i>	<i>Silene.</i>
<i>Cotoneaster.</i>	<i>Valeriana.</i>	<i>Cuscuta.</i>
<i>Malus.</i>	<i>Gerbera.</i>	<i>Paulownia.</i>
<i>Pirus.</i>	<i>Patasites.</i>	<i>Pedicularis.</i>
<i>Sanguisorbia.</i>	<i>Taraxacum.</i>	<i>Orobanche.</i>
<i>Sorbus.</i>	<i>Chimaphila.</i>	<i>Eschscholtzia.</i>
<i>Spiraea.</i>	<i>Moneses.</i>	<i>Glechoma.</i>
<i>Mitella.</i>	<i>Pieris.</i>	<i>Lamium.</i>
<i>Parnassia.</i>	<i>Pyrola.</i>	<i>Prunella.</i>
<i>Ribes.</i>	<i>Monotropa.</i>	<i>Asarum.</i>
<i>Saxifraga.</i>	<i>Primula.</i>	<i>Humulus.</i>
<i>Circaea.</i>	<i>Aconitum.</i>	<i>Ulmus.</i>
<i>Angelica.</i>	<i>Coptis.</i>	<i>Juglans.</i>
<i>Apium.</i>	<i>Podophyllum.</i>	<i>Alnus.</i>
<i>Bupleurum.</i>	<i>Nuphar.</i>	<i>Carpinus.</i>
<i>Hedera.</i>	<i>Corydalis.</i>	<i>Corylus.</i>
<i>Cornus.</i>	<i>Arabis.</i>	<i>Fagus.</i>
<i>Abelia.</i>		

Not a single genus is known to be confined to the Philippines and Formosa; furthermore, considering the proximity of the Philippines and Formosa and the distinctly similar climatic and physiographic conditions, the list of species that have this limited distribution is curiously small. After a careful examination of Hayata's list accompanied by a considerable amount of comparative work in the Bureau of Science herbarium, which contains fairly ample collections of Formosan material and much Philippine material, a list of about forty species known only from the Philippines and Formosa has been prepared. In this list the species marked (W) are adapted for dissemination by wind and those marked (B) are adapted for dissemination through the medium of birds. Many of the species, common and confined to Formosa and the Philippines, occur in the Philippines only north of central Luzon. The species are as follows:

<i>Pterospermum niveum</i> Vidal (<i>P. formosanum</i> Mats.) (W).	<i>Aralia hypoleuca</i> Presl (B).
<i>Ryssopteris cumingiana</i> Jussieu (W).	<i>Alsomitra integrifoliola</i> Hayata (W).
<i>Fagara integrifoliola</i> Merrill.	<i>Boerlagiodendron pectinatum</i> Merrill (B).
<i>Coriaria intermedia</i> Matsumura (B).	<i>Viburnum luzonicum</i> Rolfe (B).
<i>Acacia confusa</i> Merrill.	<i>Lasianthus tashiroi</i> Matsumura (B).
<i>Deutzia pulchra</i> Vidal (W).	<i>Isanthera discolor</i> Maximowicz.
<i>Astronia pulchra</i> Vidal (W).	<i>Ainslaea reflexa</i> Merrill (W).
<i>Sarcopyramis delicata</i> C. B. Robinson (B).	<i>Gynura elliptica</i> Yabe and Hayata (W).

Gaultheria cumingiana Vidal
(B).

Palaquium formosanum Hayata.

Isanthera discolor Matsumura
(B).

Hypoestes cumingiana F.-Villar.

Callicarpa formosana Rolfe
(B).

Scutellaria luzonica Rolfe.

Knema glomerata Merrill (B).

Myristica semiarum A. de Candolle (B).

Illigera luzonensis Merrill (W).

Macaranga dipterocarpifolia
Merrill (B?).

Euphorbia makinoi Hayata.

Elatostema edule C. B. Robinson.

Oreocnide trinervis Miquel (B).

Leucosyke quadrinervis C. B.
Robinson (B).

Lilium philippinense Baker
(W).

Eriocaulon merrillii Ruhland.

Isachne debilis Rendle.

Rourea volubilis Merrill.

Stellaria laxa Merrill.

Bergia serrata Blanco.

Aglaia elliptifolia Merrill (B).

Aglaia formosana Hayata (B).

There are many species, more widely distributed, which extend from Japan or the Riu Kiu Islands to China, Formosa, and the Philippines. Like those in the preceding list, however, they are found in the Philippines chiefly north of central Luzon, while many of them occur only at medium and higher altitudes in the Philippines. They are as follows:

Sageretia theezans Brongniart.

Celastrus diversifolius Hemsl.

Ilex asprella Hance.

Ilex crenata Thunberg.

Pistacia chinensis Bunge.

Acalypha australis Linnæus.

Skimmia japonica Thunberg.

Evodia meliaefolia Benth.

Rhynchosia volubilis Loureiro.

Desmodium buergeri Miquel.

Cocculus trilobus de Candolle.

Salvia scaphiformis Hance.

Bothriospermum tenellum Fisher and Meyer.

Lactuca dentata C. B. Robinson.

Lactuca indica Linnæus.

Eupatorium lindleyanum de
Candolle.

Eupatorium reevesii Wallich.

Eupatorium japonicum Thunberg.

Artemisia capillaris Thunberg.

Artemisia japonica Thunberg.

Clerodendron trichotomum
Thunberg.

Androsace umbellata Merrill.

Acanthopanax trifoliatum Merrill.

Melastoma candidum Don.

Scolopia oldhami Hance.

Columella corniculata Merrill.

Ampelopsis heterophylla Siebold and Zuccarini.

Photinia serrulata Lindley.

Polygonum benguetense Merrill.

Boehmeria densiflora Hooker
and Arnott.

Saururus chinensis Baillon.

Potamogeton maackianus A.
Bennett.

Tripogon chinensis Hackel.

Carex ligata Boott.

Carex tristachya Thunberg.

Phoenix hanceana Naudin.

Acorus gramineus Solander.

Asparagus cochinchinensis Merrill.

Aletris spicata Franchet.

Lilium longiflorum Thunberg.

Liriope graminifolia Baker.

Ophiopogon japonicus Ker.

Representatives of even more widely distributed species in *Solidago*, *Aster*, *Anemone*, *Benninghausenia*, *Deschampsia*, *Agrostis*, *Viola*, *Ellisiophyllum*, *Peracarpa*, *Senecio*, and *Hemiphragma*, some of which must certainly be considered as Himalayan types (for example, *Anemone vitifolia* Ham., *Peracarpa*, *Ellisiophyllum*, *Hemiphragma*), occur also in Formosa and in the mountains of northern Luzon.

Botel Tobago shows some distinct alliance with the Philippines, especially with the Batan and Babuyan groups, that are not presented by the Formosan flora, in that the Philippine species *Timonius arboreus* Elmer, *Dysoxylum cumingianum* C. de Candolle, *Psychotria cephalophora* Merrill, *Boerlagiodendron pectinatum* Merrill, and *Coleus pubescens* Merrill occur there; the last three are confined to the small islands between Luzon and Formosa (Batan and Babuyan groups) and Botel Tobago.

AUSTRALIAN ELEMENT IN THE PHILIPPINE FLORA

The Australian element is relatively well developed in the Philippines; in many cases the various species extend as far as northern Luzon. The following genera may be mentioned as representative Australian types:

<i>Calogyne</i> (also in	<i>Stackhousia</i> .	<i>Xanthostemon</i> .
Fukien Province,	<i>Microlaena</i> .	<i>Osbornia</i> .
China).	<i>Cladium</i> .	<i>Campostemon</i> .
<i>Stylidium</i> .	<i>Pleiogynum</i> .	<i>Patersonia</i> .
<i>Centrolepis</i> .	<i>Phrygilanthus</i> .	<i>Didiscus</i> .
<i>Eucalyptus</i> .	<i>Quintinia</i> .	<i>Pimelea</i> .

This Australian element is very weak in Formosa; *Halorrhagis*, *Acacia confusa* Merrill (Formosan and Luzon), a phyllodinous species, and *Ipomoea polymorpha* Roemer and Schultes (Formosa, northern Luzon, and northern Australia) are about the only "Australian" types known from Formosa. *Oreomyrrhis* has one species in Formosa, one in Borneo, and several in Australia, New Zealand, and South America, but none in the Philippines; while *Myoporum*, largely but not wholly an Australian genus, is represented in Formosa by one species, but has no representative in the Philippines or in Malaysia. The even stronger New Guinean, Celebesian, and Moluccan elements in the Philippine flora are absent from Formosa, although many extend to northern Luzon and some (*Wallaceodendron*) into the Babuyan Islands.

SUMMARY OF THE PHILIPPINE FLORA

Broadly stated, the Philippine flora has been derived from the Sunda Islands, or western Malaysia, through Borneo; from New Guinea via the Moluccas and Celebes; and from the Himalayas via continental China and Formosa during early Tertiary time. That the western Malaysian (or Sunda) elements were present during Pliocene time is shown by the fossil dipterocarp floras of Sagada and Cagayan Valley in northern Luzon. The absence of these characteristic trees from Formosa suggests that northern Luzon was not connected with Formosa during the Pliocene, the Pleistocene, or the Recent. The presence of certain species of Himalayan origin in both northern Luzon and Formosa and the absence of many of these from Malaysia, Celebes, and the southern islands of the Philippine group indicate that only northern Luzon was connected to Formosa during early Tertiary time. The absence of many Celebesian and tropical Australasian elements from Borneo and Palawan and their presence in Mindanao and the islands to the north indicate a direct connection between Mindanao and Celebes. Any Australasian elements that are now present in Borneo or Palawan reached there after a long stop-over in Mindanao previous to a connection during early Pleistocene time. However, this would not explain the very few Kinabalu-Australian types that do not occur in the Philippine Islands.

BIRDS OF THE PHILIPPINES

At first blush birds do not seem to afford suitable criteria for judging of the zoölogic relationships of areas separated by water, at least where the water is of inconsiderable width. As birds can fly long distances, it seems as if water could be no barrier to their dispersal.

It is true that birds can and do cross wide bodies of water. The Pacific golden plover, *Pluvialis fulvus* (Gmelin), nests in northern Siberia and along the coast of Bering Sea. In the fall it moves southward and visits the Hawaiian Islands, China, the Philippines, Australia, and New Zealand. In the spring it returns to its summer home. The ticwee buzzard, *Butastur indicus* (Gmelin), is a medium-sized hawk that inhabits eastern Asia, China, Japan, and the Malay Peninsula. In the fall it appears in immense flocks in Batan and Calayan Islands, north of Luzon, and spreads over all of the Philippines; it also extends southward to Celebes and New Guinea.

It is not by any means the large birds only that make these great journeys from north to south and back again each year. For example, the northern willow warbler, *Acanthopneuste borealis* Blasius, is only 12 centimeters in length and less than 15 grams in weight, yet it travels approximately 8,000 kilometers in a single season. This species breeds in northern Siberia and western Alaska. In the fall it moves to southeastern Asia. It also invades Formosa, the Philippines, and Borneo in moderate numbers and is found as far south as Celebes. In North America familiar examples of migratory land birds are the bobolink, the robin, and many species of the wood warblers.

Some other Philippine species of wide distribution whose members migrate long distances are the following:

Dafla acuta (Linnæus); Northern Hemisphere; in winter to Africa, India, Ceylon, China, Panama, and Cuba.

Spatula clypeata (Linnæus); North America, Europe, western Asia; in winter to Africa, India, southern China, Hawaii, the West Indies, and South America.

Falco peregrinus Tunstall; America, Europe, Asia; in winter to Africa and the Indian Peninsula.

Cuculus canorus Linnæus; Europe and northern Asia; in winter to Africa, India, Malaysia, and Australia.

Riparia riparia (Linnæus); America, Asia, and Europe; in winter to South America, Africa, and India.

Of Philippine species of wide range whose members migrate little or not at all the following are examples:

Fulica atra Linnæus; Europe, Asia, Java, Sumatra, and Celebes.

Phalacrocorax carbo (Linnæus); Europe, Africa, Asia, North America, and Australia.

Cuncuma leucogaster (Gmelin); India, the Malay Peninsula, Australia, and Oceania.

Migratory birds as well as resident species of wide distribution are clearly of no value in determining the zoölogic relationships of islands and the smaller land areas. If such birds be eliminated, there remain species of more or less limited distribution; that is, species that are nonmigratory and reside in fairly definite, relatively small, geographic areas. No doubt these birds could move to other areas than those in which they are found, but they certainly do not, so far as can be determined. Such species are said to be endemic with regard to the areas in which they live.

Nonmigratory species of birds are of great value in zoögeographic studies. In fact, one may venture to say that the data afforded by the distribution of endemic land birds are the best evidence, because birds can resist accidental transportation in many cases where mammals, reptiles, insects, mollusks, etc., are at the mercy of wind and flood. This does not mean that birds are never carried long distances over seas or other barriers, for it is known that "the smaller land birds are often carried by violent gales of wind from Europe to the Azores, a distance of nearly a thousand miles," and oceanic islands have doubtless acquired their fauna and flora through such occasional extraordinary transportation of plants and animals.

For the solution of distributional problems birds afford better evidence than mammals because they are more numerous, more conspicuous, and have been more thoroughly collected. Birds are also better known than insects, mollusks, etc.; that is, the known species constitute a higher percentage of the existing species, and their generic and specific distribution is more completely known.

The first thorough zoögeographic study was made by Sclater, in 1857, who established six primary zoölogic regions from the detailed examination of the distribution of the chief genera and

families of birds. Wallace's work, likewise, is based very largely on the distribution of birds, and his limits for regions and sub-regions are followed in this chapter. It is evident, therefore, that birds have had a primary place in developing theories concerning zoögeography.

FAMILIES OF PHILIPPINE BIRDS

More than 750 species of birds are known to occur in the Philippines, and it is improbable that many more species will be found there. The known species belong to about 293 genera. A fairly good idea of the relative richness of the Philippine avifauna can be obtained from the following approximate figures: Ogawa records 502 species in 192 genera for Japan; Uchida

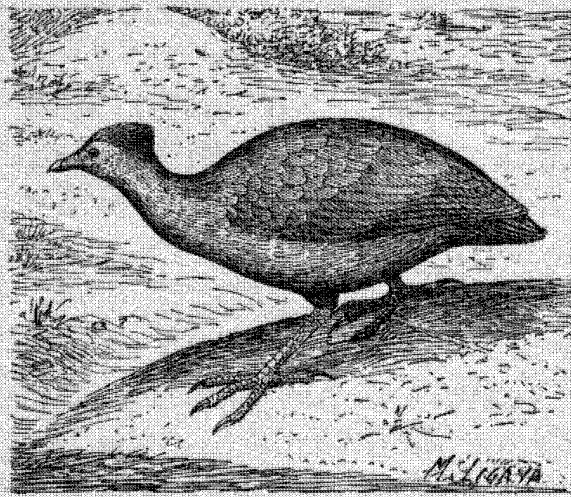


FIG. 28. Philippine megapode, *Megapodius cumingi* Dillwyn, the only Philippine species of a family that is highly developed in the Australian Region.

records 290 species in 188 genera for Formosa; the Hand-list of Genera and Species of Birds of the Indian Empire includes about 2,150 species and subspecies in 600 genera; Meyer and Wiglesworth enumerate 393 species and 83 subspecies in 207 genera for Celebes; and a manuscript list of the birds of Australia enumerates 711 species in 331 genera. In 1909 Sharpe estimated that there were known in the world, ap-

proximately, 18,939 species of birds in 2,810 genera.

The various families of Philippine birds are enumerated in the following paragraphs. Genera and species of zoögeographic significance are discussed under their respective families.

Megapodiidæ.—The species of primitive birds known as mound builders and brush turkeys are nearly all confined to the Australian Region. The genus of greatest range is *Megapodius*, one species of which is restricted to the Mariannes and another to the Nicobars. The only Philippine representative is *Megapodius cumingi* Dillwyn, which is also found in islands of northwestern Borneo.

Phasianidæ.—The pheasant family is represented in nearly all parts of the world except the Nearctic and the Neotropical. The Philippine species are *Francolinus pintadarius* (Scopoli),

introduced; *Excalfactoria lineata* (Scopoli), also in Borneo and Australia; *Gallus gallus* (Linnæus), also in India and Indo-Malayan islands; and *Polyplectron napoleonis* (Lesson), endemic in Palawan. *Gallus* and *Polyplectron* are Oriental genera.

Turnicidæ.—The button quails, or hemipods, include only two genera. *Podionomus*, a monotypic genus, is confined to Australia. *Turnix* includes about thirty species, most of which are scattered over the Oriental and Australian Regions; a few are African; and one reaches southern Europe. The five Philippine species are endemic.

Treronidæ.—The tree pigeons include about forty genera, most of which are Oriental or Australian; one genus is African. The nine species of *Sphenocercus* are Oriental; one Philippine species is confined to the Babuyan and the Batan

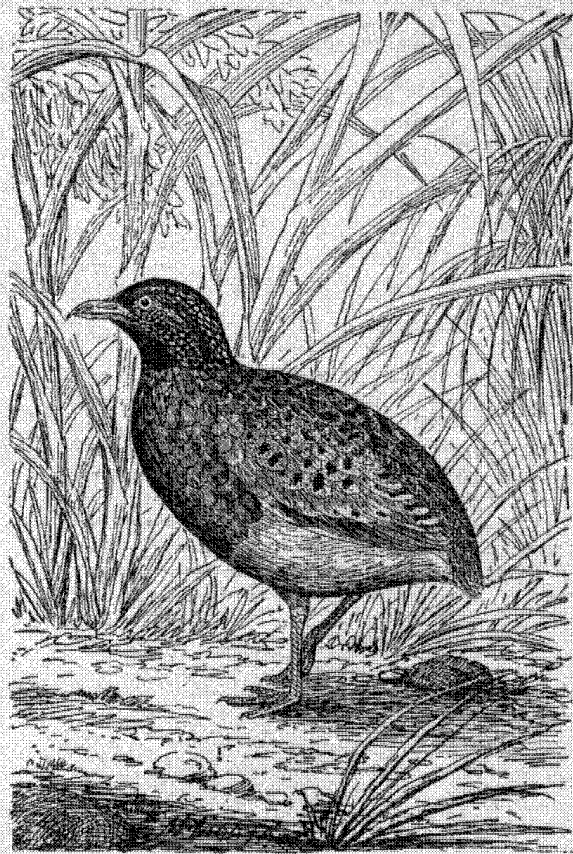


FIG. 29. Spotted button quail, *Turnix ocellata* (Scopoli), the largest Philippine species of its genus.

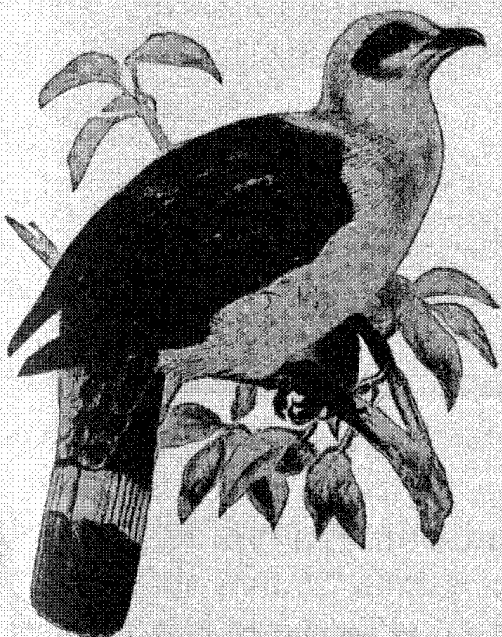


FIG. 30. Mindoro zone-tailed pigeon, *Zonophaps mindorensis* (Whitehead), a large forest bird that is confined to Mindoro.

Islands. *Treron* is Oriental, and one of the species is Philippine. The species of *Dendrophassa* (formerly called *Osmotreron*) are mostly Oriental, and a few are Austro-Malayan; two Philippine species are endemic, and another ranges to Celebes and to Indo-China. *Phapitreron* is an endemic Philippine genus of ten species. *Leucotreron* is an Australian and Oriental genus, of which *L. occipitalis* Bonaparte, *L. marchei* (Oustalet), *L. merrilli* McGregor, and *L. leclancheri* (Bonaparte) are among the most brightly col-

ored of the endemic Philippine doves. *Hæmatæna* (formerly called *Spilotreron*) is a small Austro-Malayan genus, one species of which reaches the southern Philippines. *Muscadivores* is an Indian and Austro-Malayan genus of about thirty species, of which three or four are credited to the Philippines; two or three are endemic. *Ptilocolpa* includes three species, all of which are endemic Philippine. *Zonophaps* includes nine or ten Austro-

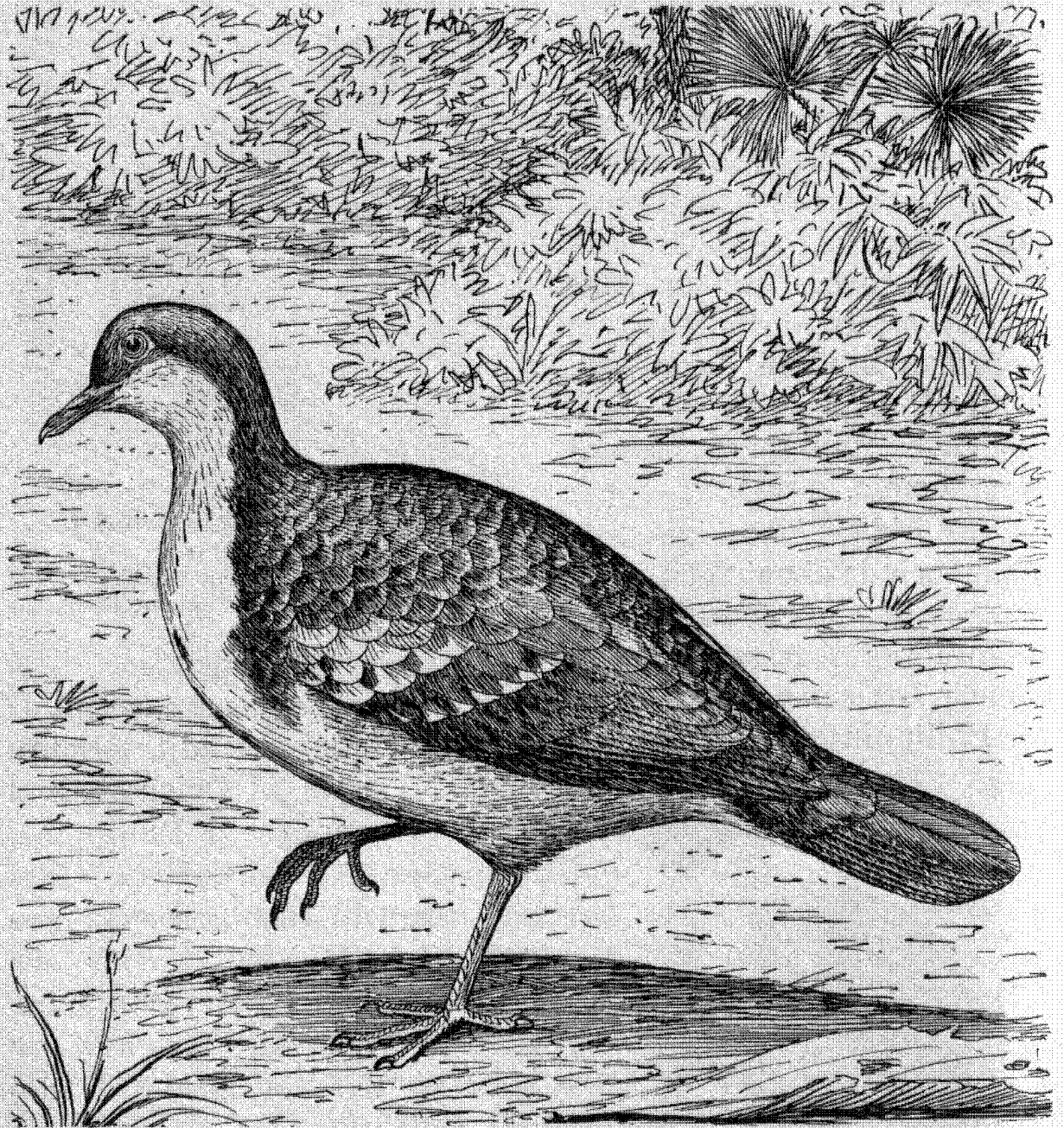


FIG. 31. Mindoro puñalada, *Gallicolumba platenæ* (Blasius), a forest dove that is restricted to Mindoro.

Malayan species, two of which are endemic Philippine. *Myristicivora* is an Australian and Oriental genus of five species; the only Philippine species is found in various parts of the Oriental Region.

Columbidae.—The typical family of the Columbiformes includes the typical genus, which has over seventy members;

Macropygia, with over thirty species; and several small genera. The family is represented in most parts of the world. *Columba griseigularis* (Walden and Layard) inhabits the Philippines and Borneo and is the only Philippine *Columba*. *Macropygia tenuirostris* Bonaparte and *M. Phæa* McGregor are Philippine; the latter has been recorded from Formosa.

Claraviidæ.—The family Claraviidæ includes about forty genera and is represented in many parts of the world. *Gallinula* (formerly called *Phlogænas*), with about thirty species, is the largest genus and the most important one of this family in the present discussion; five of its species are endemic Philip-

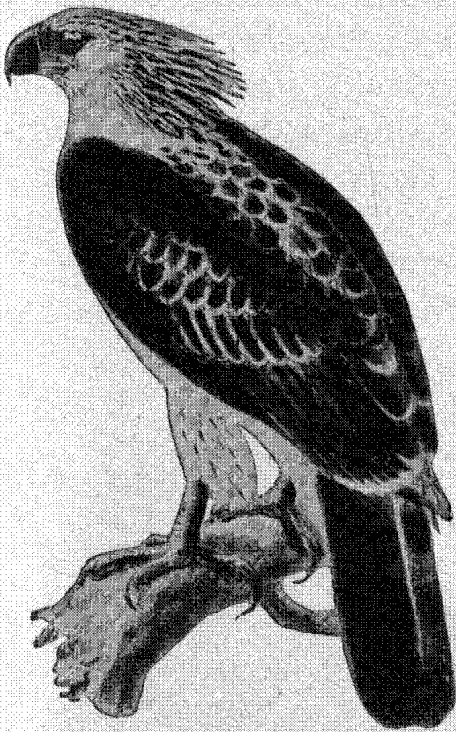


FIG. 32. Monkey-eating eagle, *Pithecophaga jefferyi* Grant, an endemic species and one of the world's largest birds of prey.



FIG. 33. Palawan barred owl, *Strix whiteheadi* (Sharpe), the only Philippine species of its genus.

pine, and nearly all of its other species are confined to single islands south and southeast of the Philippines. Other genera of this family are represented in the Philippines by the following: *Streptopelia dussumieri* (Temminck), also Borneo and Marianes; *Ænopus humilis* (Temminck), also in the Andamans, Bengal, China, and Japan; *Spilopelia tigrina* (Temminck and Knip), Palawan, also Burma, Sunda Islands, Celebes, and the Moluccas; *Geopelia striata* (Linnæus), also the Malay Peninsula, Sunda Islands, Celebes, and Amboina; *Chalcophaps indica* (Linnæus), also Ceylon, the Malay Peninsula, Celebes, and New

Guinea; *Calœnas nicobarica* (Linnæus), also the Nicobars, Greater Sunda Islands, New Guinea, and Bismarck Archipelago.

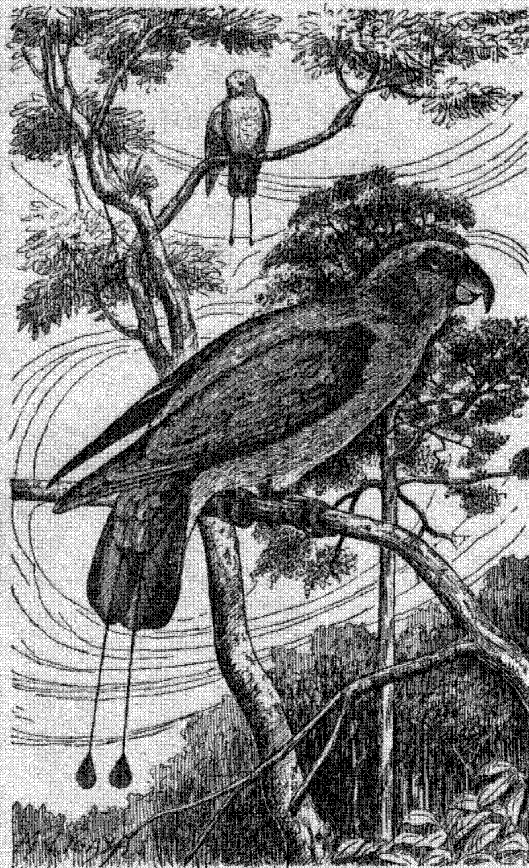


FIG. 34. Philippine racket-tailed parakeet, *Prioniturus discurus* (Vieillot), the commonest species of its genus. The genus is confined to the Philippines and Celebes.

east, but neither is known in the Australian Region; *Amaurornis olivacea* (Meyen) is endemic, and *A. phœnicura* (Forster) ranges from India to Celebes; *Gallinula chloropus* (Linnæus) is of wide distribution; *Gallicrex cinerea* (Latham) is an Oriental species; *Porphyrio pulverulentus* Temminck is endemic; *Fulica atra* Linnæus is of wide distribution.

Podicipedidæ.—The grebes include a few small genera of wide distribution. *Tachybaptus philippinensis* (Bonnaterre), the only Philippine species, is found also in Formosa, Burma, and Borneo.

Rallidæ.—The rails and their allies are represented in each of the six regions of the world, and many of the species are migratory or of wide distribution. *Hypotaenidia* contains three Philippine species, of which *H. torquata* (Linnæus) is endemic; *Rallina* has two Philippine species, of which *R. euryzonoides* (Lafresne) is endemic; *Porzana* has two Philippine species; *Poliolimnas ocularis* Ingram is endemic; *Limnobænus* has two Philippine species, both of which range north and north-

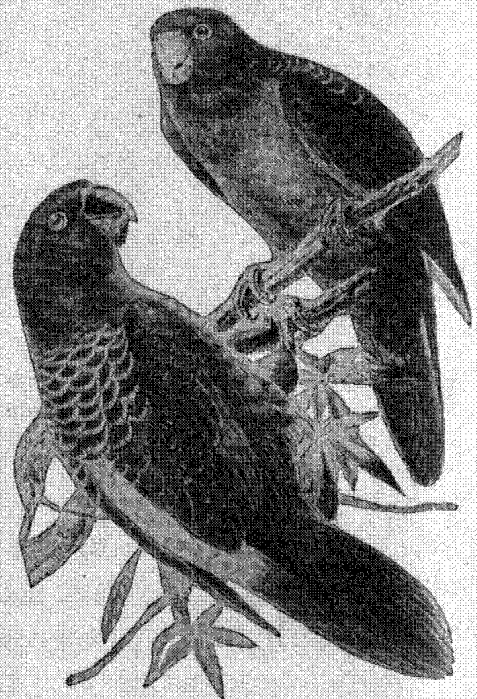


FIG. 35. Blue-backed parrot, *Tanygnathus everetti* Tweeddale, one of the largest Philippine parrots.

Procellariidæ.—The petrels are pelagic birds of wide range. The only Philippine specimen representing this family appears to be an *Oceanodroma*, of which the species has not been determined.

Puffinidæ.—The shearwaters are pelagic birds of wide range. Two species of *Puffinus* have been collected in the Philippines.

Laridæ.—Gulls and terns occur in all of the zoögeographic regions, but are poorly represented in the Philippines.

Charadriidæ.—The family of



FIG. 36. Intermediate guaiabero, *Bolbopsittacus intermedius* Salvadori, the Samar-Leyte representative of its genus.

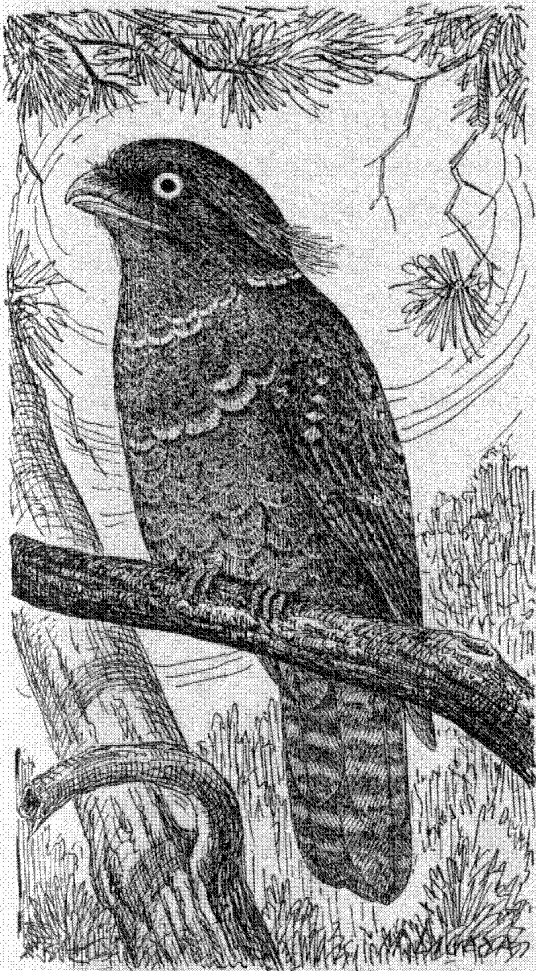


FIG. 37. Small-billed frogmouth, *Batrachostomus microrhynchus* Grant, a Luzon representative of an obscure family of the Australian and Oriental Regions.

plovers, snipes, sandpipers, and similar birds is represented in all countries, and there is a fairly large number of genera and species in the Philippines. Most of the species are migratory, and none is endemic to the Philippines.

Parridæ.—The jacanas are represented in the Philippines by two species; one is an Oriental species, the other is found in Australia, Celebes, and Borneo. The family is unknown in the Nearctic and Palæarctic Regions.

Glareolidæ.—The one Philippine species of swallow plover is migratory. The family is unknown in the Neotropical and Nearctic Regions.

Enicnemidæ.—The one Philippine stone plover ranges to Australia, Borneo, and India. The family is represented in all the regions except the Nearctic.

Gruidæ.—The one Philippine crane is probably an Indian species. The family is represented in all the regions except the Neotropical.



FIG. 38. Luzon calao, *Hydrocorax hydrocorax* (Linnæus), a large hornbill that is confined to Luzon and Marinduque.

ons and bitterns include about twenty species in fourteen genera. Few of the species are endemic, and the family is cosmopolitan.

Anatidæ.—There are twelve species of Philippine ducks in nine genera. The Luzon mallard, *Anas luzonica* Fraser, is endemic. The family is cosmopolitan.

Phalacrocoracidæ.—There is one common and nearly cosmopolitan cormorant; it is rare in the Philippines. The family is represented along the shores of all oceans.

Ibididæ.—The only Philippine ibis is a common species of wide distribution. The family is represented in each of the zoögeographic regions.

Plataleidæ.—The only Philippine spoonbill is probably a migrant from China and Japan. The family is represented in each of the regions of the world.

Ciconiidæ.—The only Philippine stork is a species of wide distribution. The family is small and is represented in each of the regions of the world.

Ardeidæ.—The Philippine her-

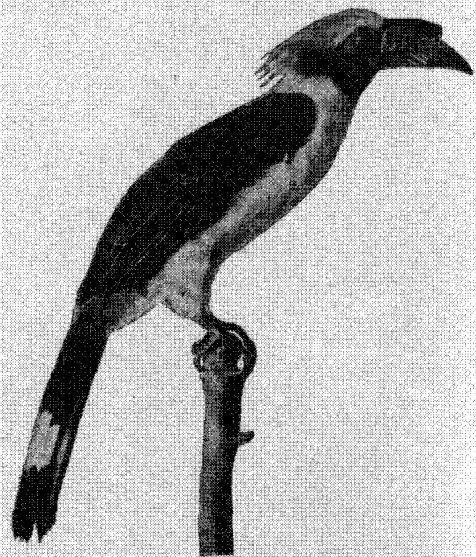


FIG. 39. Luzon tarictic, *Penelopides manillæ* (Boddaert), a small hornbill that is confined to the Luzon group of islands.

Plotidæ.—The one Philippine darter is an Oriental species that ranges to Celebes. The family consists of a single genus of four species and is represented in all zoögeographic regions.

Sulidæ.—Two or three species of gannets are found in Philippine waters. The family is cosmopolitan and includes one genus of a dozen species.

Fregatidæ.—Two or more species of man-of-war birds are found in Philippine waters. The one genus of this family is represented in all tropical and subtropical oceans.

Pelecanidæ.—The only Philippine pelican is an Oriental species. The one genus of this family is cosmopolitan.

Falconidæ.—The Philippine falcons, hawks, and eagles include thirty species representing thirteen genera. Some are of wide range, a few are migratory, and others are endemic. The family is cosmopolitan. *Lopho-*

triorchis kieneri (Geoffroy) is an Oriental species, also in Celebes; *Spizaetus philippinensis* Gurney is endemic and *S. limnaetus* (Horsfield) is Oriental; *Pithecophaga jefferyi* Grant, one of the largest eagles known, is endemic; *Spilornis* is represented by two endemic species; *Butastur indicus* (Gmelin) is migratory; *Cuncuma* (formerly called *Haliaeetus*) *leucogaster* (Gmelin) ranges from India to Australia; *Haliastur intermedius* Gurney is Oriental, also in Celebes; *Elanus hypoleucus* Gould is found in the Philippines, the Greater Sunda Islands, and Celebes; *Pernis ptilonorhynchus* (Temminck) is Oriental; *Baza magnirostris* Gray and *B. leucopais* Sharpe are endemic; *Microhierax* is an Oriental genus, and the two Philippine species are endemic; two or three species of *Falco* are Philippine; *Ichthyophaga* (formerly called *Polioaetus*) *ichthyætus* (Horsfield) is Oriental, also in Celebes.

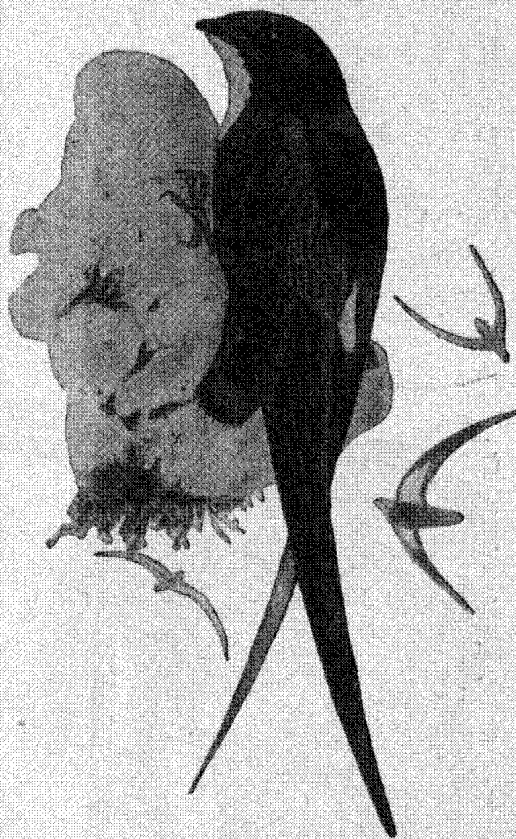


FIG. 40. Tweeddale's spine-tailed swift, *Chatura picina* Tweeddale, a rare endemic species.

Bubonidæ.—Most of the Philippine owls are endemic. *Pseudoptynx* is an endemic genus of three species; the large and

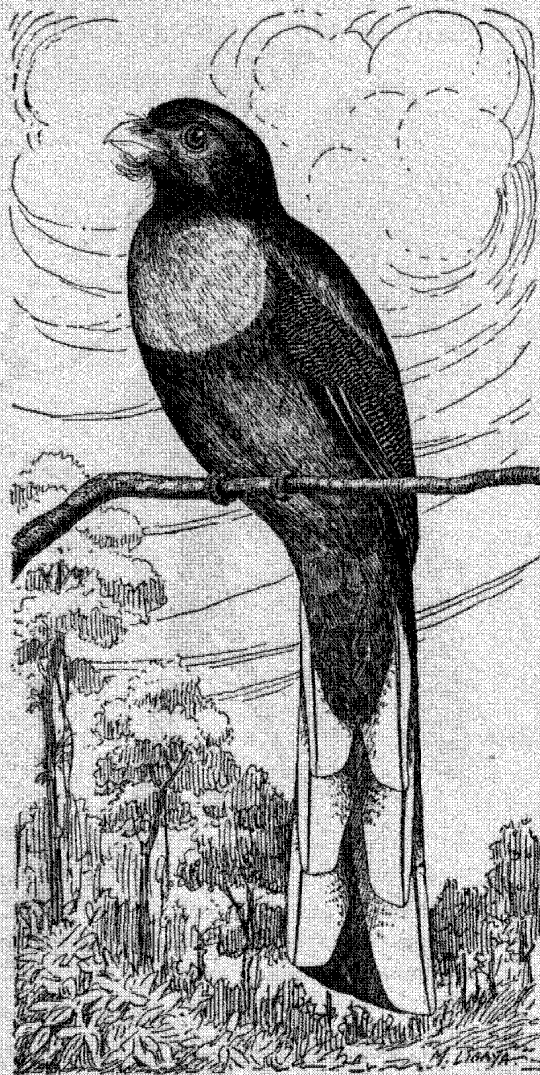


FIG. 41. Philippine trogon, *Pyrotrogon ardens* (Temminck), a brilliant forest-inhabiting species.

widespread genus *Otus* contains ten endemic Philippine species. *Ninox* contains seven endemic Philippine species; *Ninox japonica* (Temminck and Schlegel) is probably migratory from the north; *Strix* includes one species that is confined to Palawan; *Phodilus*, an Oriental genus, is represented by one endemic species.

Tytonidæ.—The only genus in this family includes about thirty species of barn owls and grass owls; one species is Philippine.

Loriidæ.—The lorries include about fifteen genera and are characteristic of the Australian Region; one endemic species inhabits Mindanao.

Cacatoidæ.—The cockatoos include seven genera and about thirty species. They are confined to the Australian Region, except one endemic Philippine species.

Psittacidæ.—The family of parrots, macaws, and parrakeets, with about sixty genera, is represented in nearly all tropical and subtropical regions. The four Philippine genera have developed numerous endemic species. *Prioniturus* includes eight Philippine and three Celebesian species (Plate 26); *Tanygnathus* is represented in Celebes, the Philippines, the Moluccas, and Borneo; *Bolbopsittacus* contains but three species, all endemic Philippine; *Loriculus* contains about forty-five species, one-third of which are Philippine, the other species are either Indo-Malayan or Austro-Malayan.

Podargidæ.—The family Podargidæ includes three genera of birds known as frogmouths, which are somewhat like rollers

and somewhat like nightjars. The species of *Podargus* and of *Aegotheles* are confined to the Australian Region. *Batrachostomus* contains twelve species, which are confined to the Oriental Region; three of the species are endemic to the Philippines.

Coraciidæ.—Four genera of the roller family are confined to Madagascar. The other genera, *Coracias* and *Eurystomus*, are represented in the African, Oriental, and Australian Regions. The only Philippine species, *Eurystomus orientalis* (Linnæus), is Indo-Malayan.

Alcedinidæ.—The kingfishers comprise about twenty genera and are known in most parts of the world. However, the species are most numerous in the Oriental and Australian Regions. *Pelargopsis* has ten species in the Oriental Region (two of these are confined to the Philippines) and three species in Sula and Celebes; *Ceyx* is Oriental and Australian, and several of the species are endemic to the Philippines; *Halcyon* includes seventy species of the African, Oriental, and Australian Regions, and three of these are endemic to the Philippines.

Bucerotidæ.—The hornbills (Plate 25) include about twenty genera and are characteristic African and Oriental birds; a few species are restricted to the Austro-Malayan Subregion. *Hydrocorax*, three species; *Penelopides*, seven species; and *Gymnolæmus*, one species, are endemic Philippine genera.

Meropidæ.—The species of the Meropidæ are most numerous in the African Region, moderately numerous in the Oriental Region, and scarce in the Australian Region. There are two Philippine species, one of which is endemic.

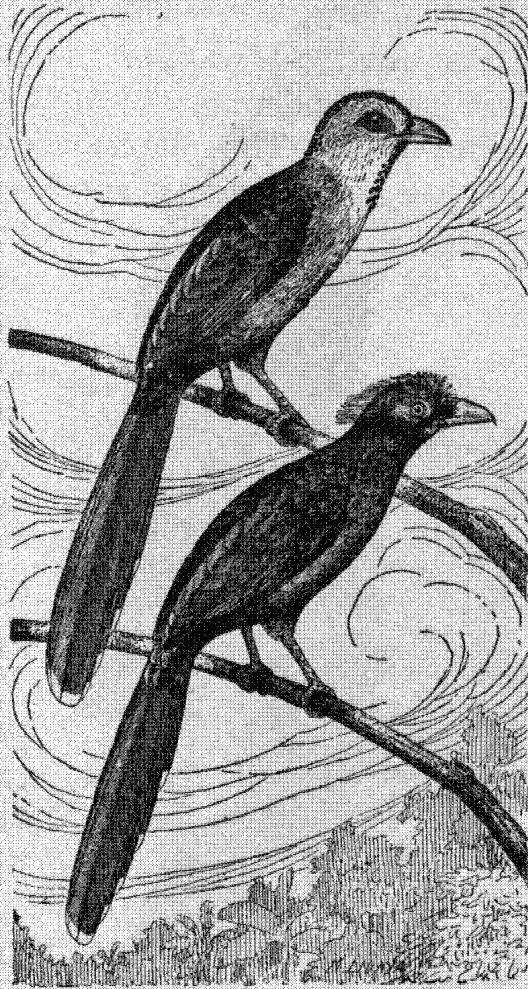


FIG. 42. Scale-feathered cuckoo, *Lepidogrammus cumingi* (Fraser), upper figure; rough-crested cuckoo, *Dasylophus superciliosus* (Cuvier), lower figure. These are among the most curious endemic Philippine birds; they are found only in the Luzon area.

Caprimulgidæ.—The goatsuckers, or nightjars, are represented in all parts of the world. *Lyncornis* is Oriental and Austro-Malayan; one of the species is restricted to the Philippines. *Caprimulgus*, with about seventy species, is represented in most regions of the world; two species are confined to the Philippines.

Macropterygidæ.—The seven species of tree swifts are Oriental and Austro-Malayan. There are two Philippine species, one of which is endemic.

Cypselidæ.—The swifts are nearly cosmopolitan. *Collocalia* includes about twenty species; some of these build the edible

nests of commerce, and several are confined to the Philippines. *Chætura* includes the spine-tailed swifts; three or four are Philippine, and one or two are endemic. One species of *Tachornis* is endemic to the Philippines. Two of the twenty-five species of *Cypselus* are found in the Philippines as migrants.

Trogonidæ.—The trogons are pantropic. *Pyrotrogon*, an Oriental genus of about fifteen species, is represented in the Philippines by one endemic species.

Cuculidæ.—Cuckoos are found in nearly all countries. The genera and the species are numerous in the Oriental Region. There are about twenty-five Philippine species in twelve genera, and they are either Indo-Malayan or endemic.

Capitonidæ.—The barbets are most numerous in Africa, two genera are confined to tropical America, and about eight genera are restricted to the Oriental Region. None is known from Australia. There are two Philippine species; one of these is endemic.

Picidæ.—The woodpeckers include about fifty genera and are nearly cosmopolitan, but the family is not represented in Australia. In the Philippines *Yungipicus* is represented by four endemic species; *Tiga*, by one endemic species in Palawan; *Chrysocolaptes*, by five endemic species; *Thriponax*, by four or five endemic species and one that ranges to the Malay Peninsula;

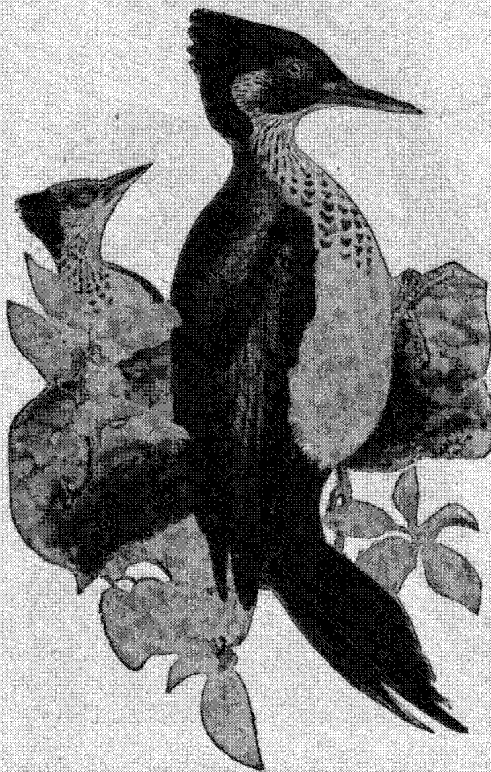


FIG. 43. Tweeddale's black woodpecker, *Thriponax pectoralis* Tweeddale, the Samar-Leyte representative of its genus.

Mulleripicus pulverulentus (Temminck), an Indian, Sumatran, and Bornean species, is found in Palawan. *Lichtensteinipicus* includes only four species; two of these are restricted to Celebes, and two are restricted to the Philippines.

Eurylæmidæ.—All the species of broadbills are restricted to the Oriental Region. There are seven genera; one genus, with two species, is restricted to the eastern Philippines.

Pittidæ.—The pittas, or ant thrushes, are confined to the Australian and Oriental Regions, and are most numerous in species in the Austro-Malayan and Indo-Malayan Subregions. There are five genera. *Pitta*, the only large genus, includes over fifty species; seven Philippine species are endemic and one is migratory.

Hirundinidæ.—The swallows are nearly cosmopolitan in distribution. Three genera and seven species are found in the Philippines.

Muscicapidæ.—The flycatchers include nearly one hundred genera and are widely distributed. About fifteen genera are represented in the Philippines. A few of the Philippine species are migratory; for example, *Xanthopygia narcissina* (Temminck), *Alseonax latirostris* (Raffles), *Cyanoptila bella* (A. Hay), and *Hemichelidon griseosticta* Swinhoe; most of them are endemic. *Cyornis*, with about thirty-five species, is nearly restricted to the Oriental Region; a few of the species are endemic to Formosa or to Celebes; three or four are endemic to the Philippines. *Muscicapula* is an Oriental genus only two species of which reach Celebes; there are four endemic Philippine species. *Gerygone* is well represented in the Australian Region; at least one species is restricted to the Philippines, one to Borneo, and one to Sumatra and the Malay Peninsula. *Hypothymis* is about equally Oriental and Austro-Malayan; there are two endemic Philippine species. *Cyanomyias* and *Camiguinia* are monotypic endemic genera. *Rhipidura*, with about one hundred species, is more Australian, especially Austro-Malayan,



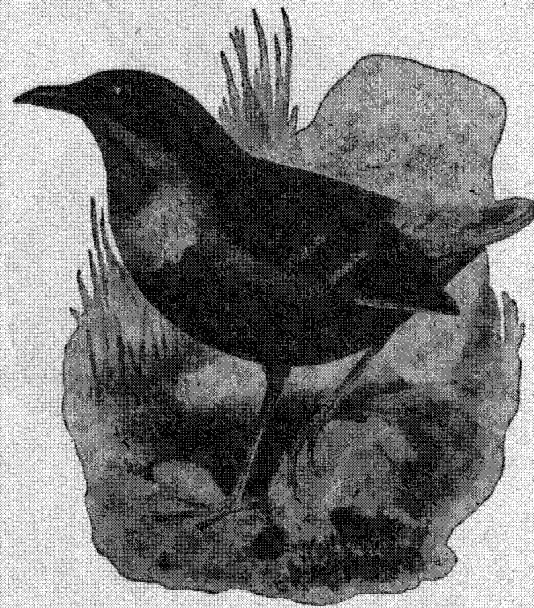
FIG. 44. Steere's broadbill, *Sarcophanops steeri* Sharpe, one of the two Philippine species of its genus, family, and order. The order is restricted to the Oriental Region.

than Oriental; there are about eight endemic Philippine species. *Xeocephus* has one species in Talaut and three in the Philippines; this genus and *Callaeops* are doubtfully distinct from *Terpsiphone*; *Callaeops*, if valid, is endemic Philippine and monotypic; *Terpsiphone affinis* (Blyth), as a Philippine species, is migratory or accidental. *Rhinomyias* is almost purely Oriental; five species are confined to the Philippines. *Culicicapa* is Oriental and Austro-Malayan; two of the three species are Philippine. *Cryptolopha* is African, Oriental, and Australian; four of the species are confined to the Philippines. *Eumyias* is strongly Oriental,

but two species are restricted to Celebes; two or three are restricted to the Philippines.

Campophagidæ.—The species of the Campophagidæ are almost all African, Oriental, or Australian. *Artamides*, which has thirty-five species, is about equally Indo-Malayan and Austro-Malayan; seven species are confined to the Philippines. *Malindangia* is a monotypic endemic genus. *Edolisoma*, with about thirty-five species, is almost purely Austro-Malayan; one species is Australian, six are endemic Philippine. *Pericrocotus*, with about thirty species, is purely Oriental; one Philippine species is a winter visitant and three are endemic. *Lalage* is Oriental and Australian; two of the Philippine species are endemic, and the third extends to Borneo, Java, and the Malay Peninsula.

FIG. 45. Koch's pitta, *Pitta kochi* Brüggemann, a large ground thrush of the highlands of northern Luzon.



Pycnonotidæ.—The bulbul family contains about thirty-five genera, equally divided between the Oriental and the Ethiopian Region. Nine genera are represented in the Philippines.

Timeliidæ.—Over one hundred twenty genera have been included in the Timeliidæ. Nearly all of them are either Ethiopian or Oriental; a few genera are restricted to the Australian Region. Ten genera are represented in the Philippines, and five or six of these are endemic.

Turdidæ.—The thrush family is almost cosmopolitan. Most of the Philippine species are of wide distribution in the Oriental

Region. *Chaimarrornis* has one species in the Himalayas and China and one in Luzon; *Copsychus mindanensis* (Gmelin) is endemic; *Kittacincla* is an Oriental genus with five endemic Philippine species; *Pratincola caprata* (Linnæus) is Philippine, Bornean, Javan, and Indian.

Sylviidæ.—The family Sylviidæ is almost cosmopolitan. *Trichura*, almost purely Oriental, has one endemic species in Luzon.

Artamidæ.—The swallow shrikes include only *Artamus*, with twenty species about equally Oriental and Australian, and *Pseudochelidon*, a monotypic African genus.

Laniidæ.—The shrikes are found in the Eastern Hemisphere and North America. There are seven Philippine species in three genera. *Cephalophoneus validirostris* (Grant) is an endemic species in an almost purely Indo-Malayan genus; *C. nasutus* (Scopoli) is Philippine and Bornean. *Enneoctonus tigrinus* (Drapiez) is an Oriental species; it occurs in Sulu—no member of this genus is found in the Australian Region. The subfamily Pachycephalinæ is characteristic of the Australian and Oriental Regions; the species are numerous in Austro-Malaya and Polynesia. *Hyloterpe*, the only Philippine genus of this subfamily, has two species in Celebes, three in Sumatra, one in Borneo, and six or seven endemic to the Philippines.

Paridæ.—The titmice are nearly cosmopolitan. *Pardaliparus* has two species in China and four or five endemic to the Philippines. *Penthornis* is an endemic Philippine genus of two species.

Sittidæ.—The nuthatches are found in the Palæarctic, Nearctic, Oriental, and Australian Regions and in Madagascar. The nine species of *Callisitta* are confined to the Oriental Region, and four of them are confined to the Philippines.

Certhiidæ.—The creepers are found in the Palæarctic, Nearctic, and Australian Regions. *Rhabdornis*, with four species, is confined to the Philippines.



FIG. 46. Tweeddale's fairy bluebird, *Irena tweeddalei* Sharpe, the Palawan representative of an Oriental genus.

Zosteropidæ.—The silvereyes are found in the Ethiopian, Oriental, and Australian Regions. *Zosterops*, with about one hundred sixty species, is found in all of these regions and has about fifteen endemic Philippine species; *Hypocriptadius*, monotypic, is endemic.

Dicæidæ.—The flowerpeckers are found in the Ethiopian, Oriental, and Australian Regions. *Dicæum*, with about seventy-five species, is found in the Oriental and Australian Regions; twenty-three are endemic Philippine. The Philippine species of *Prionochilus* and *Piprisoma* are endemic.

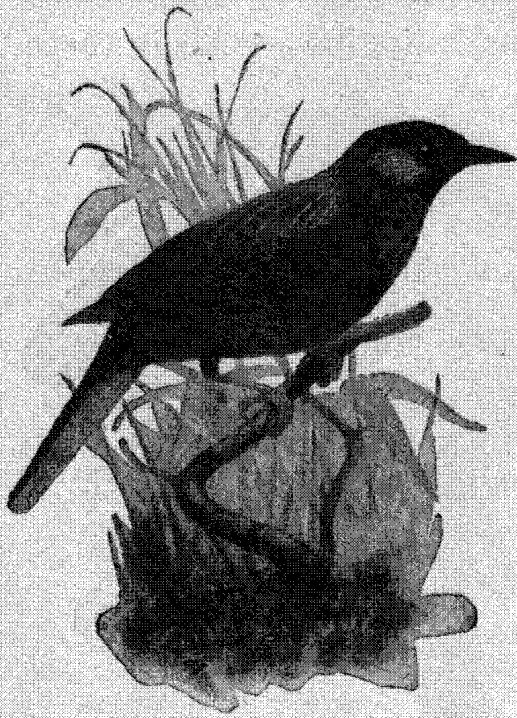


FIG. 47. Beautiful roughtemple, *Dasyrotapha speciosa* Tweeddale, the only species of its genus; confined to Negros.

Nectariniidæ.—The sunbirds are found in the Ethiopian, Oriental, and Australian Regions. *Chalcostetha calcostetha* (Jardine), monotypic, is found in the Indo-Chinese and Indo-Malayan Subregions and in Celebes. One species of *Æthopyga* is found in Celebes; the rest, about twenty-seven species, are distributed locally in various parts of the Oriental Region; the eight Philippine species are endemic. *Eudrepanis* includes but four species; one is restricted to Sangi, three are endemic Philippine. *Leptocoma* has one species in Celebes; the other species are

Oriental and three of them are endemic Philippine. *Cyrtostomus* is Oriental and Australian; five species are endemic Philippine. The Philippine species of *Leptocoma* and *Cyrtostomus* are much alike, except in colors, and were formerly included in *Cinnyris*; the last-named genus, as restricted, is African. *Anthreptes* is Ethiopian, Oriental, and Australian; three of the six Philippine species are endemic; the other three are Oriental.*

Motacillidæ.—The wagtails are cosmopolitan. The nine Philippine species are winter visitants from the north.

* A misstatement, that there are hummingbirds in the Philippines, appears in at least one book on the Islands. Probably sunbirds were mistaken for hummingbirds, although the two families are not closely related. The following statement is more surprising: "It is a curious fact that these Islands have no singing birds."—R. C. MCGREGOR.

Alaudidæ.—The larks are found in all regions except the Neotropical; only two species are Philippine. *Alauda wattersi* Swinhoe is found in Cochinchina and Formosa; I have given the same name to the Philippine skylark, but it may be different. *Mirafra philippinensis* W. Ramsay is endemic.

Fringillidæ.—Members of the sparrow family are found in all regions except the Australian. *Loxia luzoniensis* Grant, an endemic species in the pine region of Luzon, is closely related to a Himalayan species. Two species of *Pyrrhula*, endemic to the Philippines, are the most southern of this genus. *Passer montanus* (Linnæus), as a Philippine species, is probably introduced. The other Philippine sparrows are winter visitors from the north.

Ploceidæ.—The weaver finches are found in the Ethiopian, Oriental, and Australian Regions. This family contains seventy-five genera, and four of these are represented in the Philippines. *Padda orizivora* (Linnæus) is found in Java, Sumatra, and the Philippines; three species of *Munia* are endemic; *Munia* (formerly *Uroloncha*) *fuscans* (Cassin) is found in Borneo and on Cagayan Sulu; *Reichenowia* has one species in Java, one in Borneo, and one in the Philippines.

Sturnidæ.—Four species of starlings are winter visitants to the Philippines, and one has been introduced.

Eulabetidæ.—*Sarcops* is an endemic genus of two species; *Eulabes* is an Oriental genus represented in the Philippines by one species, which is restricted to Palawan; *Goodfellowia* is endemic and monotypic; *Lamprocorax*, of the Australian and Oriental Regions, has two endemic Philippine species.

Oriolidæ.—The oriole family is found in the Eastern Hemisphere. The Philippine species are endemic except *Oriolus xanthonotus* Horsfield, which is found in Palawan, Java, Sumatra, and the Malay Peninsula. The orioles of America belong to another family.



FIG. 48. Steere's oriole, *Oriolus steeri* Sharpe, is one of several small orioles having the same general color pattern.

Dicruridæ.—The drongos are found in the Ethiopian, Oriental, and Australian Regions. *Dicrurus* has four endemic Philippine species and does not extend to the Australian Region. *Dicruopsis* is Oriental and Australian; it has three endemic Philippine species and one Bornean-Philippine species.

Corvidæ.—The crow family is cosmopolitan and is represented in the Philippines by three endemic species of *Corvus*.

Twenty-five of the Philippine families of birds are nearly cosmopolitan, being represented in each of the six zoögeographic regions of the earth; twelve families are represented in four of the regions, but in neither the Neotropical nor the Nearctic. The Podargidæ are about equally Australian and Oriental, but are known from no other region. Three Philippine families are almost exclusively Australian: namely, Megapodidæ, one Philippine species and two or three others beyond the Philippines; Loridae, all species Australian except one in Mindanao; Caca-toidæ, all species Australian except one in the Philippines. The Eurylæmidæ are Indo-Chinese and Indo-Malayan only, with two Philippine species. The following Philippine families are strongly Oriental and extend to other regions but are poorly if at all represented in Australia: Trogonidæ, Neotropical and Ethiopian; Capitonidæ, Ethiopian; Fringillidæ, all regions except the Australian; Picidæ, all regions, but very weak in the Australian—*Yungipicus* in Celebes and Flores and *Mulleripicus* in Celebes. Thus the Megapodidæ, the Loridae, and the Caca-toidæ, each with one Philippine species, indicate an Australian alliance of the Philippine avifauna. The Eurylæmidæ, with two species; the Trogonidæ, with one species; the Capitonidæ, with two species; the Fringillidæ, with three species; and the Picidæ, with twenty species (including neither the Palawan nor the migratory species of any of these families), indicate a stronger Oriental alliance.

GENERA OF PHILIPPINE BIRDS

In order to get data for judging the relation of the Philippine ornithology to that of the rest of the Oriental Region and to that of the Australian Region I have constructed Table 8, which consists of an enumeration of the genera of Philippine birds, the number of Philippine species in each genus, and the alliance of each genus. For example, *Megapodius* is represented by one species in the Philippines and Borneo, one in the Nicobars, and one in the Mariannes; therefore, a plus sign appears in the last column, but as about fifteen species of *Megapodius* and six other genera

of the family are Australian there are two plus signs in the third column. *Gallus* has one plus under Australian and two under Oriental, because the genus is barely Austro-Malayan and strongly Oriental. The alliance of *Excalfactoria* is about equal with the two regions. If a genus contains only endemic Philippine species, there is a minus sign in each of the last two columns. Because many of the species are migratory the data for the shore birds, the water birds, and some of the hawks and owls are of no use and are not considered; but they are included in the table for the sake of retaining all the generic names.

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Megapodius</i>	1	++	+
<i>Excalfactoria</i>	1	+	+
<i>Gallus</i>	1	+	++
<i>Polyplectron</i>	1	—	++
<i>Turnix</i>	6	+	+
<i>Treron</i>	1	—	++
<i>Sphenocercus</i>	1	—	++
<i>Dendrophassa</i>	3	+	++
<i>Phapitreron</i>	10	—	—
<i>Leucotreron</i>	4	++	+
<i>Lamprotreron</i>	1	++	—
<i>Hæmatæna</i>	1	++	—
<i>Muscadivores</i>	3	++	+
<i>Ptilocolpa</i>	3	—	—
<i>Zonophaps</i>	2	++	—
<i>Myristicivora</i>	1	++	+
<i>Columba</i>	1	+	+
<i>Macropygia</i>	2	+	+
<i>Streptopelia</i>	1	+	++
<i>Ænopoelia</i>	1	—	++
<i>Spilopelia</i>	1	+	++
<i>Geopelia</i>	1	+	+
<i>Chalcophaps</i>	1	+	+
<i>Gallicolumba</i>	5	++	—
<i>Calænas</i>	1	+	+
<i>Hypotænidia</i>	3	+	+
<i>Rallina</i>	2	+	+
<i>Porzana</i>	2	+	+
<i>Poliolimnos</i>	1	+	+
<i>Limnobænus</i>	2	—	++
<i>Amaurornis</i>	1	+	+
<i>Gallinula</i>	1	+	+

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Gallicrex</i>	1	—	++
<i>Porphyrio</i>	1	+	+
<i>Fulica</i>	1	+	+
<i>Tachybaptus</i>	1	+	+
<i>Oceanodroma</i>	1	—	++
<i>Puffinus</i>	2	+	+
<i>Hydrochelidon</i>	2	+	+
<i>Sterna</i>	8	+	+
<i>Anous</i>	1	+	+
<i>Micranous</i>	1	+	+
<i>Larus</i>	2	+	+
<i>Arenaria</i>	1	+	+
<i>Microsarcops</i>	1	—	++
<i>Squatarola</i>	1	+	+
<i>Pluvialis</i>	1	+	+
<i>Charadrius</i>	6	+	+
<i>Himantopus</i>	1	+	+
<i>Numenius</i>	3	+	+
<i>Mesoscolopax</i>	1	+	+
<i>Limosa</i>	2	+	+
<i>Totanus</i>	2	+	+
<i>Helodromas</i>	1	—	++
<i>Heteroscelus</i>	1	+	+
<i>Actitis</i>	1	+	+
<i>Terekia</i>	1	+	+
<i>Glottis</i>	1	+	+
<i>Rhyacophilus</i>	1	+	+
<i>Crocethia</i>	1	+	+
<i>Pisobia</i>	4	+	+
<i>Heteropygia</i>	1	+	+
<i>Erolia</i>	1	+	+
<i>Tringa</i>	2	+	+
<i>Limicola</i>	1	+	+
<i>Gallinago</i>	3	+	+
<i>Rostratula</i>	1	+	+
<i>Lobipes</i>	1	(?)	++
<i>Hydrophasianus</i>	1	—	++
<i>Hydralector</i>	1	++	+
<i>Glareola</i>	1	+	+
<i>Orthorhamphus</i>	1	+	+
<i>Mathewsena</i>	1	+	+
<i>Plegadis</i>	1	+	+
<i>Platalea</i>	1	—	++
<i>Dissūura</i>	1	+	++
<i>Pyrrotherodia</i>	1	+	+
<i>Ardea</i>	1	+	+
<i>Typhon</i>	1	+	+

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Mesophoyx</i>	1	+	+
<i>Herodias</i>	1	+	+
<i>Egretta</i>	1	+	+
<i>Demigretta</i>	1	+	+
<i>Nycticorax</i>	2	+	+
<i>Gorsachius</i>	2	—	++
<i>Butorides</i>	3	+	++
<i>Bubulcus</i>	1	+	+
<i>Ixobrychus</i>	2	+	+
<i>Nannocnus</i>	1	+	+
<i>Dupetor</i>	1	+	+
<i>Botaurus</i>	1	+	+
<i>Nettapus</i>	1	+	+
<i>Dendrocygna</i>	2	+	+
<i>Anas</i>	1	+	+
<i>Polionetta</i>	1	—	++
<i>Mareca</i>	1	—	++
<i>Nettion</i>	1	+	+
<i>Dafila</i>	1	+	+
<i>Querquedula</i>	1	+	+
<i>Spatula</i>	1	+	+
<i>Marila</i>	2	—	++
<i>Phalacrocorax</i>	1	+	+
<i>Anhinga</i>	1	+	+
<i>Sula</i>	2	+	+
<i>Fregata</i>	2	+	+
<i>Pelecanus</i>	1	+	+
<i>Circus</i>	3	+	+
<i>Astur</i>	2	+	+
<i>Accipiter</i>	3	+	+
<i>Lophotriorchis</i>	1	+	+
<i>Spizaetus</i>	2	+	+
<i>Pithecophaga</i>	1	—	—
<i>Spilornis</i>	3	+	++
<i>Butastur</i>	1	+	+
<i>Cuncuma</i>	1	+	+
<i>Haliastur</i>	1	+	+
<i>Elanus</i>	1	++	+
<i>Pernis</i>	1	+	++
<i>Baza</i>	2	+	+
<i>Microhierax</i>	2	—	++
<i>Falco</i>	4	+	+
<i>Cerchneis</i>	1	+	+
<i>Pandion</i>	2	+	+
<i>Ichthyophaga</i>	1	+	+
<i>Pseudoptynx</i>	3	—	—
<i>Otus</i>	12	+	+

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Ninox</i>	10	+	+
<i>Strix</i>	1	—	++
<i>Tyto</i>	1	+	+
<i>Phodilus</i>	1	—	++
<i>Trichoglossus</i>	1	++	—
<i>Cacatoes</i>	1	++	—
<i>Prioniturus</i>	8	++	—
<i>Tanygnathus</i>	5	++	+
<i>Bolbopsittacus</i>	3	—	—
<i>Loriculus</i>	11	+	+
<i>Batrachostomus</i>	5	—	++
<i>Eurystomus</i>	1	+	+
<i>Pelargopsis</i>	3	+	+
<i>Alcedo</i>	2	+	+
<i>Ceyx</i>	10	+	+
<i>Halcyon</i>	8	+	+
<i>Hydrocorax</i>	3	—	—
<i>Anthracoceros</i>	1	—	++
<i>Gymnolæmus</i>	1	—	—
<i>Penelopides</i>	7	—	—
<i>Craniorrhinus</i>	2	+	+
<i>Merops</i>	2	+	+
<i>Lyncornis</i>	1	+	+
<i>Caprimulgus</i>	5	+	+
<i>Hemiprocne</i>	2	+	+
<i>Collocalia</i>	8	+	+
<i>Chætura</i>	4	+	+
<i>Tachornis</i>	1	—	++
<i>Micropus</i>	2	+	++
<i>Pyrotrogon</i>	1	—	++
<i>Clamator</i>	1	+	+
<i>Surniculus</i>	1	+	+
<i>Hierococcyx</i>	2	+	+
<i>Cuculus</i>	3	+	+
<i>Penthoceryx</i>	1	—	++
<i>Cacomantis</i>	1	+	+
<i>Chalcococcyx</i>	2	+	+
<i>Eudynamys</i>	3	+	+
<i>Centropus</i>	8	+	+
<i>Dryococcyx</i>	1	—	—
<i>Dasylophus</i>	1	—	—
<i>Lepidogrammus</i>	1	—	—
<i>Xantholæma</i>	2	—	++
<i>Yungipicus</i>	6	+	++
<i>Tiga</i>	1	—	++
<i>Chrysocolaptes</i>	6	—	++
<i>Lichtensteinipicus</i>	2	++	—

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Mulleripicus</i>	1	—	++
<i>Thriponax</i>	6	—	++
<i>Sarcophanops</i>	2	—	—
<i>Pitta</i>	8	+	+
<i>Chelidonaria</i>	1	—	+
<i>Riparia</i>	2	—	+
<i>Hirundo</i>	4	+	+
<i>Hemichelidon</i>	3	+	++
<i>Alseonax</i>	1	—	+
<i>Cyornis</i>	5	+	++
<i>Muscicapula</i>	6	+	++
<i>Gerygone</i>	2	++	+
<i>Zanthopygia</i>	1	—	+
<i>Cyanoptila</i>	1	—	+
<i>Hypothymis</i>	1	+	+
<i>Camiguinia</i>	1	—	—
<i>Cyanomyias</i>	1	—	—
<i>Rhipidura</i>	8	+	+
<i>Xeocephus</i>	3	+	++
<i>Terpsiphone</i>	2	+	++
<i>Rhinomyias</i>	5	+	++
<i>Culicicapa</i>	2	+	+
<i>Cryptolopha</i>	5	+	++
<i>Eumyias</i>	3	+	++
<i>Artamides</i>	7	+	+
<i>Malindangia</i>	1	—	—
<i>Edolisoma</i>	7	++	—
<i>Pericrocotus</i>	6	—	++
<i>Lalage</i>	3	+	+
<i>Ægithina</i>	1	—	++
<i>Chloropsis</i>	2	—	++
<i>Irena</i>	4	—	++
<i>Hypsipetes</i>	3	—	++
<i>Iole</i>	10	—	++
<i>Poliolophus</i>	1	—	+
<i>Microtarsus</i>	1	—	++
<i>Trichophorus</i>	2	+	+
<i>Pycnonotus</i>	3	—	++
<i>Pseudotharrhaleus</i>	4	—	—
<i>Turdinus</i>	1	+	+
<i>Ptilocichla</i>	4	—	—
<i>Anuropsis</i>	1	—	++
<i>Dasycrotapha</i>	1	—	—
<i>Zosterornis</i>	8	—	—
<i>Mixornis</i>	2	—	++
<i>Macroncus</i>	4	—	++
<i>Leonardina</i>	1	—	—

TABLE 8.—The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Brachypteryx</i>	4	—	++
<i>Planesticus</i>	6	+	+
<i>Turdus</i>	3	—	++
<i>Geokichla</i>	3	+	+
<i>Zoothera</i>	1	+	++
<i>Oreocincla</i>	1	+	+
<i>Petrophila</i>	1	—	++
<i>Chaimarrornis</i>	1	—	++
<i>Calliope</i>	1	—	++
<i>Copsychus</i>	1	—	++
<i>Kittacincla</i>	5	—	++
<i>Pratincola</i>	1	—	++
<i>Saxicola</i>	1	—	++
<i>Locustella</i>	3	—	++
<i>Acrocephalus</i>	2	+	++
<i>Tribura</i>	1	—	++
<i>Orthotomus</i>	10	+	++
<i>Cisticola</i>	2	+	+
<i>Megalurus</i>	2	+	+
<i>Acanthopneuste</i>	3	+	++
<i>Horornis</i>	3	+	++
<i>Phyllergates</i>	2	+	+
<i>Artamus</i>	1	++	+
<i>Enneoctonus</i>	1	—	++
<i>Cephalophoneus</i>	3	+	++
<i>Otomela</i>	3	+	++
<i>Hyloterpe</i>	8	+	+
<i>Pardaliparus</i>	5	—	++
<i>Penthornis</i>	2	—	—
<i>Callisitta</i>	4	+	++
<i>Rhabdornis</i>	4	—	—
<i>Zosterops</i>	16	+	+
<i>Hypocryptadius</i>	1	—	—
<i>Dicæum</i>	22	+	+
<i>Prionochilus</i>	6	+	+
<i>Piprisoma</i>	2	+	+
<i>Chalcostetha</i>	1	+	+
<i>Æthopyga</i>	10	+	++
<i>Eudrepanis</i>	3	++	—
<i>Leptocoma</i>	3	+	++
<i>Cyrtostomus</i>	7	+	+
<i>Anthreptes</i>	6	+	+
<i>Arachnothera</i>	3	—	++
<i>Motacilla</i>	2	—	++
<i>Budytes</i>	1	+	+

TABLE 8.—*The genera of Philippine birds, showing the number of Philippine species in each genus and the zoögeographic alliance of each genus—Ctd.*

Genus.	Philippine species.	Alliance of genus with—	
		Australian Region.	Oriental Region, other than Philippines.
<i>Dendronanthus</i>	1	—	++
<i>Anthus</i>	5	+	+
<i>Alauda</i>	1	—	++
<i>Mirafra</i>	1	+	+
<i>Fringilla</i>	1	—	+
<i>Spinus</i>	1	—	(?)
<i>Passer</i>	1	—	++
<i>Loxia</i>	1	—	++
<i>Pyrrhula</i>	2	—	++
<i>Emberiza</i>	3	—	++
<i>Amandava</i>	1	—	++
<i>Padda</i>	1	—	++
<i>Munia</i>	5	+	+
<i>Erythrura</i>	1	++	+
<i>Reichenowia</i>	1	—	++
<i>Spodiopsar</i>	2	—	++
<i>Sturnia</i>	2	+	+
<i>Æthiopsar</i>	1	+	+
<i>Sarcops</i>	2	—	—
<i>Eulabes</i>	1	+	+
<i>Goodfellowia</i>	1	—	—
<i>Lamprocorax</i>	2	+	+
<i>Oriolus</i>	9	+	+
<i>Dicrurus</i>	5	—	++
<i>Dicruropsis</i>	4	++	+
<i>Bhuchanga</i>	1	—	++
<i>Corvus</i>	3	+	+

The nineteen genera enumerated in Table 9 are clearly more Australian than Oriental.

TABLE 9.—*Australian-Philippine bird genera.*

<i>Megapodius.</i>	<i>Gallicolumba.</i>	<i>Lichtensteinipicus.</i>
<i>Leucotreron.</i>	<i>Elanus.</i>	<i>Gerygone.</i>
<i>Lamprotreron.</i>	<i>Trichoglossus.</i>	<i>Edolisoma.</i>
<i>Hæmatæna.</i>	<i>Cacatoes.</i>	<i>Artamides.</i>
<i>Muscadivores.</i>	<i>Prioniturus.</i>	<i>Eudrepanis.</i>
<i>Zonophaps.</i>	<i>Tanygnathus.</i>	<i>Dicruropsis.</i>
<i>Myristicivora.</i>		

The seventy genera enumerated in Table 10 are clearly more Oriental than Australian.

TABLE 10.—*Oriental-Philippine bird genera.*

<i>Gallus.</i>	<i>Thriponax.</i>	<i>Copsychus.</i>
<i>Polyplectron.</i>	<i>Hemichelidon.</i>	<i>Kittacincla.</i>
<i>Treron.</i>	<i>Cyornis.</i>	<i>Pratincola.</i>
<i>Sphenocercus.</i>	<i>Muscicapula.</i>	<i>Acrocephalus.</i>
<i>Dendrophassa.</i>	<i>Xeocephus.</i>	<i>Tribura.</i>
<i>Streptopelia.</i>	<i>Terpsiphone.</i>	<i>Orthotomus.</i>
<i>Ænopoelia.</i>	<i>Rhinomyias.</i>	<i>Horornis.</i>
<i>Spilopelia.</i>	<i>Cryptolopha.</i>	<i>Enneoctonus.</i>
<i>Spilornis.</i>	<i>Eumyias.</i>	<i>Cephalophoneus.</i>
<i>Pernis.</i>	<i>Pericrocotus.</i>	<i>Otomela.</i>
<i>Microhierax.</i>	<i>Ægithina.</i>	<i>Pardaliparus.</i>
<i>Strix.</i>	<i>Chloropsis.</i>	<i>Callisitta.</i>
<i>Phodilus.</i>	<i>Irena.</i>	<i>Æthopyga.</i>
<i>Batrachostomus.</i>	<i>Hypsipetes.</i>	<i>Leptocoma.</i>
<i>Anthracoceros.</i>	<i>Iole.</i>	<i>Arachnothera.</i>
<i>Tachornis.</i>	<i>Microtarsus.</i>	<i>Alauda.</i>
<i>Micropus.</i>	<i>Pycnonotus.</i>	<i>Loxia.</i>
<i>Pyrotrogon.</i>	<i>Anurostis.</i>	<i>Pyrrhula.</i>
<i>Penthoceryx.</i>	<i>Mixornis.</i>	<i>Padda.</i>
<i>Xantholæma.</i>	<i>Macronous.</i>	<i>Erythrura.</i>
<i>Yungipicus.</i>	<i>Brachypteryx.</i>	<i>Reichenowia.</i>
<i>Tiga.</i>	<i>Zoothera.</i>	<i>Dicrurus.</i>
<i>Chrysocolaptes.</i>	<i>Chaimarrornis.</i>	<i>Bhuchanga.</i>
<i>Mulleripicus.</i>		

All the species of the genera enumerated in Table 11 are restricted to the Philippines; therefore, the genera are endemic to the Philippines.

TABLE 11.—*Endemic Philippine bird genera.*

<i>Phapitreron.</i>	<i>Dasylophus.</i>	<i>Dasycrotapha.</i>
<i>Ptilocolpa.</i>	<i>Lepidogrammus.</i>	<i>Zosterornis.</i>
<i>Pitheophaga.</i>	<i>Sarcophanops.</i>	<i>Leonardina.</i>
<i>Pseudoptynx.</i>	<i>Camiguinia.</i>	<i>Penthornis.</i>
<i>Bolbopsittacus.</i>	<i>Cyanomyias.</i>	<i>Rhabdornis.</i>
<i>Hydrocorax.</i>	<i>Malindangia.</i>	<i>Hypocryptadius.</i>
<i>Gymnolæmus.</i>	<i>Pseudotharrhaleus.</i>	<i>Sarcops.</i>
<i>Penelopides.</i>	<i>Ptilocichla.</i>	<i>Goodfellowia.</i>
<i>Dryococcyx.</i>		

Among the twenty-five endemic Philippine genera there are very few of which I can recognize the faunal relationships. *Pseudoptynx*, *Sarcophanops*, and *Dryococcyx* are clearly related to genera west of Wallace's Line and *Malindangia* is related to a genus in Celebes, east of the line; of the others I shall venture to say nothing.

In Table 9 there are nineteen names of Philippine genera that are more Australian than Oriental. In Table 10 there are

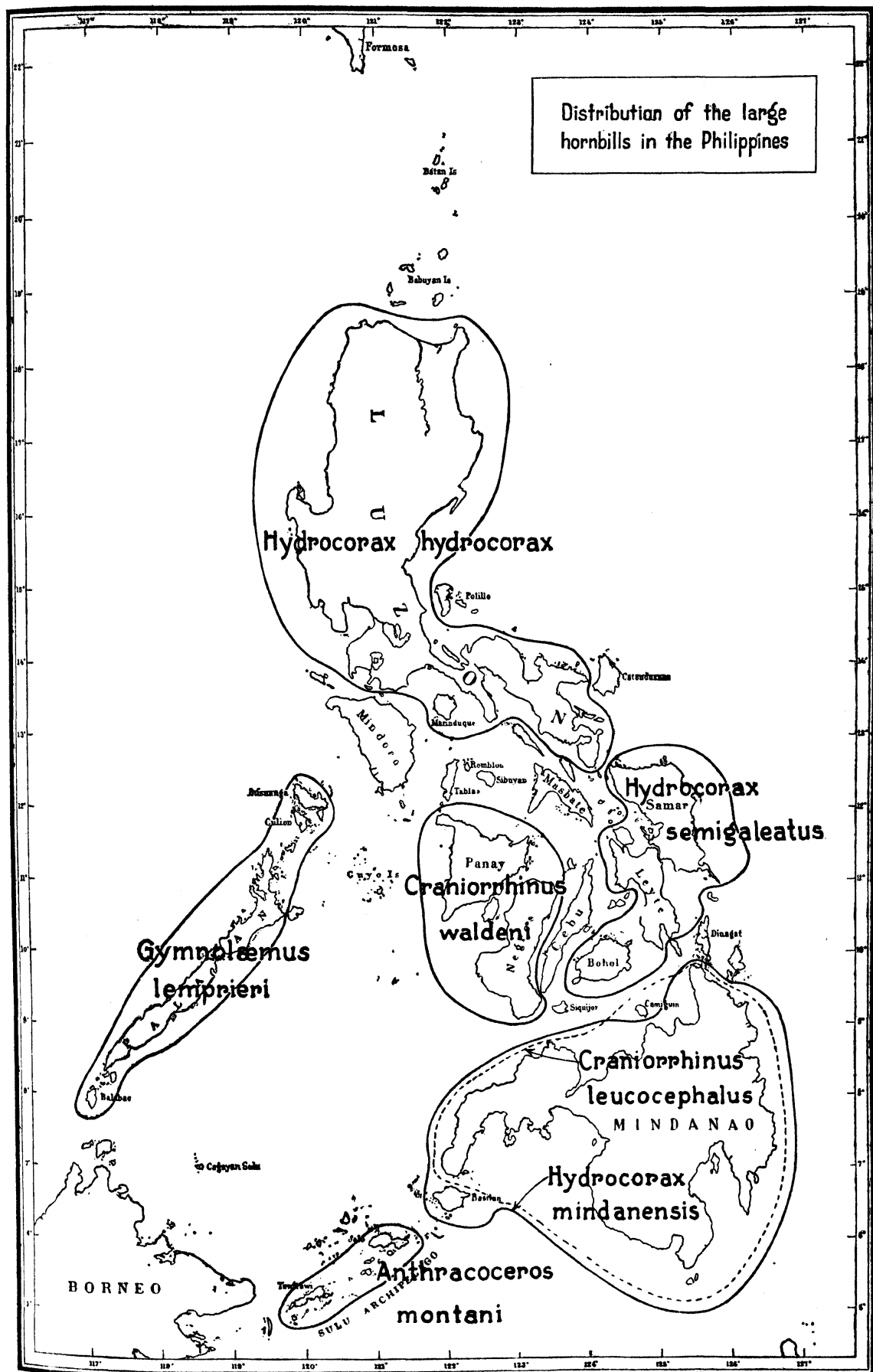


FIG. 49. The Philippine Islands, showing the distribution of various species of large hornbills.

seventy names of Philippine genera that are more Oriental than Australian. If it is thought that Palawan should not be included in the Philippines then twelve genera represented in the Palawan area but not in the rest of the Philippines must be removed from Table 10. This will leave fifty-eight Philippine-Oriental genera against nineteen Philippine-Australian genera.

ENDEMIC SPECIES OF PHILIPPINE BIRDS

The hornbills are good examples of birds that do not move about. The endemic Philippine genus *Hydrocorax* consists of three species of large, conspicuous, noisy, forest-inhabiting hornbills, locally known as "calao," "cao," or "gasalao." One of these species is confined to Luzon and Marinduque; another inhabits Samar, Leyte, Bohol, and Biliran; and the third is found in Mindanao and Basilan. There is no question here of fine specific distinctions. Each of the species is so distinct that it can be recognized by anyone. Plate 25 shows somewhat diagrammatically the characters exhibited by the bills of these three species. These are not the only characters that distinguish them, but they are the most striking ones.

The calaos are certainly capable of flying from one island to another, and just as certainly they do not. South of Luzon, distant a few kilometers, is the large heavily forested island Mindoro. If the calaos were in the habit of flying from island to island, certainly the species in Luzon would have crossed to Mindoro; and if calaos lived in Mindoro, certainly some collector would have found them there. The same condition is illustrated throughout the range of the genus. Cebu is but a short distance from Bohol; calaos are abundant in Bohol and are unknown in Cebu. In Negros there is a very distinct species of hornbill, which likewise has never been found in Cebu. A very distinct monotypic genus of this family is confined to Palawan.

It is not the large hornbills alone that show this restricted specific distribution. The species of the genus *Penelopides*, small hornbills locally known as "tarictic" or "talictic," are distributed as follows, one species in each island or group of islands:

Luzon, Marinduque, and Catanduanes; *P. manillæ* (Boddaert), bases of both mandibles with deep grooves.

Polillo; *P. subnigra* McGregor, similar to the preceding species, but larger and darker.

Mindoro; *P. mindorensis* Steere, base of upper mandible only with grooves, no black at base of tail, sexes alike in plumage.

Samar, Leyte, Biliran, and Bohol; *P. samarensis* Steere, base of lower mandible only with grooves, upper tail coverts white, tinged with buff.

Negros, Guimaras, Panay, Masbate, and Ticao; *P. panini* (Boddaert), abdomen rufous, thighs chestnut.

Mindanao and Dinagat; *P. affinis* Tweeddale, upper tail coverts black, a black patch on basal half of upper mandible.

Basilan; *P. basilanica* Steere, upper tail coverts black, upper mandible flesh colored.

The brief characters given refer to the males only, except for the Mindoro species in which the sexes are similar in colors.

It should be noted that *Penelopides* is unknown north of Luzon and is unrepresented in Cebu and in Palawan. The Philippine hornbills illustrate well the kind of evidence afforded by the distribution of bird species. The calaos and the tarictics are mentioned in some detail because they are large and easily seen. A genus of small birds that shows similar distribution as to its Philippine species is *Loriculus*, the hanging parrakeets, locally known as "colasisi." The Philippine species of this genus are distributed as follows:

Luzon and small adjacent islands; *L. philippensis* (P. L. S. Müller).

Mindoro; *L. mindorensis* Steere.

Romblon, Tablas, and Sibuyan; *L. bournsi* McGregor.

Negros, Guimaras, Panay, Masbate, and Ticao; *L. regulus* Souancé.
Cebu; *L. chrysonotus* Sclater.

Siquijor; *L. siquijorensis* Steere.

Samar, Leyte, Biliran, and Bohol; *L. worcesteri* Steere.

Mindanao and small adjacent islands; *L. apicalis* Souancé.

Basilan; *L. dohertyi* Hartert.

Sulu, Tawitawi, and Bungau; *L. bonapartei* Souancé.

There are numerous extra-Philippine species of *Loriculus*, and the genus extends over a large part of the Oriental Region and the Austro-Malayan Subregion; but the birds of this genus do not migrate and do not leave the areas that their respective species inhabit.

Plate 26 shows the most conspicuous specific characters of nearly all the members of the genus *Prioniturus*. Three species, *P. waterstradti*, *malindangensis*, and *suluensis*, are not figured, but none of these differs greatly from *P. discurus*, which is represented as fig. 1 on the plate. The crown of *P. discurus* is verditer blue; that of *P. mindorensis* is blue with a violet tinge, and the tail rackets are shorter than in *P. discurus*. In Palawan there is a blue species, called *P. cyaneiceps*. The commonest species in Luzon is *P. discurus*; in addition there is a

small species, *P. luconensis*, with yellowish green plumage; *P. montanus*, with a red spot on the crown, is abundant in northern Luzon. In Tawitawi there is another red-crowned species, *P. verticalis*. The last two species illustrated are *P. flavicans* from Menado, northern Celebes, and *P. platurus* from Bangi Islands, between Sula and the eastern peninsula of Celebes. *Prioniturus flavicans* appears to be a highly developed offshoot of *P. montanus*, but the old rose and light blue on the head of *P. platurus* give this species a striking appearance, so that it is not difficult to agree with Meyer and Wigglesworth that "*P. platurus* may fairly be regarded as the most highly differentiated of the group." One may suggest that *Prioniturus* originated in the Philippine Islands and that the two Celebesian species are the most recent and most highly developed of the series. It is somewhat difficult to suggest a reason for a red-headed species in northern Luzon and another in Tawitawi with the various other species in intervening islands.

Many genera with local species showing distributions similar to those already given might be enumerated.

FAUNAL AREAS OF THE PHILIPPINES

The distribution of the endemic species of many smaller genera affords evidence in accord with that derived from large genera. As a result the Philippines have been divided into several areas, sometimes called subprovinces, by no means of equal size, each characterized by the presence of certain species of birds and by the absence of others. Text fig. 50 shows what islands pertain to the various areas, or subprovinces.

The approximate number of species of land birds confined to each area is noted in Table 12.

Neither Table 12 nor the map, fig. 50, conveys the full force of the evidence, as the reader cannot learn from them that the twelve endemic species in Cebu are as significant as seventeen in Mindoro or twenty-seven in Samar-Leyte. Cebu is small, poorly wooded, and without highlands; Mindoro is large, heavily wooded, and contains high mountains. The wonder is that Mindoro has not nearer thirty-seven endemic species. A brief discussion of each group of islands and its birds follows.

1. The Palawan area consists of Palawan, the small islands adjacent to it, Balabac, the Calamianes, and the Cuyos. The fauna of this group contains a large extra-Philippine element, mostly Oriental, and lacks some of the genera that are conspicuous in the other islands of the Philippine Archipelago.

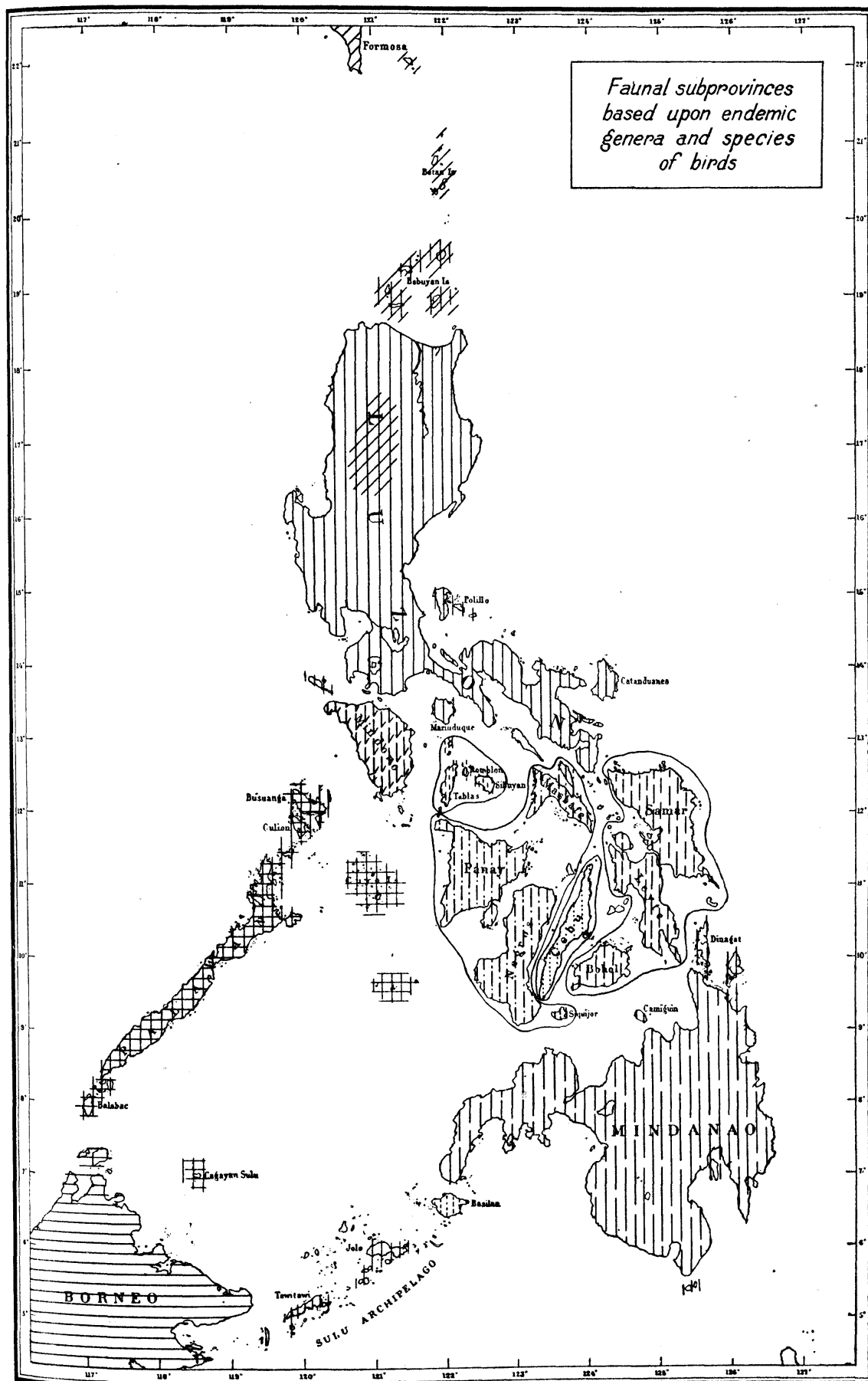


FIG. 50. The Philippine Islands, showing the division of the Archipelago into zoögeographic subprovinces on the basis of the endemic genera and species of birds.

TABLE 12.—*Faunal divisions * of the Philippines, the islands included in each area, and the number of endemic bird species restricted to each area.*

	Species.
1. Palawan area (Palawan, Culion, Busuanga, Cuyo, Balabac, Cagayancillo)	40
2. Central islands (Negros, Guimaras, Panay, Masbate, Ticao)	32
3. Mindoro area (Mindoro, Maestre de Campo, Lubang, Ilin, Semirara)	17
4. Luzon area (Luzon, Polillo, Catanduanes, Marinduque, Lubang, Verde?)	61
5. Samar-Leyte area (Samar, Leyte, Bohol, Biliran)	27
6. Mindanao area (Mindanao, Dinagat, Siargao, Sarangani)	51
7. Basilan	7
8. Sulu-Tawitawi area (Bungau, Sulu, Tawitawi, Lapac, Sibutu)	30
9. Romblon area (Romblon, Tablas, Sibuyan, Banton)	9
10. Cebu	12
11. Babuyanes-Batanes	14

The species enumerated in Table 13 are found in Palawan, Balabac, and the Calamianes and are not known in the other islands of the Archipelago. An E indicates that the species is confined to the Palawan islands; a G indicates that the genus is not represented in the rest of the Philippines.

TABLE 13.—*Species of birds known from the Palawan area but not from other Philippine islands.*

- Polyplectron napoleonis* Lesson; an Oriental genus. EG
Spilornis bacha (Daudin); an Indo-Malayan and Austro-Malayan genus.
Ninox scutulata Raffles; an Oriental species.
Strix whiteheadi (Sharpe). EG
Prioniturus cyaneiceps Sharpe; a Philippine and Celebesian genus. E
Batrachostomus javensis (Horsfield); an Oriental species.
Batrachostomus affinis Blyth; an Oriental species.
Gymnolæmus marchei (Sharpe); a monotypic genus. EG
Caprimulgus macrurus Horsfield; an Indo-Malayan and Austro-Malayan species.
Surniculus lugubris (Horsfield); an Oriental genus.

* These divisions should not be called provinces, because the Philippines constitute a faunal province of the Indo-Malayan Subregion. Another objection is that "province" and "subprovince" are used for political divisions and lead to confusion if used in a geographic sense. Perhaps "district," used by Semper, is the best term.—R. C. MCGREGOR.

TABLE 13.—Species of birds known from the Palawan area but not from other Philippine islands—Continued.

- Eudynamys honorata* (Linnæus); an Oriental genus.
Tiga everetti Tweeddale; an Oriental genus. EG
Chrysocolaptes erythrocephalus Sharpe; an Oriental genus. E
Mulleripicus pulverulentus (Temminck); monotypic and Oriental. G
Thriponax hargitti Sharpe; most of the species are Oriental. E
Pitta propinqua Sharpe. E
Cyornis lemprieri Sharpe. E
Cyornis platenæ (Blasius); an Austro-Malayan and Oriental genus. E
Xeocephus cyanescens Sharpe; two other endemic Philippine species; another species in the Talaut Islands. E
Cryptolopha xanthopygia Whitehead. E
Artamides difficilis (Hartert); an Austro-Malayan and Indo-Malayan genus. E
Pericrocotus igneus Blyth; an Oriental species.
Ægithina viridis (Bonaparte); an Oriental genus; the species in Sumatra and Borneo. G
Chloropsis palawanensis (Sharpe); an Oriental genus. E
Irena tweeddalei Sharpe; an Oriental genus. E
Iole striaticeps Sharpe; an Oriental genus. E
Microtarsus atriceps (Temminck); an Oriental genus and species. G
Trichophorus frater (Sharpe). EG
Trichophorus palawanensis (Tweeddale). EG
Pycnonotus cinereifrons (Tweeddale); the species of this genus are mostly African and Oriental. E
Turdinus rufifrons Tweeddale. EG
Ptilocichla falcata Sharpe; three other species; all are endemic Philippine. E
Anurophasis cinereiceps (Tweeddale); one other species, in Malay Peninsula, Sumatra, and Borneo. EG
Mixornis woodi Sharpe; another species is confined to Cagayan Sulu; the other species are Oriental. EG
Kittacincta nigra Sharpe; an Oriental genus. E
Orthotomus ruficeps (Lesson); an Indo-Malayan species; about half of the species of *Orthotomus* are endemic to the Philippines.
Hyloterpe whiteheadi Sharpe; an Indo-Malayan and Austro-Malayan genus. E
Pardaliparus amabilis (Sharpe); a Palearctic and Oriental genus. E
Callisitta palawana (Hartert); an Oriental genus. E
Prionochilus johannæ Sharpe; the genus is almost purely Indo-Malayan. E
Chalcostetha calcostetha (Jardine); a monotypic Indo-Malayan and Austro-Malayan genus. G
Æthopyga shelleyi Sharpe; the genus is almost exclusively Oriental. E
Cyrtostomus aurora Tweeddale; the genus is Austro-Malayan and Oriental. E

TABLE 13.—*Species of birds known from the Palawan area but not from other Philippine islands*—Continued.

Arachnothera dilutior Sharpe; an Oriental genus. E

Eulabes palawanensis Sharpe; the genus is almost exclusively Oriental. EG

Oriolus xanthonotus Horsfield; an Indo-Malayan species.

Dicruropsis palawanensis (Tweeddale); the genus is Australian and Oriental. E

Bhuchanga palawanensis Whitehead; the genus is almost exclusively Oriental. EG

Cuyo may be grouped with Palawan because of the presence of *Cyrtostomus aurora* Tweeddale, a conspicuous Palawan species. *Dicruropsis cuyensis* (McGregor) is confined to Cuyo.

Cagayan Sulu has a marked Bornean element in its fauna. Of course, not many species are to be expected on such a small island. *Munia fuscans* (Cassin) and *Pycnonotus plumosus* Blyth are Bornean species not known in the Philippines except in Cagayan Sulu; *Mixornis cagayanensis* Guillemard is endemic to that island.

2. The central Philippines consist of Negros, Panay, Bantayan, Guimaras, Masbate, and Ticao. Marilison and Batbatan, off the coast of Antique Province, Panay, were visited by me, but they yielded no species that would indicate their faunal relationships. The central Philippines form a well-marked group, although there are indications of infiltration from Luzon into Masbate and Ticao. Table 14 gives the distribution of the species that are characteristic of the central Philippines. Table 19, given under Cebu, also is of interest in this connection.

All of the thirty-two species listed in Table 14 are known from Negros, and twenty-three are known from Panay. Guimaras and Masbate are much smaller islands, and each supports about one-half the species known from Negros. Ticao has half the number of species known from Panay. Only nine of these thirty-two species range beyond the five central islands.

Siquijor is an island of recent origin; it has three endemic species and lacks some of the species that are characteristic of Negros, but it would be grouped with the central islands if with any. The fauna of Cagayancillo is puzzling; *Cyrtostomus aurora* Tweeddale, a characteristic Palawan species, is as abundant on Cagayancillo as it is on Cuyo; but *Dicruropsis*, which is common on Cuyo, is not found on Cagayancillo. *Zosterops rich-*

mondi McGregor, endemic to Cagayancillo, represents a genus unknown in the Palawan group; *Centropus viridis* (Scopoli), also found on Cagayancillo, is non-Palawan.

TABLE 14.—Distribution of thirty-two species of birds that are characteristic of the central Philippines.

Species.	Negros.	Panay.	Guimaras.	Masbate.	Ticao.	Tablas.	Romblon.	Sibuyan.	Cebu.
<i>Phapitreron maculipectus</i>	×	—	—	—	—	—	—	—	—
<i>Phapitreron nigrorum</i>	×	×	×	×	×	×	—	×	×
<i>Ptilocolpa nigrorum</i>	×	—	—	—	—	—	—	—	—
<i>Spilornis panayensis</i>	×	×	×	×	—	×	×	×	—
<i>Loriculus regulus</i>	×	×	×	×	×	—	—	—	—
<i>Batrachostomus menagei</i>	×	×	—	—	—	—	—	—	—
<i>Ceyx nigrirostris</i>	×	×	—	—	—	—	—	—	×
<i>Halcyon moseleyi</i>	×	—	—	—	—	—	—	—	—
<i>Penelopides panini</i>	×	×	×	×	×	—	—	—	—
<i>Craniorrhinus waldeni</i>	×	×	×	—	—	—	—	—	—
<i>Xantholæma roseum</i>	×	×	—	×	—	×	×	—	×
<i>Yungipicus maculatus</i>	×	×	×	—	—	—	—	—	×
<i>Chrysocolaptes xanthocephalus</i> ...	×	×	×	×	×	—	—	—	—
<i>Rhipidura albiventris</i>	×	×	×	×	×	—	—	—	—
<i>Rhinomyias albigularis</i>	×	—	×	—	—	—	—	—	—
<i>Eumyias panayensis</i>	×	×	—	—	—	—	—	—	—
<i>Artamides panayensis</i>	×	×	×	×	×	—	—	—	—
<i>Edolisoma panayensis</i>	×	×	×	—	—	—	—	—	—
<i>Dasycrotopha speciosa</i>	×	(?)	—	—	—	—	—	—	—
<i>Brachypteryx brunneiceps</i>	×	—	—	—	—	—	—	—	—
<i>Planesticus nigrorum</i>	×	—	—	—	—	—	—	—	—
<i>Kittacincla superciliaris</i>	×	×	—	×	×	—	—	—	—
<i>Orthotomus castaneiceps</i>	×	×	×	×	×	—	—	—	—
<i>Hyloterpe winchelli</i>	×	×	—	×	×	×	—	×	×
<i>Zosterops nigrorum</i>	×	×	—	×	×	—	—	—	—
<i>Dicaeum hæmatostictum</i>	×	×	×	—	—	—	—	—	—
<i>Dicaeum dorsale</i>	×	×	—	×	—	—	—	—	—
<i>Æthopyga bonita</i>	×	—	—	×	×	—	—	—	×
<i>Æthopyga magnifica</i>	×	×	—	—	—	×	—	×	×
<i>Cyrtostomus guimarasensis</i>	×	×	×	—	—	—	—	—	—
<i>Oriolus stceri</i>	×	—	—	×	—	—	—	—	—
<i>Dicrurus mirabilis</i>	×	×	×	×	×	—	—	—	×
Total.....	32	23	15	16	12	5	2	4	8

3. The Mindoro area includes Mindoro, Semirara, and probably Ylin, Caluya, Sibay, Libagao, and other small islands adjacent to Mindoro. The birds of these small islands and of other small islands near large islands are, in general, species of wide distribution and of little interest.

The following species, except the *Artamides* which has been collected in Tablas, are confined to Mindoro and small neighboring islands. Each of the genera, except *Geocichla*, is represented in Luzon.

Zonophaps mindorensis (Whitehead).

Gallicolumba platenæ (Blasius).

Otus mindorensis (Whitehead).

Ninox mindorensis Grant.

Ninox plateni Blasius.

Prioniturus mindorensis Steere.

Loriculus mindorensis Steere.

Penelopides mindorensis Steere.

Centropus mindorensis Steere.

Centropus steeri Bourns and Worcester.

Thriponax mindorensis Steere.

Artamides mindorensis Steere.

Iole mindorensis Steere.

Planesticus mindorensis Mearns.

Geocichla cinerea Bourns and Worcester.

Zosterops halconensis Mearns.

TABLE 15.—Genera represented in Luzon and other islands but not in Mindoro.

Genus.	Samar-Leyte.	Mindanao.	Basilan.	Sulu-Tawitawi.	Bohol.	Negros.	Cebu.	Sibuyan.	Palawan.
<i>Pithecophaga</i>	×	×							
<i>Baza</i>	×	×							×
<i>Pseudoptynx</i>	×	×							
<i>Bolbopsittacus</i>	×	×							
<i>Batrachostomus</i>	×	×	×			×			×
<i>Hydrocorax</i>	×	×	×		×				
<i>Pyrotrogon</i>	×	×	×		×				
<i>Chrysocolaptes</i>	×	×	×		×	×			×
<i>Lichtensteinipicus</i>	×	×							
<i>Cyanomyias</i>		×	×					×	
<i>Rhinomyias</i>	×	×	×	×	×	×			
<i>Culicicapa</i>	×	×		×		×	×		×
<i>Pericrocotus</i>	×	×		×		×			×
<i>Irena</i>	×	×	×						×
<i>Pseudotharrhaleus</i>		×							
<i>Zosterornis</i>	×	×	×		×				
<i>Orthotomus</i>	×	×	×		×	×			×
<i>Phyllergates</i>		×							
<i>Penthornis</i>		×				×			
<i>Callisitta</i>	×	×				×	×		×
<i>Rhabdornis</i>	×	×			×	×			
<i>Eudrepanis</i>	×	×			×				
<i>Pyrrhula</i>		×							
<i>Oriolus</i> (small species).....	×	×	×	×		×	×		×
Total.....	19	24	10	4	8	10	3	1	9

Two Indo-Malayan species, *Treron nipalensis* (Hodgson) and *Hemichelidon ferruginea* Hodgson, and one Javan species, *Cyornis banyumas* (Horsfield), are known from Mindoro and

Palawan; one endemic Philippine species, *Corvus pusillus* (Tweeddale), is restricted to Mindoro and Palawan.

Every genus enumerated in Table 15 is represented in Luzon and in Mindanao, all but four of them are found in Samar or in Leyte, and ten are known from Basilan. The data in Table 15 serve to emphasize the difference between Luzon and Mindoro and to show that there is a remarkable similarity among the islands that form the eastern front of the Archipelago. The birds of Luzon and of Mindanao are more nearly alike than are the birds of Luzon and of Mindoro.

4. Luzon, Catanduanes, Marinduque, Lubang, and Polillo have more endemic species than any other area. The following species are confined to this area, and most of them are restricted to Luzon:

Turnix ocellata (Scopoli).
Turnix whiteheadi Grant.
Turnix worcesteri McGregor.
Leucotreron marcheii (Oust.).
Leucotreron merrilli McGregor.
Gallicolumba luzonica (Scopoli).
Pseudopteryx philippensis Kaup.
Otus megalotus (Gray).
Otus longicornis (Grant).
Otus whiteheadi (Grant).
Prioniturus luconensis Steere.
Prioniturus montanus Grant.
Bolbopsittacus lunulatus (Scopoli).
Loriculus philippensis (P. L. S. Müller).
Batrachostomus microrhynchus Grant.
Halcyon lindsayi (Vigors).
Hydrocorax hydrocorax (Linnaeus).
Penelopides manillæ (Bodd.).
Centropus unirufus (Cabanis and Heine).
Dasylophus superciliosus (Cuvier).
Lepidogrammus cumingi (Fraser).
Chrysocolaptes hæmatribon (Wagler).
Microstictus funebris (Valenciennes).
Pitta kochi Brüggemann.

Thriponax confusus Stresemann.
Cyornis herioti Ramsay.
Rhipidura cyaniceps (Cassin).
Rhinomyias insignis Grant.
Artamides striatus (Boddaert).
Pericrocotus novus McGregor.
Irena cyanogastra Vigors.
Pseudotharrhaleus caudatus Grant.
Zosterornis striatus Grant.
Zosterornis whiteheadi Grant.
Zosterornis dennistouni Grant.
Zosterornis affinis McGregor.
Chaimarrornis bicolor Grant.
Kittacincla luzoniensis (Kittl.).
Tribura seebohmii (Grant).
Orthotomus derbianus Moore.
Orthotomus chloronotus Grant.
Horornis seebohmii (Grant).
Callisitta mesoleuca (Grant).
Zosterops luzonica Grant.
Dicæum luzoniense Grant.
Dicæum obscurum Grant.
Prionochilus anthonyi McG.
Eudrepanis jefferyi Grant.
Leptocoma henkei (Meyer).
Cyrtostomus flagrans (Oustalet).
Loxia luzoniensis Grant.
Pyrrhula leucogenys Grant.
Oriolus albiloris Grant.
Oriolus isabellæ Grant.

The following species that are known to occur in Marinduque show that the island is a fragment of Luzon:

Prioniturus luconensis.
Loriculus philippensis.
Hydrocorax hydrocorax.
Penelopides manillæ.
Dasylophus superciliosus.

Lepidogrammus cumingi.
Chrysocolaptes hæmatribon.
Lichtensteinipicus funebris.
Kittacincla luzoniensis.

Catanduanes, like Marinduque, yields no distinctive species of birds; and the following, which are known from there, are Luzon species:

Phapitreron leucotis.
Loriculus philippensis.
Dasylophus superciliosus.
Yungipicus validirostris.

Lichtensteinipicus funebris.
Kittacincla luzoniensis.
Cyrtostomus flagrans.
Orthotomus derbianus.

Polillo supports the following characteristic Luzon species:

Leucotreron merrilli.
Gallicolumba luzonica.
Loriculus philippensis.
Centropus unirufus.
Dasylophus superciliosus.

Chrysocolaptes hæmatribon.
Lichtensteinipicus funebris.
Artamides striatus.
Irena cyanogastra.

Tanygnathus freeri McGregor, *Penelopides subnigra* McGregor, and *Kittacincla parvimaculata* McGregor are confined to Polillo and are similar to species in Luzon. *Æthopyga rubri-nota* McGregor is confined to Lubang.

5. Samar, Leyte, Biliran, and Bohol form a well-defined area. The differences between these islands and Cebu are presented under Cebu. Table 15 shows the similarity of the birds of Luzon, Samar-Leyte, and Mindanao. The following species are confined to the Samar-Leyte area:

Bolbopsittacus intermedius Salvadori.
Loriculus worcesteri Steere.
Ceyx flumenicola Steere.
Ceyx samarensis Steere.
Hydrocorax semigaleatus (Tweeddale).
Penelopides samarensis Steere.
Yungipicus leytenensis Steere.
Chrysocolaptes rufopunctatus Hargitt.
Thriponax pectoralis Tweeddale.
Sarcophanops samarensis Steere.

Muscicapula samarensis Bourns and Worcester.
Rhipidura samarensis (Steere).
Pericrocotus leytenensis Steere.
Irena ellæ Steere.
Ptilocichla minuta Bourns and Worcester.
Zosterornis pygmæus Grant.
Zosterornis nigrocapitatus (Steere).
Orthotomus samarensis Steere.
Rhabdornis inornatus Grant.
Oriolus samarensis Steere.
Corvus samarensis Steere.

6. Mindanao and the small islands adjacent to it form a distinct area. The following species are confined to this area:

Muscadivores langhornei Mrns.
Ptilocolpa mindanensis Grant.
Pseudoptynx gurneyi Tweeddale.
Pseudoptynx mindanensis Gr.
Trichoglossus johnstoniæ Hartert.
Prioniturus waterstradti Hartert.
Bolbopsittacus mindanensis (Steere).
Loriculus apicalis Souancé.
Ceyx goodfellowi Grant.
Halcyon hombroni (Bonaparte).
Penelopides affinis Tweeddale.
Craniorrhinus leucocephalus (Vieillot).
Caprimulgus mindanensis Mrns.
Collocalia origenis Oberholser.
Chrysocolaptes montanus Grant.
Muscicapula montigena Mearns.
Rhipidura nigrocinnamomea Hartert.
Rhipidura hutchinsoni Mearns.
Rhinomyias goodfellowi Grant.
Cryptolopha mindanensis Hartert.
Eumyias nigriloris (Hartert).
Malindangia mcgregori Mearns.
Pericrocotus johnstoniæ Grant.
Pseudotharrhaleus unicolor Hartert.
Pseudotharrhaleus griseipectus Mearns.

Pseudotharrhaleus malindangensis Mearns.
Ptilocichla mindanensis Steere.
Zosterornis plateni (Blasius).
Macronous montanus (Mearns).
Leonardina woodi Mearns.
Brachypteryx mindanensis Mearns.
Brachypteryx malindangensis Mearns.
Planesticus kelleri Mearns.
Planesticus malindangensis Mearns.
Geocichla mindanensis Mearns.
Orthotomus nigriceps Tweeddale.
Phyllergates heterolæmus Mrns.
Pardaliparus mindanensis Mrns.
Penthornis tessacourbe (Scopoli).
Zosterops vulcani (Hartert).
Zosterops goodfellowi Hartert.
Zosterops malindangensis (Mearns).
Hypocryptadius cinnamomeus Hartert.
Dicæum apo Hartert.
Dicæum davao Mearns.
Dicæum nigrilore Hartert.
Prionochilus bicolor Hartert.
Æthopyga boltoni Mearns.
Pyrhula steerei Mearns.
Lamprocorax todayensis Mrns.
Goodfellowia miranda Hartert.

7. Basilan has much in common with Mindanao. The following species are known from these two islands and small neighboring islands and from nowhere else:

Ninox spilocephala Tweeddale.
Batrachostomus septimus Tweeddale.
Ceyx argentata Tweeddale.
Ceyx mindanensis Steere.
Hydrocorax mindanensis (Tweeddale).
Yungipicus fulvifasciatus Hartert.
Chrysocolaptes lucidus (Scopoli).

Thriponax multilunatus McGregor.
Sarcophanops steeri Sharpe.
Rhipidura superciliaris (Sharpe).
Edolisoma mindanense (Tweeddale).
Irena melanochlamys Sharpe.
Iole ruficularis (Sharpe).
Orthotomus cinereiceps Sharpe.
Oriolus basilanicus Grant.

Seven species are confined to Basilan, and there is a corresponding species for each of these in Mindanao.

TABLE 16.—*Genera that are represented by different species in Basilan and in Mindanao.*

Species confined to Basilan.	Corresponding species in Mindanao.
<i>Phapitreron brunneiceps</i> .	<i>P. amethystina</i> .
<i>Phapitreron occipitalis</i> .	<i>P. brevirostris</i> .
<i>Loriculus dohertyi</i> .	<i>L. apicalis</i> .
<i>Penelopides basilanica</i> .	<i>P. affinis</i> .
<i>Ptilocichla basilanica</i> .	<i>P. mindanensis</i> .
<i>Macronous striaticeps</i> .	<i>M. mindanensis</i> .
<i>Orthotomus mearnsi</i> .	<i>O. frontalis</i> .

8. Bungau, Tawitawi, and Sulu form a well-marked area to which Lapac and Sibutu must probably be added. The species enumerated in Table 17 have the distribution shown therein.

TABLE 17.—*Distribution of the species that are characteristic of the Sulu-Tawitawi area.*

Species.	Sulu.	Tawitawi.	Bungau.	Lapac.	Sibutu.	Siasi.
<i>Turnix suluensis</i>	×					
<i>Dendrophassa everetti</i>	×		×		×	
<i>Phapitreron cinereiceps</i>		×				
<i>Gallicolumba menagei</i>		×				
<i>Otus sibuensis</i>					×	
<i>Ninox everetti</i>						×
<i>Ninox reyi</i>	×		×			
<i>Prioniturus verticillatus</i>		×	×		×	
<i>Tanygnathus burbidgei</i>	×	×	×			
<i>Loriculus bonapartei</i>	×	×	×			
<i>Anthraceros montani</i>	×	×				
<i>Yungipicus ramsayi</i>	×	×	×			
<i>Thriponax suluensis</i>		×	×			
<i>Rhinomyias ocularis</i>	×	×				
<i>Artamides guillemardi</i>	×	×	×	×	×	
<i>Edolisoma everetti</i>	×	×	×			
<i>Pericrocotus marchesi</i>	×					
<i>Iole haynaldi</i>	×	×	×			
<i>Macronous kettlewelli</i>	×	×	×			
<i>Cephalophoneus suluensis</i>	×					
<i>Hyloterpe homeyeri</i>	×	×	×		×	
<i>Dicaeum assimile</i>	×	×				
<i>Dicaeum sibuense</i>						
<i>Aethopyga arolasi</i>	×	×				
<i>Anthreptes wigglesworthi</i>	×	×	×			
<i>Oriolus cinereogenys</i>		×	×			
<i>Dicrurus suluensis</i>	×			×		

9. Romblon, Tablas, and Sibuyan, although they shelter some of the central-island species, as is shown in Table 14, may well be considered a separate area.

TABLE 18.—*Species of birds that are confined to Romblon, Tablas, and Sibuyan.*

	Romblon.	Tablas.	Sibuyan.
<i>Loriculus bournsi</i>	×	×	×
<i>Yungipicus menagei</i>			×
<i>Rhipidura sauli</i>		×	
<i>Iole cinereiceps</i>		×	
<i>Dicaeum intermedium</i>	×	×	
<i>Dicaeum sibuyanicum</i>			×
<i>Dicruroopsis menagei</i>		×	

Banton is very slightly related to Romblon. Cresta de Gallo, south of Sibuyan, is little more than a sand bar; I found only seven species of birds on the island, and none of them, except *Zosterops nigrorum* Tweeddale, has a restricted range in the Philippines.

Seven species are confined to these islands, but only one of the species occurs in all three islands. Some families and many genera of the central Philippines are unrepresented in Romblon, Tablas, or Sibuyan; for example, the hornbills, the woodpeckers (except *Yungipicus*), the tailorbirds, the titmice, the creepers, and the shamas.

The avian fauna of Romblon, Tablas, and Sibuyan, of the Batanes, and of the Babuyanesis present some common features; namely, abundance of a few endemic species most of which do not inhabit all the islands of the group and lack of many genera that are well represented in neighboring islands. These conditions suggest that the islands of each group may have been separated from other islands for a long time or that they were never joined to each other or to any other island.

10. Cebu, although it shelters several of the characteristic central-island species (see Table 14), shows well-marked individual features and cannot be united with either Negros or Bohol. The following genera are represented in Bohol and are lacking in Cebu:

Hydrocorax.

Penelopides.

Pyrotrogon.

Chrysocolaptes.

Rhinomyias.

Poliolophus.

Zosterornis.

Macronous.

Orthotomus.

Eudrepanis.

Arachnothera.

Evidence of the fundamental difference between Negros, Cebu, and Bohol is afforded by Table 19, in which are enumerated genera represented in the three islands by different species; see also Table 15, under Mindoro.

TABLE 19.—Seven avian genera and the species by which they are represented in Negros, Cebu, and Bohol, respectively.

Negros.	Cebu.	Bohol.
<i>Phapitreron maculipectus</i>	<i>P. frontalis</i>	<i>P. amethystina</i> .
<i>Phapitreron nigrorum</i>	<i>P. nigrorum</i>	<i>P. albifrons</i> .
<i>Loriculus regulus</i>	<i>L. chrysnotus</i>	<i>L. worcesteri</i> .
<i>Yungipicus maculatus</i>	<i>Y. maculatus</i>	<i>Y. leytensis</i> .
<i>Artamides panayensis</i>	<i>A. cebuensis</i>	<i>A. kochi</i> .
<i>Hyloterpe winchelli</i>	<i>H. winchelli</i>	<i>H. apoensis</i> .
<i>Zosterops signiforensis</i>	<i>Z. everetti</i>	<i>Z. boholensis</i> .
<i>Dicaeum dorsale</i>	<i>D. pallidus</i>	<i>D. cinereigulare</i> .

11. The Batanes and the Babuyan, two groups of small islands north of Luzon, support some characteristic Philippine species, have several species confined to them, and lack many characteristic Philippine genera. Although Camiguin, Calayan, and Batan show differences from each other, they form an area quite as distinct as most of the others.

Some species are abundant in one island and absent from another. *Leptocoma henkei* is abundant in Fuga, Calayan, and Camiguin; no species of sunbird is known in Batan. *Corvus philippinus* is abundant in Fuga and in Calayan but lacking from Camiguin and Batan. *Lamprocorax panayensis* was seen in Fuga but not in Calayan. *Oriolus chinensis* is found in Calayan and Camiguin, but not in Batan. None of the following conspicuous Philippine families and genera is known north of Luzon: Hornbills, woodpeckers, parrots, sunbirds (but one), flowerpeckers (but one), *Dicrurus*, *Callisitta*, *Megalurus*, *Orthotomus*, *Kittacincta*, *Pycnonotus*, *Artamides*, *Hypothymis*, *Rhipidura*, *Sarcops*, and *Pitta*.

The species confined to the Batanes and the Babuyan are scattered somewhat as are the endemic species of the Romblon area. This parallel may or may not be significant of similar causes.

During a single season in Calayan I collected the first Philippine specimens of eight species, all strays from the north, as follows:

Polionetta zonorhyncha (Swinhoe).
Chelidonaria dasypus (Bp.).
Riparia riparia (Linnæus).
Turdus pallidus Gmelin.

Saxicola ænanthe (Linnæus).
Horornis minuta (Swinhoe).
Fringilla montifringilla Linn.
Spinus spinus (Linnæus).

I have since found *Horornis minuta* in Luzon, and any of the others may turn up in more-southern islands. As the Batanes and the Babuyanes are subject to heavy wind storms, it is easy to imagine that those islands may have received some of their bird population from strays.

TABLE 20.—*Endemic birds of the Batanes and the Babuyanes.*

	Fuga.	Camiguin.	Calayan.	Batan.
<i>Sphenocercus australis</i>		×	×	×
<i>Macropygia phæa</i>			×	×
<i>Otus calayensis</i>			×	
<i>Eudynamis frater</i>	×		×	
<i>Centropus carpenteri</i>				×
<i>Hypsipetes fugensis</i>	×		×	
<i>Hypsipetes camiguinensis</i>		×		
<i>Hypsipetes batanensis</i>				×
<i>Muscicapula calayensis</i>			×	
<i>Terpsiphone periophthalmica</i>				×
<i>Zosterops batanis</i>				×
<i>Zosterops meyeri</i>		×		
<i>Hyloterpe fallex</i>			×	
<i>Hyloterpe illex</i>		×		
<i>Pardaliparus edithæ</i>		×	×	

Sphenocercus and *Hypsipetes* are not known in the Philippines except as here noted, but are well represented in Japan and Formosa. *Macropygia phæa* has been recorded from Formosa. *Centropus carpenteri* Mearns is slightly larger than *C. mindorensis* Steere, but otherwise is nearly the same thing; no species of this type is known from Luzon. A more-remarkable species is *Camiguinia helenæ* (Steere), of Camiguin, Samar, and Mindanao. This beautiful blue flycatcher is abundant in Camiguin, and I described it as a new species of a new genus; when I compared specimens with Steere's *Cyanomyias helenæ* I could find no difference. I had a somewhat similar experience with a long-tailed flycatcher that is abundant in Batan. This seems to be a perfect *Terpsiphone* and I described it as *T. nigra*, but I now believe that it is the same as *Callaeops periophthalmica* Grant, which was based upon a short-tailed immature individual that was collected in Luzon. As a result Grant's generic name and my specific name must be discarded. The other species in Table 20 are local species of common Philippine genera.

SUMMARY OF THE PHILIPPINE AVIFAUNA

Twenty-five of the seventy avian families represented in the Philippines are nearly cosmopolitan, twelve others are represented in four of the zoögeographic regions of the world but not in the Neotropical or the Nearctic. The Megapodidæ, the Loriidæ, and the Cacatoidæ, each with one Philippine species, indicate an Australian alliance of the Philippine avifauna. The Eurylæmidæ, with two species; the Trogonidæ, with one species; the Capitonidæ, with two species; the Fringillidæ, with three species; and the Picidæ, with twenty species, indicate a stronger Oriental alliance.

The resident land birds of the Philippines contain a large Austro-Malayan element, represented by nineteen genera, and a much stronger Indo-Malayan element, represented by seventy genera. If the Palawan genera that are not represented in the rest of the Philippines be disregarded, there are still fifty-eight Philippine genera that have little or no Austro-Malayan alliance. A few genera of the highlands probably came into the Philippines from the north, possibly through Formosa.

Some of the twenty-five endemic genera are unmistakably allied to Australian genera and others are just as surely Oriental, but most of them are highly specialized and not very nearly related to extra-Philippine genera.

The Philippine bird fauna includes about seven hundred fifty species in two hundred ninety-three genera. There is a high percentage of endemism among the species.

Few of the endemic species or genera range over the whole or over a large part of the Archipelago. A study of the endemic forms leads to the division of the Archipelago into eleven zoögeographic areas, districts, or subprovinces; these areas are equal neither in size nor in number of restricted bird forms, and some of them are more clearly cut off than others.

The Palawan group of islands is the most distinct area and exhibits a strong Indo-Malayan element.

The Babuyanes-Batanes area is almost as distinct as the Palawan area, but this is mainly due to the lack of many of the characteristic Philippine genera and species; this area contains a small Formosan element.

The Luzon area has the largest number of endemic species, and a few of these from the highlands of northern Luzon are boreal types related to Himalayan genera or identical with them. Some of these genera are represented in the highlands of Mindanao.

The eastern islands; namely, Luzon, Samar, Leyte, Mindanao, and Basilan, have numerous genera in common that are not represented in the other islands.

The bird faunæ of Luzon, Mindoro, and Palawan are very distinct from each other; the faunæ of Bohol, Cebu, and Negros are also remarkably unlike.

The bird fauna of the Romblon area, as well as that of the Batanes and the Babuyanès, was probably derived from storm-driven strays or from neighboring areas during brief land connections. The bird fauna of Cagayancillo was probably derived from strays.

The evidence derived from the distribution of resident Philippine land birds leads to conclusions, in regard to probable former land connections among the islands and between the Archipelago and surrounding land masses, that are pleasingly similar in many details to the deductions from the evidence afforded by geology, hydrography, and phytogeography.

AMPHIBIANS, LIZARDS, AND SNAKES OF THE PHILIPPINES

AMPHIBIANS

LIFE HISTORY AND HABITS OF AMPHIBIANS

A brief consideration of the biology of the Philippine amphibians is necessary in order to make clear the limitations of the line of reasoning it is desired to undertake. Frogs, toads, and salamanders reproduce by eggs which are fertilized extraneously. After a given period the young escapes from the egg and passes through a larval stage. During this stage the young animal lives for the most part in the water and appears more like a fish than an amphibian. In the salamanders and cæcilians true external gills are developed. Usually the eggs of the amphibian are deposited in or near fresh water, and the larval and youthful stages develop in fresh water. A few species lay eggs that are surrounded by a thick gelatinous mass in which the larval stage is passed, and the young frog emerges direct from the egg. None is adapted to a marine habitat, and salt water is particularly injurious to the eggs and to immature amphibians.

Some of the Philippine amphibians have particularly peculiar habits. Thus, the females of the species of the genus *Ichthyophis*, a representative of the cæcilians, place their eggs in underground holes near water. The more or less oval eggs of these species are from 6 to 9 millimeters in diameter. The female of *Ichthyophis glutinosus* (Linnæus) coils about the eggs, evidently for the purpose of protecting them from their enemies. The eggs increase in size before the embryo hatches. Not only is there a definite increase in size, but the embryo in its development absorbs so much food material from the glutinous substance which surrounds the eggs that its weight is increased to four times that of the freshly laid egg. When the larvæ are hatched, the gills are lost, and the young take to the water, coming occasionally to the surface to breathe. This species attains almost adult size while still in the larval stage; with the closure of the gill slit and the disappearance of the fin on the tail, the

animal becomes a burrowing land creature. So thoroughly is this form then adapted to the land habitat that it drowns very quickly when placed in fresh water.

Amphibians of the order Salientia and some species of Caudata in other parts of the world, like Philippine frogs, for the most part lay their eggs directly in water, where the eggs hatch. The young passes through a larval stage of varying length, during which a large finlike tail develops, the tadpole stage. Later it emerges from the water with four well-developed legs, which are absent in the tadpole, and the tail disappears.

In connection with the distribution of these forms, it is well to note that amphibians are very definitely confined to land areas. Even short stretches of the sea prevent the spread of these animals, since salt water is inimical to both the adult and the young. The eggs after fertilization develop within a few hours and, since they will not withstand desiccation, it is not probable that these eggs could be transported by birds that inhabit fresh water. However, there are a few exceptions to these limitations, as in the case of the banana frog (palacang-saging), *Polypedates leucomystax* (Gravenhorst), which lays its eggs in a mass of froth or foam deposited along the edges of small pools of water, on reeds or plants growing in the water, or on an overhanging bough of a tree at some distance above the water. In about three days, under the meteorologic conditions prevailing in the Philippines, the eggs hatch; the young emerge from the mass, fall into the water, and become free-swimming larvæ.

A close relative of this species, *Polypedates pardalis* (Günther), often lays its eggs in water collected in holes in trees, while *Polypedates appendiculatus* (Günther) frequently deposits its eggs in water collected in the axils of the leaves of abacá (*Musa*) or *Alocasia*. It is possible that man may accidentally transport the eggs of such species for short distances. A species of *Cornufer*, a specimen of which was collected on Little Govenen Island, near Basilan, probably emerges from the egg fully developed into the adult stage, as is known to occur in at least one Philippines species. This is probably true of the *Cornufer* on Little Govenen, since the area of this island is only a few hundred square meters on which there is neither standing nor running water, even after a heavy rain. Considering even these exceptional cases, it is obvious that, on the whole, amphibians are particularly well adapted for the determination of past land connections. Unfortunately, no extensive collection of

amphibians has been made in the Philippine Islands, and many of the larger islands have not a single record for specimens. Palawan and Mindanao appear to be better known than Luzon or the Visayan or the Sulu group. Meager collections have been made in Samar, Leyte, and Mindoro, and apparently none has been made in Bohol, Cebu, or Panay. Even so, the Philippines are rich in species of Amphibia, no less than sixty-six having been enumerated in a monograph,* and since its publication twenty-two new species have been discovered and described. Probably not more than half the species existing within the Archipelago are known. Approximately eighty species are known from Borneo, seventy from New Guinea, forty-two from Sumatra, and forty-seven from Java. Japan and Formosa together have only fifty recorded species.

DISTRIBUTION OF THE ORDERS OF AMPHIBIA IN THE ORIENT

The order Apoda is composed of a single family, the Cæci-liidæ, represented in the East Indian region by three genera, which contain four or five species. Of the eleven genera of this family recorded in Boulenger's Catalogue, the distribution is as follows: Two genera are Malaysian, one of which occurs in India and Ceylon, and the other in southern Asia and Africa; five genera are American; two are African; one is American, African, and Asian; one is confined to southern Asia.

TABLE 21.—*Distribution of the orders of Amphibia in the Orient.*

Country or island.	Apoda.	Caudata.	Salientia.
Australia.....			×
New Guinea.....			×
Celebes.....			×
Mindanao.....			×
Luzon.....			×
Palawan.....	×		×
Borneo.....	×		×
Java.....	×		×
Sumatra.....	×		×
Malay Peninsula.....	×		×
Asia.....	×	×	×
Japan.....	×	×	×

There is no authentic record of the occurrence of a species of the order Caudata in either the Philippine, the East Indian, or the Australian Archipelago. Within the order Apoda, the

* Taylor, E. H., *Amphibians and Turtles of the Philippine Islands*, Bur. Sci. Pub. No. 15 (1921).

family Cæciliidæ is restricted to Palawan, Borneo, and the Sulu Archipelago. One of the species has been found in Basilan. This unique family, with the peculiar biology of one of its species, *Ichthyophis glutinosus*, practically requires definite land connections for its dispersal and, undoubtedly, members of

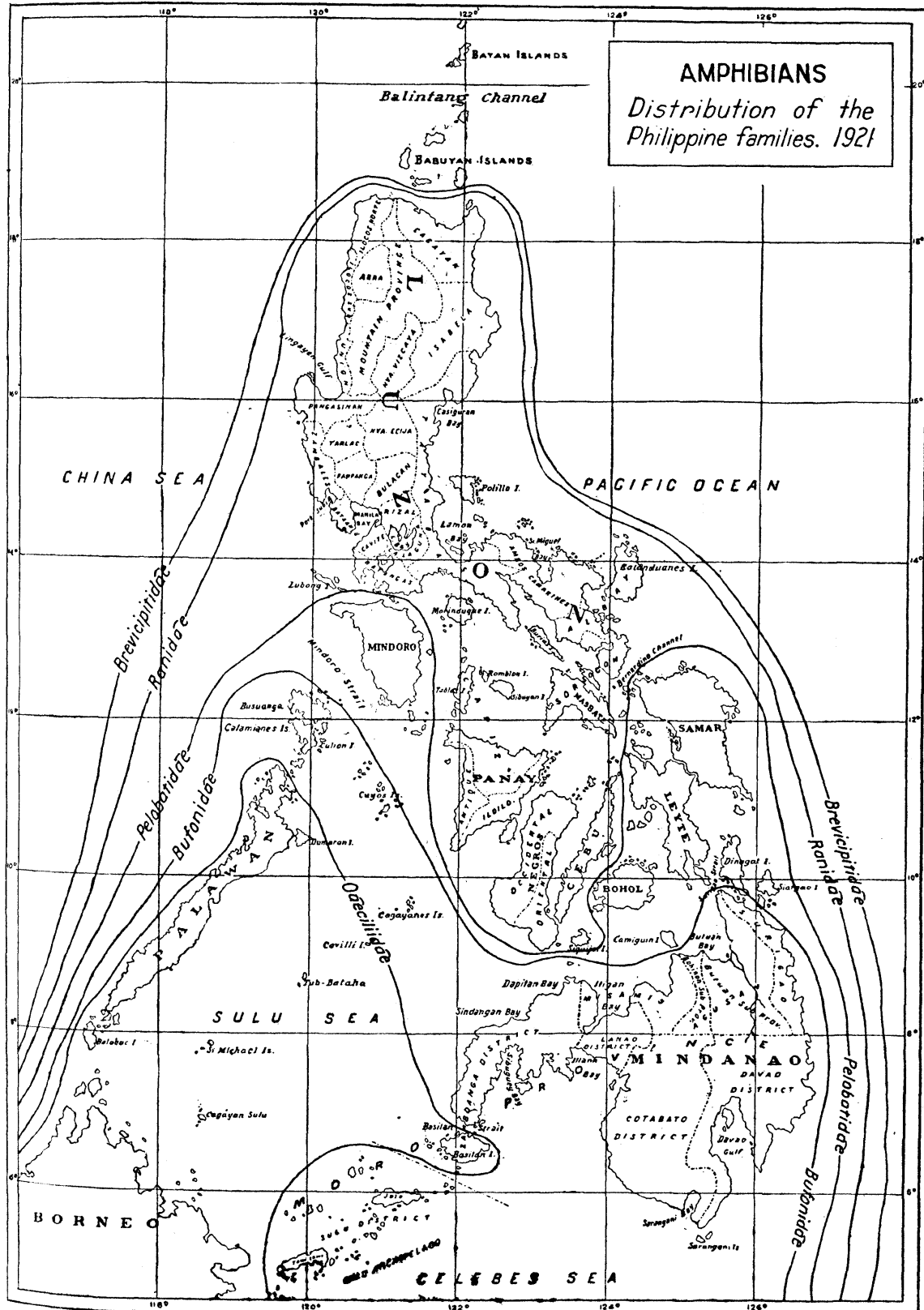


FIG. 51. Distribution of Philippine families of Amphibia.

the family spread from Borneo northward into Palawan and the Sulu Archipelago when the Sulu Archipelago and Palawan were land-tied to Borneo. The distribution of Philippine families of Amphibia is shown in fig. 51.

DISTRIBUTION OF THE FAMILIES OF SALIENTIA

Most of the Philippine species of Amphibia belong in the order Salientia, which is represented in western Malaysia, and among its families and genera we may expect to find evidences of faunal relationships. Of the seven families represented in the Oriental Region only four have been found in the Philippines and of these but two occur in Luzon, where as yet no member of the Bufonidæ or Pelobatidæ has been found. Table 22 shows the distribution of the families of Salientia in the Orient. As will be seen from the study of this table both Borneo and Celebes have representatives of these families and no others, thus indicating that Borneo, Celebes, and the Philippines in a broad fundamental way constitute an amphibian faunal unit, in contrast to New Guinea where the Bufonidæ are replaced by the Hylidæ. Cystignathidæ, a family characteristic of Australia and South America, also occurs in the latter island. In Japan and Formosa, the families Ranidæ, Brevicipitidæ, Bufonidæ, and Hylidæ are found, but Pelobatidæ is lacking.

Hazelia is the only genus confined to the Philippines, which indicates that the Philippine Islands have not been disconnected for a great geologic time from Borneo and Celebes, for otherwise a much higher generic endemism would be expected.

DISTRIBUTION OF GENERA OF SALIENTIA IN THE PHILIPPINES

Table 23 shows the distribution of the genera of Salientia in the Philippine Islands. This generic distribution is even better shown in fig. 52. All of the fifteen genera represented in the Philippines occur in Mindanao, six have been discovered in Luzon, and eleven in Palawan. All of the five genera known from Luzon occur in both Celebes and Borneo, and two of them, the widely spread genera *Rana* and *Polypedates*, occur in Japan. New Guinea has four genera in common with Mindanao and Borneo. Celebes has six genera in common with Mindanao, but of these only two occur in New Guinea, while all are found in Borneo. Three (*Phrynixalus*, *Chaperina*, and *Cornufer*) of the fifteen genera might have been derived from New Guinea, but this possible source is somewhat negatived by the fact that single representatives of two of these three genera are known in Borneo.

Eleven of the Philippine genera of the Salientia, which are for the most part southern Asiatic or Malaysian in distribution,

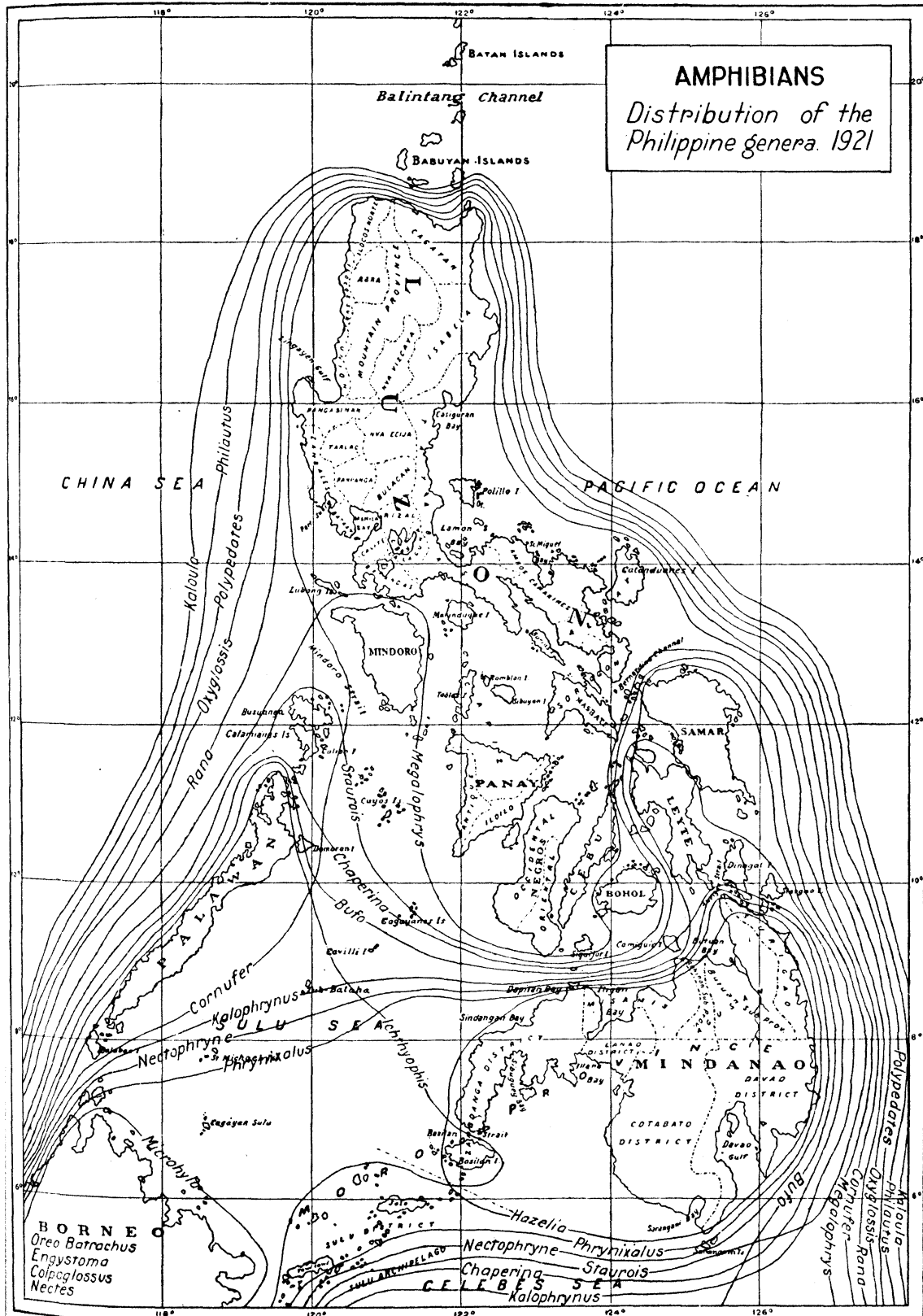


FIG. 52. Distribution of Philippine genera of Amphibia, 1921. *Nectophryne* was found in Palawan and *Ichthyophis* in Zamboanga, Mindanao, in 1923.

TABLE 22.—*Distribution of the families of Salientia.*

Country or island.	Ranidæ.	Brevicipitidæ.	Cystignathidæ.	Bufonidæ.	Hylidæ.	Pelobatidæ.	Discoglossidæ.
Oceania.....	×						
New Zealand.....							×
Australia.....	^a ×	×	×	×	×		
New Guinea.....	×	×			×	^b ×	
Celebes.....	×	×		×		×	
Mindanao.....	×	×		×		×	
Luzon.....	×	×					
Palawan.....	×			×		×	
Borneo.....	×	×		×		×	
Java.....	×	×		×		×	
Sumatra.....	×	×		×		×	
Malay Peninsula.....	×	×		×		×	
Southern Asia.....	×	×		×	×	×	
Central Asia.....	×	×		×	×		×
Japan.....	×	×		×	×		×
Europe.....	×			×	×	×	×
Madagascar.....	×	×					
Southern Africa.....	×	×		×			
Northern Africa.....	×	×		×	×		×
North America.....	×	×	^c ×	×	×	×	×
South America.....	^a ×	×	×	×	×		

^a In only the extreme northern part.^b Depending on the final disposition of *Ranaster convexusculus* MacLeay.^c In Mexico and Florida.

have probably entered the Philippines from Borneo by way of the Sulu and Palawan bridges. The western Malaysian alliance is clearly indicated by a detailed consideration of these genera. *Megalophrys* is represented by three species in the Philippines, one of which also occurs in Burma, the Malay Peninsula, Sumatra, Borneo, and Java. The seven known species of this genus, except the three that have penetrated the Philippines, are confined to Asia and western Malaysia. *Kalophrynus* is known from Burma to China, Sumatra, and Borneo, with two species in the Philippines but none in New Guinea and Halmahera. *Nectophryne* occurs in Africa and India, with eight species in Borneo, one of which occurs also in Singapore and the Natuna Islands; there are three species in the Philippines, but none is known from eastern Malaysia. *Staurois*, with four species, has one representative in the Philippines and three in Borneo; one of the Bornean species extends to the Malay Peninsula. *Rana palavanensis* Boulenger occurs in Borneo, Palawan, and Celebes; *R. erythræa* (Schlegel), in southeastern Asia, Sumatra, Java, Borneo, Philippines, and Celebes; and *R. glandulosa* Boulenger,

TABLE 23.—*Distribution of the genera of Salientia represented in the Philippine Islands.*

Country or island.	<i>Oxyglossus</i> .	<i>Rana</i> .	<i>Staurois</i> .	<i>Polypedates</i> .	<i>Hazelia</i> .	<i>Philautus</i> .	<i>Cornufer</i> .	<i>Microhyla</i> . ^a	<i>Kaloula</i> .	<i>Kalophrynus</i> .	<i>Chaperina</i> .	<i>Phrynixalus</i> .	<i>Nectophryne</i> .	<i>Bufo</i> .	<i>Megalophrys</i> .
Oceania.....		×					×								
New Zealand.....															
Australia.....		×					×								
New Guinea.....		×					×				×	×			
Celebes.....	×	×	?	×			×		×					×	
Mindanao and Sulu.....	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Luzon.....	×	×		×		×	×		×						
Palawan.....	×	×	×	×		×				×	×			×	×
Borneo.....	×	×	×	×		×	×	×	×	×	×	×	×	×	×
Java.....	×	×		×		×		×	×				×	×	×
Sumatra.....	×	×		×				×	×	×			×	×	×
Malay Peninsula.....	×	×	×	×		×		×	×	×			×	×	×
Southern Asia.....	×	×		×			×	×	×	×				×	×
Central Asia.....	×	×		×					×	×				×	
Japan.....		×		×				×						×	
Europe.....		×												×	
North Africa.....		×											×	×	
South Africa.....		×											×	×	
Madagascar.....		×													
North America.....		×												×	
South America.....		×												×	

^a Very doubtful in the Philippine Islands.

in the Malay Peninsula, Sumatra, Borneo, and Palawan. The genus *Rana* extends to New Guinea and Queensland, but there are many more species in western Malaysia than in eastern. *Oxyglossus laevis* Günther extends from Burma through the Malay Peninsula to Sumatra, Borneo, the Philippines, and Celebes, while the only other species of the genus extends from India to China and Java. *Ichthyophis* has two species in the Philippines and two in Asia, Sumatra, Java, and Borneo. *Philautus* extends from India to Sumatra, Java, and Borneo; there are several endemic species in the Philippines, but none is known from eastern Malaysia. *Polypedates* presents numerous species in western Malaysia, a few in eastern Malaysia, and six in the Philippines. The genus *Bufo* presents about twenty species in western Malaysia, only two or three extend as far east as Celebes, and four occur in the Philippines.

The Philippine special alliances with eastern Malaysia are practically limited to the three genera *Phrynixalus*, *Chaperina*, and *Cornufer*. The general alliances of Philippine amphibians

are hence overwhelmingly with western Malaysia and in remarkably close conformity with the Malaysian-Philippine distribution of fresh-water fishes, and with the generic distribution of plants in the same regions. The amphibians present clear evidences of longer-continued or more-pronounced connections between the Philippines and western Malaysia than between the Philippines and eastern Malaysia, as do the fresh-water fishes, the Dipterocarpaceæ, and the genera of all families of flowering plants as a whole.

The sparsity of western Malaysian amphibians in New Guinea may be explained by what appear to be circuitous routes between New Guinea and the western Malaysian region. A narrow land bridge probably for a short geologic time joined Halmahera with New Guinea and with Celebes, and in turn Celebes joined Mindanao by way of the Sarangani bridge; certain Bornean species passed across the Sulu bridge to Mindanao south of this eastern passage, and from Celebes eastward to New Guinea. The Saragins suggest that Celebes was likewise connected in the Tertiary to Java on the south.

Careful collecting in Mindoro will probably develop some interesting relationships between Palawan and Luzon.

LIZARDS

HABITS OF LIZARDS

The large numbers of lizards in the houses is one of the first things that arrests the attention of the tourist who visits the Philippines. He quickly finds that, far from being regarded as pests, the small geckos are welcome guests and almost indispensable adjuncts to the menage. This is because several species, probably *Hemidactylus frenatus* Duméril and Bibron, *Peropus mutilatus* (Wiegmann), and *Cosymbotus platyurus* (Schneider), are skillful hunters of cockroaches, mosquitoes, moths, and other insect pests except ants. These lizards belong to the family Gekkonidæ. The species *Hemidactylus frenatus*, *Hemidactylus garnotii* Duméril and Bibron, *Peropus mutilatus*, *Cosymbotus platyurus*, *Gekko gekko* (Linnæus), and *Gekko monarchus* (Duméril and Bibron) are carried from place to place through the agency of man. Their habit of dwelling in houses enables them to accommodate themselves readily to boats. In this way some species have been carried all over the world during the past four hundred years. For example, the type locality of *Hemidactylus frenatus* is Manila, but it is also found in Mexico where it was renamed by Duges *Hemidactylus navarri*.

Its introduction into Mexico probably occurred not earlier than the sixteenth or seventeenth century when direct commerce was carried on between the Philippines and Mexico. Many members of this genus are world-wide travelers. Several species are found in nearly all the important Philippine ports, but some are evidently recent immigrants, for they have not yet penetrated the interior portions of some islands. For example, *Cosymbotus platyurus* (Schneider) was found in the seacoast towns of Mindanao, but no specimen was found in the interior.

The arboreal habits of certain members of this family also render them easily susceptible to accidental transport. Thus, all the captured specimens of *Hemiphyllodactylus insularis* Taylor were found along the seashore under the bark of trees whose bases were even lapped by ocean waters. In one instance two dirty, brownish white eggs of this species, joined together, were found beneath the bark. Evidently such species could be transported from island to island by floating trees that had been toppled over into the sea during storms. Because of the habits of some of the species of the Gekkonidæ, and the consequently great chances for their accidental transport, it is clear that certain species must be regarded as valueless in determining former land connections.

Likewise, *Hydrosaurus* and the five Philippine members of the genus *Varanus*, whose species are the largest and the most striking in appearance of Philippine reptiles, have great powers of adaptability, so far as means of migration are concerned, and because of the facility with which they swim and dive they are not restricted in their movements by streams or possibly even narrow stretches of ocean. In certain habits the species of *Varanus* do not differ greatly from other lizards. Their eggs are laid in tree trunks or in the hollow roots of stumps, usually near water. They seem to prefer rotting animal flesh, but they will feed also on bugs, small mammals, chickens, or eggs. Animals with such habits and catholic tastes are capable of rapidly extending their range within an archipelago, but the great body bulk of *Varanus salvator* (Laurenti) would largely prohibit its migration across even a moderately wide sea.

The habit that lizards of many Philippine species have of laying eggs under the bark of live trees and of logs subjects them to accidental dispersal; on this account, alone, lizards in general are by no means as good material for distributional studies as are the amphibians.

DISTRIBUTION OF PHILIPPINE LIZARDS

It now becomes necessary to examine the recorded distribution of Philippine lizards in order to discover what light it throws on migration routes north of the Bornean-Celebesian area.

It should be noted that only five saurian families (Gekkonidæ, Agamidæ, Varanidæ, Scincidæ, and Dibamidæ) are represented in the Philippines, Celebes, and the Moluccas. These families also occur in Borneo together with three other sparsely represented families, namely: Helodermatidæ, represented by the extremely rare *Lanthanotus borneensis*; the Lacertidæ, by a single widespread species, *Takydromus sexlineatus* Daudin; and the Anguidæ by a single species, *Ophisaurus buttikoferi*, known from a single specimen. Representatives of these three families may yet be found in Palawan, since the reptilian fauna of that island is essentially Bornean. *Takydromus sexlineatus* is probably a recent immigrant to Borneo, since this species is known in Sumatra and the Malay Peninsula, the intervening land masses between Borneo and the Afro-Asian regions in which the family probably originated. The single representatives of Helodermatidæ and Anguidæ obviously are remnants of older faunas. This is to be inferred since the nearest relative of *Lanthanotus borneensis* is found in southern North America with no connecting link representative of the Helodermatidæ in Eurasia, and also because the probable origin of the Anguidæ was in Central America where this family is best represented. The Anguidæ also occur in the West Indies, South America, and North America; but only two genera, each with one species, are found in Europe, while *Ophisaurus* has only one recorded species, *Ophisaurus gracilis*, an Indian form, in all of Asia.

DISTRIBUTION OF SAURIAN FAMILIES

The general world distribution of saurian families is shown in Table 24.

The distribution of the saurian families in the Philippines and Borneo is graphically shown in fig. 53. This family distribution shows that the five family stocks represented in the Philippines are old and have been well established throughout the Australasian region for a comparatively great geologic time—probably since at least the beginning of the Tertiary period.

As a result of these irregularities, it becomes necessary to examine the generic distribution within the families in order

TABLE 24.—*Distribution of saurian families.*

Family.	Polynesia.	New Zealand.	Australia.	New Guinea.	Celebes.	Philippines.	Palawan.	Borneo.	Java.	Sumatra.	Malay Peninsula.	Japan.	Asia.	Africa.	Madagascar.	Europe.	North America.	Central America.	South America.
Gekkonidæ	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Eublepharidæ																			
Uroplatidæ																			
Pygopodidæ			×	×															
Agamidæ			×	×	×			×	×	×	×	×	×	×	×		×	×	×
Iguanidæ	×																		
Zonuridæ																			
Anguidæ																			
Helodermatidæ																			
Varanidæ	×		×	×	×	×	×	×	×	×	×		×	×			×	×	
Amphisbaenidæ																			
Lacertidæ																			
Gerrhosauridæ																			
Anelytropidæ																			
Scincidæ	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Dibamidæ																			
Xenosauridæ																			
Aneliidæ																			
Xantusiidæ																			
Teiidæ																			

GENERIC DISTRIBUTION OF LIZARDS

LIZARDS
Distribution of the Philippine families, 1921

The map illustrates the geographical distribution of lizard families in the Philippines as of 1921. It features a grid of latitude and longitude lines. Major islands and archipelagos are labeled, including Luzon (with sub-regions like Ilocos, Cagayan, and Mountain Province), Mindoro, Panay, Samar, Leyte, Bohol, and Mindanao (divided into Northern, Central, and Eastern districts). Surrounding bodies of water include the China Sea, Pacific Ocean, Sulu Sea, and Celebes Sea. Contour lines represent the distribution ranges of several lizard families: Scincidae (widely distributed), Gekkonidae (along the western coast), Agamidae (in the north and west), Varanidae (in the south and west), Dibamidae (in the south), and Anguillidae (in the south). Specific locations and islands are marked, such as Manila, Cebu, Iloilo, Zamboanga, and various smaller islands like Palawan, Calamian, and the Sulu Archipelago.

FIG. 53. Distribution of Philippine families of lizards.

twenty-eight genera are recognized in the Philippines, about twenty-five in the Celebes-Moluccas group, and thirty in Borneo. Twenty-one are common to the Philippines and Borneo, and nineteen of these occur in Celebes. Of the two exceptions, *Hemiphyllodactylus* probably occurs there but is unreported. *Ptychozoon* is represented by only one known species in the Philippines; only the type specimen was captured. On account of its rarity, its nonoccurrence in Celebes is of no significance. *Otosaurus* and *Hydrosaurus* occur in both the Philippines and Celebes, but are not known from Borneo. However, the genus *Lygosoma* (as restricted by Stejneger) is represented in Palawan by *Lygosoma chalcides* (Linnæus) and probably will be found in Borneo. *Otosaurus cumingii* Gray is the only representative of the genus *Otosaurus* in the Philippines. *Hydrosaurus* is likewise represented in the Philippines by only one species, *Hydrosaurus pustulosus* (Eschscholtz). This aquatic, herbivorous species has been collected from the following widely separated areas: Polillo, Mindoro, Negros, and Mindanao; it has a wide extra-Philippine distribution as well. The genus *Perochirus* is known from only Mindanao and the Caroline Islands.

The mere number of genera in the Philippines is of little significance in the study of zoögeography, since many of them range throughout Celebes and Borneo. Possibly the Philippine endemic genera *Brachymeles*, *Luperosaurus*, and *Pseudogekko* and the fact that certain Bornean and Celebesian genera are lacking may throw some light upon distributional problems.

Brachymeles, the most important and most distinctive of the three endemic Philippine genera, is represented by eight species, which exhibit a great diversity of size and development or degeneration of legs. No species is known to occur in Palawan, but the genus appears to be represented with fairly uniform frequency elsewhere in the Islands. No closely related genus is known in any adjacent territory. The absence of this genus from northern Borneo (if it is indeed absent) would suggest that it is of comparatively recent development. There are three species of the genus in the Sulu region, which lies nearest Borneo. Some of these species should certainly have reached the northern Bornean coast while the transfer of species represented by the twenty-one genera common to the Philippines and Borneo was being made, unless they are a later development or the transfer was made over a different route. This theory of a late development of this genus, however, is hardly substantiated by its wide distribution in the Philippines.

Luperosaurus has three known species. One on Calayan, Babuyan Islands, in the extreme northern part of the Philippine group; one on Jolo Island, in the extreme southern part of the Archipelago; and one, the exact type locality of which is unknown. All of these species are known only from the types and cotypes. The apparent rarity of the lizards of this genus in the Philippines supports the belief that they may easily have remained undiscovered in Borneo and neighboring islands.

Pseudogekko is extremely rare; only three specimens of the single known species have been taken. Its nearest relative appears to be *Thecadactylus*, which has been recorded from New Guinea and certain adjacent islands.

Of the nine Bornean genera not found in the Philippines, *Takydromus*, *Ophisaurus*, *Japalura*, and *Aphaniotis* are common to Borneo, to the islands lying south and west, and to Asia; *Homolepida* is common to Borneo, Celebes, Java, and Sumatra; *Gonatodes* and *Aleuroscalabotes* have representatives in Australia, Borneo, and the Malay Peninsula, but are apparently absent from Celebes, Java, and Sumatra; *Mimetozone* is common to Borneo and the Malay Peninsula; and *Lanthanotus* is endemic.

Of the three Celebes-Moluccan genera not known in the Philippines *Cryptoblepharis* is widely distributed over Polynesia, Australia, Africa, Asia, and Japan, but appears to be wanting in Borneo, the Philippines, and even in Celebes proper; *Homolepida* occurs in Borneo; and *Tiliqua* has representatives in Australia and New Guinea.

While this consideration of endemism does not lead to very definite conclusions, it is evident that the lizard fauna of Palawan and the dependent islands is distinctly Bornean, and that it stands apart from the varied saurian fauna found in the remainder of the Philippine Archipelago.

The map of generic distribution shows that many genera are extensively distributed over Borneo, Celebes, and the Philippines; others, fewer in number, appear to be limited to Borneo, Palawan, and the Sulu Archipelago. Such distribution would indicate an early saurian invasion—fundamentally western Malaysian—that became widespread as the result of a very late penetration of certain genera from Borneo into Palawan and the Sulu Archipelago after the remainder of the Philippines had become separated from these later Bornean connections. It is not unlikely that some of the forms from New Guinea and Australia may have been brought northward on natural rafts or logs in the Kuro-Siwo. However, it seems improbable that any

[illegible]

FIG. 54. Distribution of Philippine genera of lizards, 1921. Since 1921, *Hemiphyllodactylus*, *Gymnodactylus*, *Sphenomorphus*, *Siaphos*, and *Riopa* have been found in Palawan and the Calamianes, and *Gonyocephalus* has been found in Luzon.

SNAKES

HABITS OF SNAKES

Snakes, like lizards, are in many cases arboreal and natatorial in habit. Consequently certain forms, such as water snakes, are of wide distribution and hence useless in postulating former land connections. The arboreal forms and the swamp dwellers are likely to be transported on natural rafts.

DISTRIBUTION OF PHILIPPINE GENERA OF SNAKES

Very little information or guidance of value can be gained by a study of the family distribution of snakes (see fig. 55).

Seven of the eleven or twelve families of snakes have been reported from the Philippine Islands, and Borneo has representatives of one other family, the Anillidæ, which is widespread in the southern East Indies and may eventually be discovered in the Philippines. Of the subfamilies of the Natricidæ, the Philippines may have a representative of Langahinæ,* which apparently has not been discovered in the other islands of the Malay Archipelago. The other genera of this subfamily are confined largely to Madagascar and South Africa.

There are thirty-two genera of land snakes in the Philippine Islands, five of which are endemic. One of the endemic genera has three species, and each of the other four is represented by only a single species. There are four other genera in the Philippines not found in Borneo. One of these, *Hemibungarus*, has three species in the Philippines and possibly may have entered from the north, as the genus is represented on the mainland of Asia, India, and the Riu Kiu Islands. Stejneger states that no species has been found in Formosa, but suggests the possibility of later discovery, as little is known of the fauna of that island. A very closely related genus, *Callophis*, also a mainland form, strengthens the possibility that *Hemibungarus* may have arrived through the northern chain of islands. *Stegonotus*, with two species in the Islands, appears to have arrived from the south via the chain of islands that connects with the Moluccas. This is certainly a not unreasonable supposition when we consider that the genus is absent from both Celebes and Borneo. The Moluccas have two species, New Guinea has two others, and the

* There may be some doubt as to the propriety of including the subfamily Langahinæ in the Philippine fauna on the strength of the little-known species *Hologerrhum philippinum* Günther. It may have no actual relationship to the forms found in Madagascar and Africa and may actually be an aberrant natricid.—E. H. TAYLOR.

[illegible]

[illegible]

Australian mainland two. Another hypothesis is that the ancestors of these forms have been transported from New Guinea on natural rafts in the Kuro-Siwo which bathes the eastern coast of Samar. For the most part, the genera that occur in the Philippine Islands are widely distributed in the Philippines.

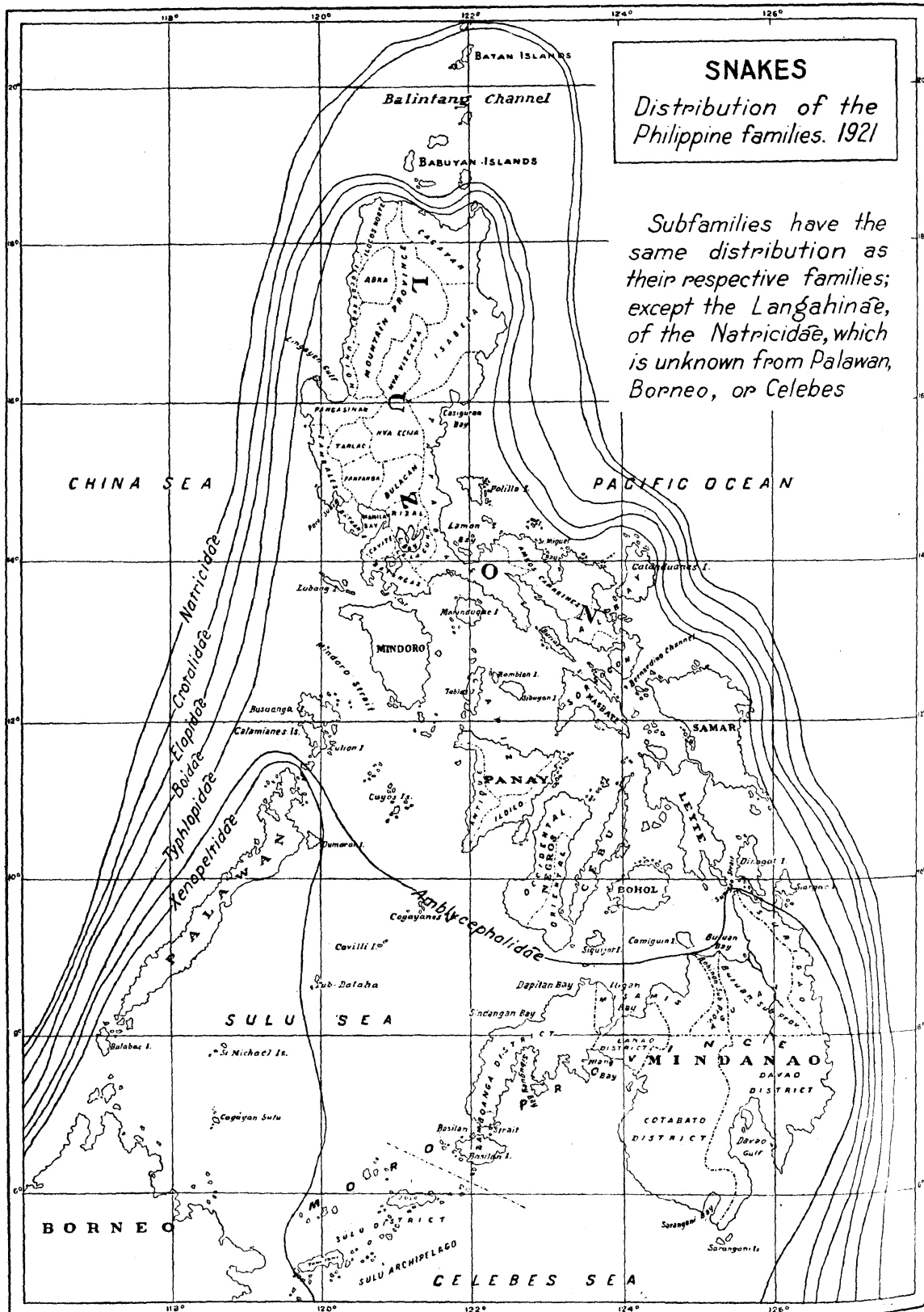


FIG. 55. Distribution of Philippine families of snakes.

Thus, of the thirty-two terrestrial and arboreal forms, only eight have not been discovered in Luzon, and only ten are lacking from the Visayan Islands; three are known only from Palawan and the southern Sulu islands; one appears to be confined to Mindanao and the neighboring islands; and one is restricted to Mindanao and Palawan.

RELATIONS OF PHILIPPINE AMPHIBIANS, SNAKES, AND LIZARDS TO THOSE OF THE MOLUCCAS AND NEW GUINEA

It is clear that most of the Philippine species of amphibians, snakes, and lizards show definite relations to those of Borneo or the larger Sunda islands. Certain reptilian and amphibian representatives show relationships with the Moluccas and New Guinea. They are the snake genus *Stegonotus*; one lizard of the genus *Perochirus*, which appears to be confined to Mindanao and the Caroline Island group; another genus of lizards, *Pseudogekko*, which has its closest affinity with a New Guinea genus, *Thecadactylus*; and another, *Otosaurus*, whose relation is with Celebes. In the Amphibia, the three genera *Cornufer*, *Chaperina*, and *Phrynixalus* show marked relationships with New Guinea. The only other genus common to the Philippines and New Guinea is *Rana*, of nearly world-wide distribution and lacking only in New Zealand.

HERPETOLOGIC FAUNAL AREAS OF THE PHILIPPINES

The amphibian, reptilian, and saurian faunas of the Islands are still largely unknown and future discoveries will make changes in the limits of the proposed faunal areas. At any rate, marked overlapping along their boundaries will be shown.

However, the existence of two well-marked faunal areas is well established—Borneo, Palawan, and its dependent islands form one, and the remaining Philippine islands the other. In fig. 56 the first-named area is represented by horizontal rulings, and the second by vertical rulings with square checks over the Sulu Archipelago to indicate a possible mingling of the two major faunas. The tentative subdivisions of the eastern faunal area are very suggestive. Thus, that the configuration of Mindanao Island is recent is clearly indicated by the fact that the reptilian and saurian faunas have not been completely dispersed over the island. This fact accords with Mr. Moody's palæogeographic conception of a Mindanao archipelago composed of at least five islands during late Pleistocene time.

The minor faunal region consisting of Surigao (eastern Mindanao), Leyte, Samar, and Bohol is easily explained by the

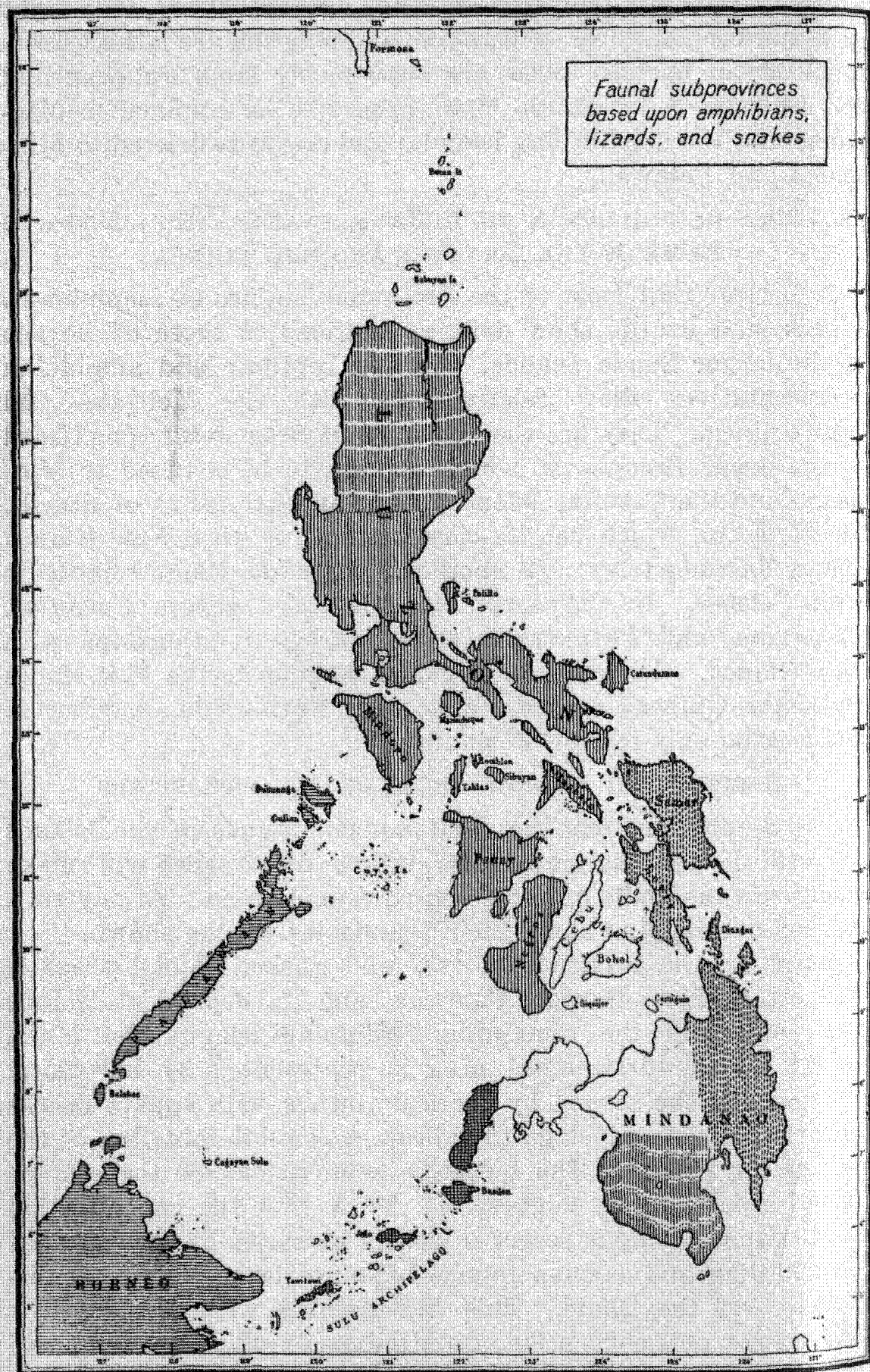


FIG. 56. Faunal subprovinces of the Philippines based on the distribution of amphibians, lizards, and snakes. Bornean (horizontal rulings), Philippine (vertical rulings), both Bornean and Philippine (checkered design).

conclusions, derived from a study of hydrographic conditions, that one large island existed in this region during the Pleistocene and that the present separation is due to the last restoration of glacial waters of the Pleistocene.

Former land connections of the Philippines are clearly indicated by the reptilian, saurian, and amphibian faunas of Palawan and the Sulu Archipelago; an isthmian connection with Celebes is likewise highly probable. Direct land connections between Mindanao and New Guinea via Halmahera, Talaut, and dependent islands is less probable, since some of the Philippine representatives of the New Guinean genera may have been rafted northward in the Kuro-Siwo. Possibility of northern connections is but slightly indicated by the three Philippine species of the snake genus *Hemibungarus*, which also occurs on the Riu Kiu Islands and the Asiatic mainland. This genus may be found in Formosa, as the reptilian fauna of that island is as yet but little known. The sparseness of amphibian, saurian, and reptilian forms of northern origin indicates that, if Luzon was once connected to Formosa, such connection was far more ancient than were the two or three southern connections of Pleistocene age.

TRUE FRESH-WATER FISHES OF THE PHILIPPINES

The exceedingly rich marine fish fauna of the Philippines is the same in general as that of the rest of the East Indies, though a few northern species extend from Japan to the Visayas. While no light can be thrown upon the geologic history of the Philippines by a study of its marine fauna, an examination of the fresh-water fishes leads to some interesting and positive conclusions.

Many species are found in the Philippine lakes and rivers, but most of them are marine or brackish-water species, or else they spawn in salt water and spend only a part of their life in fresh water. Examples of the first are sharks, rays, sawfishes, and various ophichthyoid and murænoid eels, which ascend rivers 250 kilometers or more from the sea. Examples of the second group are the mullets, or banak, Mugilidæ; some snappers, Lutianidæ; eels, Anguillidæ; bañgos, *Chanos chanos* (Forskål); some pompanos, Carangidæ; the ten-pounder *Megalops cyprioides*; some Holocentridæ; many Apogonichthyidæ; some Tera-ponidæ; the Kuhliidæ; *Scatophagus argus* (Gmelin); some pipefishes, Syngnathidæ; and many gobies. Some of those just named ascend rivers but a short distance or to some lake; but others, as the eels, mullets, and gobies, go to the most remote headwaters of Luzon and Mindanao, more than 300 kilometers from the sea. All return to the ocean when spawning time approaches, and this annual movement, whether of adults downstream or the influx of myriads of young at the river mouths, has given rise to very important fisheries, especially in Luzon, Mindoro, and Mindanao.

In nearly every stream can be found curious little fishes with elongated beaks, which on examination are seen to have but the lower half extended while the upper beak seems to have been cut off. These halfbeaks, near relatives of the flying fishes, spend their whole lives in fresh water. In most streams, too, there are gobies that do not go down to the sea; but since their affinities are all marine the fresh-water halfbeaks and gobies can be regarded as recent immigrants and can be

dismissed from consideration as having little bearing upon a study of the geologic history of the Philippines and the land connections of the various islands.

The catfishes, though a fresh-water group, include several representatives which have adapted themselves to life in either brackish or salt water, or to living indifferently in fresh or salt water. Omitting these, there are in the Philippines the following exclusively fresh-water fishes thus far known: One group of catfishes of four species, the Clariidæ; the dalag, or Ophiocephalidæ, with five nominal species; the climbing perch, or lawalo, *Anabas testudineus* (Bloch); the Osphromenidæ, with one species; and the carp family, or Cyprinidæ, with about twenty-seven species.

The first three are of very doubtful utility in a study of distribution. The dalag, or haluan, *Ophiocephalus striatus* Bloch, is a fish of remarkable tenacity of life, grows rapidly to a large size, is of fair food quality, and has therefore been widely distributed by the Malays in their wanderings. As a result it occurs in all parts of the Philippines. I have authentic records of dalag being placed in remote mountain lakes by both Christian and pagan Filipinos; in one instance no other fish was living in the lake. Of even greater ability to live without water is the climbing perch, and it too has been carried about by Malays, though not to the same extent perhaps, as owing to its smaller size it is less desirable. The commonest of the fresh-water catfishes, the hito, *Clarias batrachus* (Linnæus), has also been widely distributed by man. Though it is a better food fish than the climbing perch, it is apparently not able to adapt itself to such a variety of conditions as either of the two others and hence its Philippine range is not so wide.

THE GOURAMI OF CAGAYAN SULU

On Cagayan Sulu, which lies 64 kilometers off the coast of Borneo, is a species of *Trichopodus* which is confined to a small fresh-water lake there. This fish is evidently a survival of the days when Cagayan Sulu was an integral part of Borneo and is the sole representative in the Philippines of the widespread gourami, the only other species, which occurs from Borneo to Java and Siam. Cagayan Sulu lies at the outer edge of the Bornean shelf, and the great deep of the Sulu Sea north of it has effectually prevented the further extension of this species.

PHILIPPINE CYPRINIDÆ

There remains, accordingly, only the Cyprinidæ. The distribution of this family is strongly marked and corroborates to a remarkable degree the conclusions reached by a study of plants and other groups of animals in western Malaysia. The Cyprinidæ is the largest family of fishes and is undoubtedly of Asiatic origin, with a secondary center of distribution in eastern North America. Sumatra and Borneo are the chief centers of cyprinid life in Malaysia. Cyprinids are totally lacking in Celebes and occur nowhere east of Borneo except in the Philippines, and nowhere east of Wallace's Line except on Lombok Island and, perhaps, on the neighboring island Sumbawa, a single widespread species of *Rasbora* having succeeded in extending its range thus far eastward, previous to the formation of Lombok Strait. In the Philippines, Cyprinidæ are apparently confined to Mindanao and to Balabac, Palawan, Busuanga, and Mindoro. We are thus forced to the conclusion that there has been no land connection between Mindoro and Luzon, or else none since the Cyprinidæ reached northern Mindoro. It is likewise evident that Leyte, Bohol, Cebu, and Negros have also been separated from Mindanao for a very long time, if indeed any of them except Leyte was ever connected with it. Leyte and Samar seem to have been formed by the fusion of smaller islands, which have been alternately above and below sea level several times, so that Cyprinidæ would have been exterminated by salt water, if indeed the ancient islets ever possessed permanent streams of sufficient size to allow their immigration.

CYPRINIDÆ OF MINDANAO

A study of the Cyprinidæ of Mindanao also leads to some interesting conclusions. This great land mass was once five separate islands, but cyprinids abound in all parts of Mindanao, whether lowland or elevated plateau regions. In the Lanao Plateau, a volcanic district with a large lake as the central feature, occur thirteen species of Cyprinidæ, although the fishes of Lake Lanao and its tributaries are separated from all other regions by the impassable barrier of Maria Cristina Falls. That this isolation took place a long time ago is shown by the fact that three of the genera and all of the species of Cyprinidæ living there occur nowhere else.

It is self evident that Palawan and Mindoro were populated by Cyprinidæ from Borneo, via Balabac. It is likewise evident that the migration must have occurred when Palawan

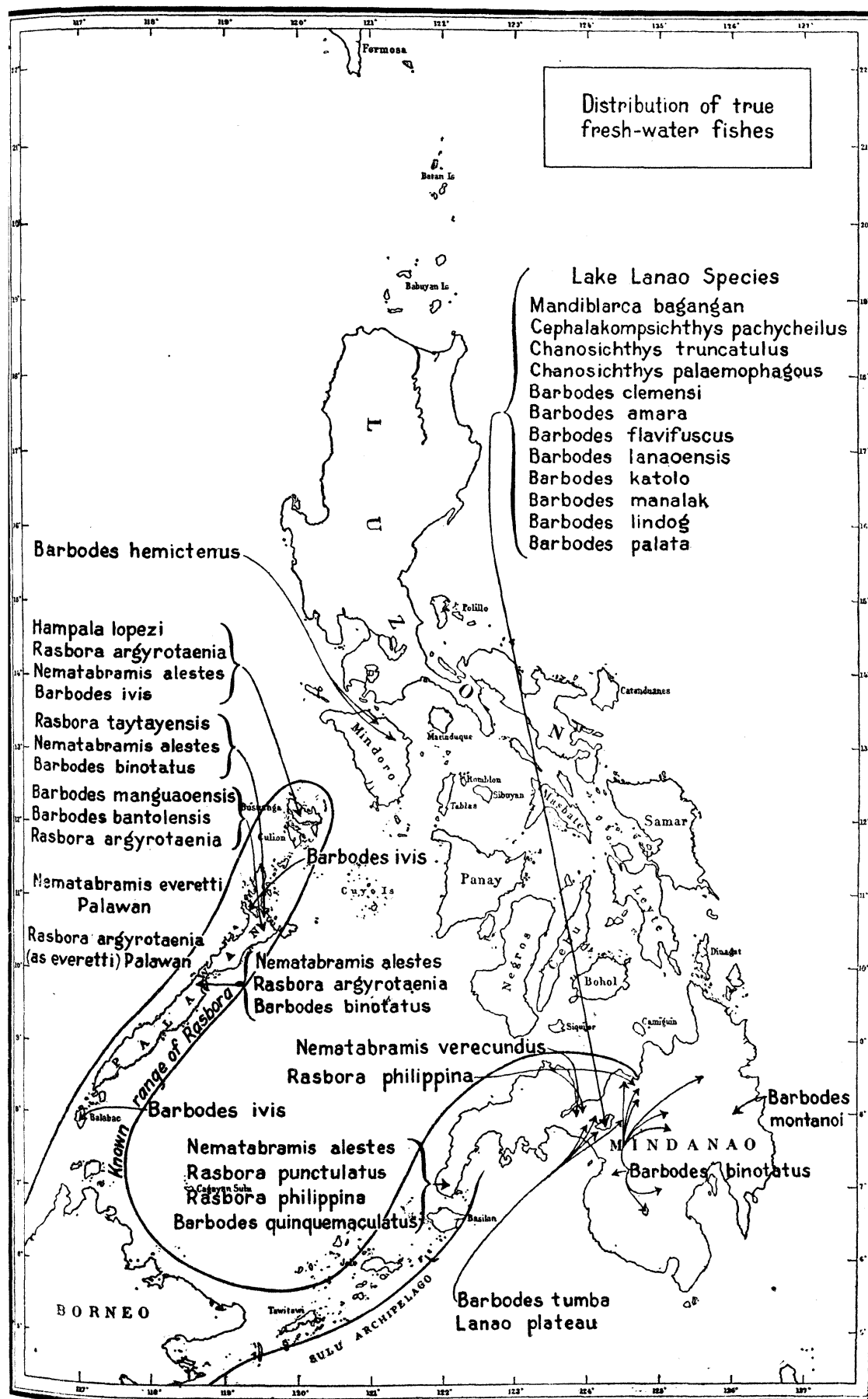


FIG. 57. Distribution of true fresh-water fishes in the Philippines.

had a greater area than at present and probably at a time when the southern end of the China Sea was land, and a great river flowed northward, draining western Borneo and Sumatra. At that time, with larger streams in Palawan, it would have been comparatively easy for fresh-water minnows to extend their range northward. The relatively large number of endemic species in Palawan shows that this condition ceased long ago.

The Cyprinidæ of Mindanao entered from Borneo over a Sulu land bridge. Cyprinids occur on Tawitawi and Basilan, but Jolo, the only other Sulu island with permanent fresh-water creeks, apparently lacks Cyprinidæ, as numerous collectors have failed to obtain them there; this is probably due to the great amount of volcanic activity on this small land mass in late Pleistocene or Recent time. The ubiquitous dalag and various gobies, eels, and other salt-water immigrants are apparently the only fresh-water fishes in Jolo.

The endemic species at Zamboanga, the nearest point of Mindanao to Borneo, furnish proof that connection ceased a long time ago, and the numerous changes in elevation that most of the Sulu islands have undergone have destroyed the cyprinids if any ever occurred there.

BORNEAN CYPRINIDS COMPARED WITH PHILIPPINE CYPRINIDS

There are approximately one hundred eight species of Cyprinidæ known from Borneo, in contrast to the twenty-nine* native Philippine species thus far collected. One of these is common to Borneo, Mindanao, and the Palawan islands. One species is known only from Zamboanga and Borneo; one from the Palawan islands and Borneo; one is confined to Mindoro, and one to Busuanga; one is thus far known from Palawan, Balabac, and Busuanga, while three species are confined to Palawan. Thirteen are limited to the plateau of the Lake Lanao region in Mindanao.

FORMOSAN FRESH-WATER FISHES

An examination of the fresh-water fishes of Formosa shows that there is no specific relationship between them and the fresh-water fishes of the Philippines and Malaysia. Of the fresh-water fishes of Formosa more than 61 per cent are endemic, excluding those artificially introduced or those that are wholly or partially marine or are really brackish-water forms.

* The carp, *Cyprinus carpio* Linnæus, has become established in Pulangi River, Cotabato, and in Lake Nunungan, Lanao, having been introduced from China a few years ago.

The nearest relatives of these endemic species are found in China, Korea, or Japan, and the majority of the fishes belonging to their genera occur in British India, Indo-China, and China. The whole fresh-water fauna, endemic and widespread species alike, shows close relationship to the neighboring continental forms. Eleven species are of more or less general distribution, from southern China to Korea and Japan, one only on the Chinese mainland, and one only in Japan. Seven species belong to a more southerly realm, occurring in Indo-China and southern China northward to, but not beyond, the Yangtze. An examination of the related species shows that all Formosan species with Chinese affinities have changed into more or less distinct species, while those ranging also southward into Indo-China are unchanged. Of the species not peculiar to Formosa, 80 per cent occur on the Chinese mainland. It would seem, therefore, that the fresh-water streams of Formosa were first occupied by fishes from the streams of China, long enough ago to give them time to be altered, while the species with southern affinities came up through southern China at a much later date and are consequently unaltered.

There is but one species recorded from both the Philippines and Formosa; as it is also found in southern China, there is no reason to believe that it reached Formosa via Luzon. The absence of recent land connections between Formosa and the Philippines is thus shown by a comparison of the fresh-water fishes of Formosa with those of the Philippines.

BORNEAN AFFINITIES OF PHILIPPINE FRESH-WATER FISHES

The absence of trout from the Baguio Plateau, where the conditions are not greatly unlike conditions in the highlands of Formosa in which a species of trout does occur, would seem to corroborate the statement that the Bashi Channel is an old one and that there has been no connection between Luzon and Formosa since Miocene time or even earlier. Fossil trout are known from Pliocene and Pleistocene deposits in Idaho, and from the Miocene in Bohemia. We may be reasonably certain therefore that if there ever was any connection between Formosa and Luzon it was a very ancient one and was broken a long time ago, so that the only land connection by which fresh-water fishes could arrive in the Philippines was that with Borneo. The true fresh-water fishes of the Philippines must then be considered as having been wholly derived from western Malaysia via Borneo.

INSECTS OF THE PHILIPPINES

Due to the enormous development of insects in genera and in species, and the imperfect knowledge of geographic distribution of Malaysian insects, it is hardly possible to draw general conclusions as to faunistic alliances from a study of this group alone, although the distribution data now available conform remarkably to the distribution of plants and the various groups of animals. A large amount of work remains to be done in the field and in the museum before the essential data on geographic distribution for most orders of insects will become generally available. Present knowledge of Philippine and Malaysian insects and of the geographic distribution of the various groups indicates that alliances exist between the insect fauna of the Philippines and that of both eastern and western Malaysia. As in other groups of animals and the various groups of flowering plants and cryptogams, a definite Asiatic element, which is apparently absent from Malaysia, is also found in the Philippines, especially in northern Luzon. In its insect fauna, as with other groups of both animals and plants, the Philippine Archipelago is characterized by a high percentage of endemism.

With the insects, as with other groups of both animals and plants, the value of distribution data varies in the several orders. No attempt has here been made to cover the entire field, but a few major groups have been selected on which intensive work has been recently done; some of these indicate close relations with the islands south and southeast of the Philippines and some with the islands to the southwest, while others present definite continental (Asiatic) types. In this group of organisms, probably more than in any other discussed in this book, it seems to be evident that the distribution data of any one subgroup, be it order, family, or genus, cannot be taken alone as showing the true biologic relationships of the fauna of the Philippines with that of surrounding regions.

GENERAL ALLIANCES OF PHILIPPINE INSECTS

The relationships of the Philippine insect fauna suggest previously existing land bridges to the south connecting Sangi, the Moluccas, Morotai, Gilolo, Ternate, and Batchian with the

Philippines, with perhaps a northern extension through the Babuyan Islands to Formosa and thence to the mainland of Asia.

The insect fauna of the Philippines is in general more closely related to that of Malaysia as a whole than to that of China. The most manifest alliances are apparently with the southern part of eastern Malaysia, that is, Celebes, with less-pronounced relationships with the Moluccas and the eastern part of New Guinea and still less-pronounced relationships with Borneo and Sumatra or western Malaysia. The least evident relationships are with the mainland of Asia by way of China.

The Philippine insect fauna presents a high percentage of endemic elements, and thus the relatively great antiquity of the present fauna is demonstrated. The orders of insects that are generally considered to be of great antiquity, such as Orthoptera, are particularly well developed in the Archipelago as to number of species; especially in the families Phyllidæ, Phasmidæ, Acridiidæ, subfamily Tetriginæ, and Blattidæ. In these families, furthermore, are many species that present strong mimetic characters; that is, a general resemblance to surroundings, such as leaves, bark, and mossy stones. This feature is present in a much more-pronounced degree in these families than in any other group of Philippine insects. The following examples will demonstrate the geographic alliances of the Philippine Orthoptera:

The Phyllidæ (leaf-insects) presents three genera with sixteen species. The genus *Phyllium* Illiger presents eleven species, of which four are found in the Philippines, although none is endemic. They are indigenous, however, and their general distribution is eastern Africa, the Mascarene Islands, Seychelles, Ceylon, India, the Sunda Islands, Moluccas, Philippines, and New Guinea. *Chitoniscus* Stål presents five species in Fiji, New Caledonia, the Loyalty Islands, and New Britain. The genus *Nanophyllum* Hedt is monotypic and confined to New Guinea.

The Phasmidæ is found in the warmer parts of the world, but particularly in the warmer and damp tropical and subtropical regions. The largest number of phasmids is found in the Indo-Malaysian-Australian region and then, in order of abundance, in the following regions: Tropical Central and South America, Australia, Africa, North America, Europe. The subfamily Obrismininæ presents thirteen genera, seven of which occur in the Philippines; three are endemic. The largest, a

very highly specialized genus, *Obrimus* Stål, presents eight species, seven of which are found in the Philippines; six are endemic, and one is common to Palawan and Borneo; one is confined to Borneo.

The subfamily Tetriginæ of the Acridiidae is another group of highly specialized orthopteroid insects, is extraordinarily well represented in the Philippines, and presents a group that is of special value in reference to geographic distribution. This group presents about ninety-eight genera and about four hundred fifty species. It is of world-wide distribution, but is especially developed in the Tropics where many diverse forms occur, in contrast to the less bizarre or specialized forms of temperate regions. Bruner lists one hundred four species in thirty-one genera as occurring in the Philippines, of which ninety-seven species in nine genera are endemic; only seven of the Philippine species occur outside of the Archipelago, ranging as follows: One, Philippines and Burma; one, Philippines, Java, and Burma; one, Philippines and Celebes; one, Philippines and Sumatra; one, Philippines and (?) Australia; one, Philippines, Java, Sumatra, Borneo, Australia, Caledonia, and Japan; and one, Philippines, Java, Sumatra, Siam, Ceylon, and Burma. Twenty-three per cent of the species belonging to this subfamily, known from the entire world, occur in the Philippines and of the ninety-eight genera thirty-one, or 32 per cent, occur there.

Hebard * makes the following significant statement on the distribution of the Orthoptera in Malaysia:

We have found that Wallace's line separates quite as large a percentage of species of Tettigoniidae as of the Mantidae, clearly delimiting the Malayan from the Melanesian fauna.

An examination of his extensive paper on the orthopterous groups of Tettigoniidae shows that of the ninety-four genera considered thirty-five occur in the Philippines. Nine of these are endemic; thirteen are common to the Philippines and western Malaysia and do not occur in eastern Malaysia (Melanesia of Hebard); while four genera occur in the Philippines and eastern Malaysia but are unknown from western Malaysia. The geographic distribution of this particular group of insects is thus in striking conformity with the Philippine phytogeographic relationships with both western and eastern Malaysia, and is definitely much stronger with the former than with the latter.

* Proc. Acad. Nat. Sci. Philadelphia 74 (1922) 121.

Philippine blattids (cockroaches) find their closest allies in the Moluccas. Certain very striking elements are represented by the genus *Prosoplecta* Saussure. Shelford speaks of this genus as follows: *

The geographical distribution of *Prosoplecta* is as follows:—Eight of the species are found in the Philippine Islands, one in Celebes, the remaining three in Batchian and Ceram. None has yet been discovered in the Great Sunda Islands, so that the distribution is discontinuous and serves to emphasize the view that if the Philippines are to be regarded as a part of the Indo-Malayan region, their separation from adjacent land is of very great antiquity. The Philippine Islands constitute an area in which insect mimicry has attained great perfection. That is shown not only by these wonderful cockroaches mimicking Coleoptera, but Professor Poulton tells me that some of the most wonderful examples of mimicry amongst butterflies are known from these islands only, e. g. the distasteful Danaine genus *Hestia* † is mimicked very closely by a Satyrine and an Elymniine. Again, the gorgeous little Curculionidæ of the genus *Pachyrhynchus* [sic] are mimicked by other weevils, by Longicorns, by Cetoniids, and by a cricket. A comparative study of mimetic insects in geographically adjacent but zoologically distinct areas, such as Borneo, the Philippines, and Celebes, is a piece of research that would surely yield some very interesting results.

KNOWN NUMBERS OF PHILIPPINE SPECIES OF THE VARIOUS INSECT ORDERS COMPARED WITH THE PROBABLE NUMBERS

The insects (Insecta), the largest class of the animal kingdom, together with the spiders (Arachnida), centipedes (Chilopoda), millipedes (Diplopoda), and lobsters and crabs (Crustacea), form the great subkingdom Arthropoda. In order to give an approximate idea of how large a field entomology has in the Philippine Islands and what is actually known concerning insects and their allies, a rough estimate follows as to the number of unknown species, and the actual number of species known and determined belonging to the more important orders of Insecta in the Philippine Islands.

The largest order, the Coleoptera (beetles), is estimated to contain about 7,500 Philippine species of which up to 1915 about 2,500 were known and at present (1925), about 4,600 species.

Lepidoptera (butterflies and moths); estimated, about 3,800; known, 1,825.

* Proc. Zool. Soc. London (1912) 368.

† The most striking mimic of *Hestia leuconoë* Erichson, in the Philippines, is *Papilio idaeoides* Hewitson.—W. SCHULTZE.

Rhynchota (true bugs, water bugs, cicadids, fulgorids, lice, plant lice, and scale insects); estimated, about 3,500; known, 1,600. The order Rhynchota is best represented specifically in the Philippines and has the greatest diversity of forms in its components.

Diptera (flies, gnats, and mosquitoes); estimated, about 2,500 species; known, about 500. The mosquitoes comprise about 200 species, 90 known.

Hymenoptera (bees, wasps, ants, and gall flies); estimated, 2,500 species; known, about 800.

Orthoptera (grasshoppers, locusts, crickets, praying mantes, bark insects, leaf insects, walking sticks, and cockroaches); estimated, 2,500 species; known, 750.

Mallophaga (bird lice); estimated, 500 species; known, 75.

Neuroptera (raphidians, aphid lions, and ant lions); estimated, 200 species; known, 20.

Dermoptera (earwigs); estimated, 100 species; known, 25.

Odonata (dragon flies); estimated, 100 species; known, 25.

Trichoptera (caddis flies); estimated, 100 species; known, 5.

Isoptera (termites, or white ants); estimated, 100 species; known, 40.

Mecoptera (scorpion flies); estimated, 25 species; known, 3.

Thysanura (silver fishes); estimated, 25 species; known, 3.

Corrodentia, family Psocidæ (book lice); estimated, 10 species; described, none.

The total number of insect species of the Philippine Islands is estimated at 25,000; of which about 10,000 species, or approximately 40 per cent, are known.

The classes Arachnida, or spiders, scorpions, etc.; Chilopoda, or centipedes; and Diplopoda, or millipedes, are closely related to the insects; their Philippine species are estimated to number 1,000, of which about 50 are known.

PHILIPPINE LEPIDOPTERA AND SEMPER'S PROVINCES AND SUBPROVINCES

Since the Lepidoptera of the Philippines is the best known of all the different insect orders, it is from this group more than from others that we can obtain data on distribution of species among the different islands of the Philippines, as well as in neighboring regions outside the Archipelago. Furthermore, this order furnishes excellent data on the indigenous and endemic elements in the Philippines, and this is particularly true of the

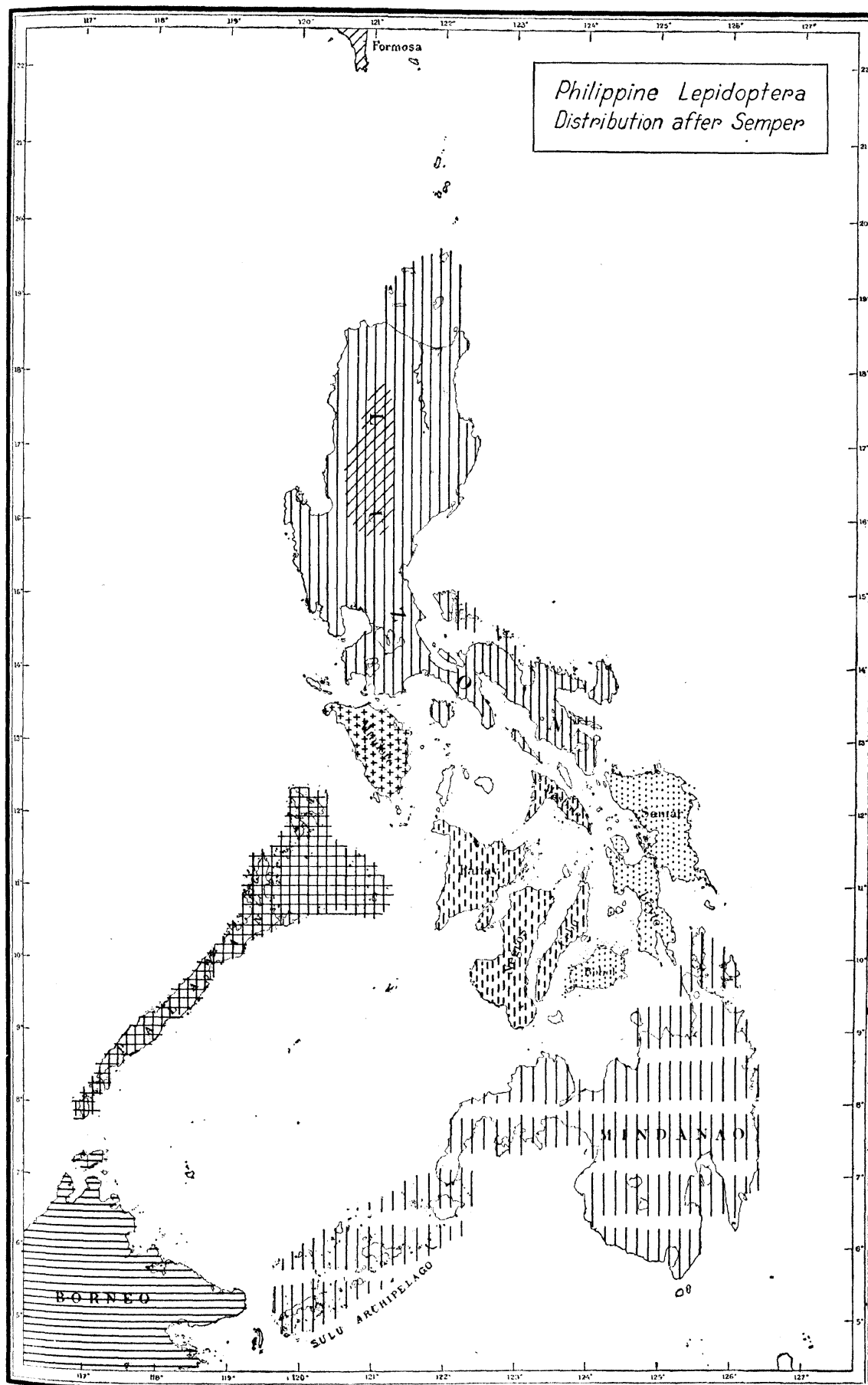


FIG. 58. Distribution of Philippine Lepidoptera according to Semper.

butterflies. Of those who have studied Philippine Lepidoptera, George Semper obtained the best results. His observations and statements concerning the Lepidoptera of the Philippine Islands are based on actual examination of over 50,000 specimens; suborder Rhopalocera, butterflies, over 33,000 specimens, 612 species; suborder Heterocera, moths, 20,000 specimens, 907 species. On the basis of the specimens studied by him Semper divides the islands of the Archipelago into six faunal districts, as follows:

First district.—Luzon, Marinduque, Burias, Catanduanes, Polillo, Babuyan, and Batanes. He mentions especially for the first district the presence of several Indo-Chinese or Asiatic genera that seem to be missing from other parts of the Philippine Islands; namely, *Debis*, *Vanessa*, *Pyrameis*, *Argynis*, *Pieris*, and *Colias*. Since the time of his writing several still more striking European and Central-Asiatic genera have been found in the high mountain ranges.

Second district.—Mindoro. In many respects similar to the first district, but with some species in common with the districts southwest and southeast of it.

Third district.—Busuanga, Culion, Palawan, Dumarang, Cuyo, and Balabac. The fauna of this district has a comparatively very large number of genera not represented in the other islands of the Philippines and, in its faunistic values, has closest relation with Borneo and the large Sunda Islands. According to Pagenstecher's statement, approximately 50 per cent are Philippine and 50 per cent Bornean.

Fourth district.—Panay, Guimaras, Negros and Cebu, and doubtfully Masbate and Ticao. Semper mentions particularly that Panay has several rather peculiar indigenous species in common with Luzon.

Fifth district.—Samar, Leyte, Bohol, Camotes, and Panaon. From this district he reports no endemic genera but does report very well defined local species along with others which reach over to Mindanao.

Sixth district.—Mindanao, together with Camiguin, Dinagat, Siargao, Sarangani, Basilan, Sulu, and Tawitawi.

The distribution of Rhopalocera, or butterflies, in the Philippines is shown in text fig. 58. The approximate average number of species in a given district in the Philippine Islands is estimated to be two hundred fifty-five. On this basis the percentages are given in Table 27.

Some comparison between the number of species of Lepidoptera in the Philippines and in adjoining faunistic regions is of interest. The approximate number of butterfly species of British India, Ceylon, and Burma is eight hundred. The Philippine butterfly species are estimated at about seven hundred, of which six hundred twenty-five are exactly identified. The approximate number of moth species of British India, Ceylon, and Burma is fifty-five hundred. The Philippine moth species are estimated at about three thousand, of which about twelve hundred have been identified. Probably comparatively few of the large and medium-sized Lepidoptera remain undiscovered, but the smaller moths are not so well known.

TABLE 27.—*The endemic elements in the Lepidoptera-Rhopalocera (butterflies) in the Philippine Islands, based on Semper's study of over 33,000 specimens.*

District.	Species.	Percentage based on an average of 255 species to a district.
Luzon alone.....	61	25
Luzon and Mindoro.....	13	
Mindoro alone.....	18	7
Mindoro and Palawan.....	2	
Mindoro and Visayas.....	3	
Palawan alone.....	128	55
Visayas alone.....	11	
Visayas and Mindanao.....	38	
Mindanao alone.....	83	32
Several.....	255	
Total.....	612	

During the last ten years some very striking indigenous species of Lepidoptera have been found in Luzon, particularly in the higher mountains. For example, a very large moth, *Actias maenas* Doubleday, cannot fly farther than a few hundred meters and is dependent on the oak family (Fagaceæ) for its food. This species is known from Sikhim, Darjeeling, Bhutan, Khasi Hills, Burma, and Siam. Another species of this genus, *Actias selene* Hübner, is known from India, Sylhet, Java, China, and Poona. However, no species of *Actias* is reported from Borneo, Sumatra, or Celebes and, since *Actias* species are easily recognized, it could hardly have escaped observation by entomologists who collected in those regions. From the mountains of Benguet the genus *Agrotis*, with seven indigenous species, is recorded.

Its wide range of distribution is as follows: Europe, Asia, China, Japan, and the Philippines. The great distribution may be conditioned by its food supply, the Umbelliferæ. At Pauai (Haight's place, 2,400 meters), Benguet Subprovince, McGregor collected the indigenous swallow-tail butterfly *Papilio xuthus* subsp. *benguetana* Joic and Talbot, which probably feeds on plants of the family Umbelliferæ, possibly *Oenanthe* or *Pimpinella*. Its distribution is also very peculiar; namely, Persia, Siberia, Thibet, China, Korea, Japan, Formosa, the Riu Kiu Islands, the Bonins, Guam, and now northern Luzon but not farther south. The distribution of Philippine Lepidoptera in general, as well as the large number of endemic and indigenous species in northern Luzon from the north that range scarcely beyond that island, indicates that these northern types entered Luzon at a time when there were still land connections with the mainland of Asia by way of Formosa or China. Furthermore, a land connection extended through the Philippines to the Moluccas and Celebes as the relations of Philippine species to the species of those islands show. The large percentage of endemic elements in the different islands indicates that islands in the Philippine region have existed for a long time, a fact established particularly by endemic genera. This fact will be brought out still more clearly in the discussion of the Coleoptera. The high percentage of endemism shows, furthermore, that island character was assumed almost simultaneously among the different islands of to-day, even among some of the small islands like Polillo, Catanduanes, Siargao, and Bucas. The endemic elements are clearly demonstrated in the comparative table of Semper, Table 27.

In principle I agree with Semper on the endemic elements of Lepidoptera; however, his figures are entirely too conservative, mainly due to the fact that his collector, Prof. Carl Semper, his brother, was limited to certain localities. Such regions as the high mountains along the northeast coast of Luzon, in central Mindoro, and in central Mindanao could not be explored at that time. In such regions many more endemic species have been collected since and many more will be discovered. Therefore, the actual percentage of endemic species is relatively much higher than Semper's table indicates.

Pagenstecher * states that Palawan may be accepted as a bridge between Borneo and the Philippines; he bases his con-

* Die geographische Verbreitung der Schmetterlinge (1909).

clusion on the distribution of the true butterflies, after Staudinger.* Of the two hundred eighty-three known Palawan species about one hundred thirty are found in the rest of the Philippines and one hundred twenty in Borneo, while about sixty-five are common to the three regions. Pagenstecher states that the Palawan moths have a geographic distribution similar to that of the butterflies. The moth fauna of Palawan appears to be a mixture of species from the large Sunda Islands (especially Borneo) and the Philippines, with a number of endemic species; but the Bornean element predominates. My conception of the Lepidoptera fauna of Palawan is that it is by far more closely related to that of Borneo than to that of the rest of the Philippines.

PHILIPPINE COLEOPTERA

The Coleoptera of the Philippines are not so well known as are the Lepidoptera. The estimated number of species is about seventy-five hundred, about forty-six hundred of which are known and identified. In Schultze's catalogue of the Coleoptera of the Philippine Islands about twenty-five hundred species are mentioned (1915). Since that time about twenty-one hundred species have been added by identification and description. The Coleoptera fauna of the Philippine Islands in its general aspect is also most nearly related to that of Celebes, Sumatra, and Borneo. It also has a rather large number of endemic genera and species. Coleoptera of Palawan are distinctly set off from those of the rest of the Philippine Islands by being pronouncedly Bornean in character.

The largest family of the Coleoptera, Curculionidæ, is well represented in the Philippine Islands by about eight hundred twenty-five known species at the time of writing. One of the outstanding features of the Philippine Curculionidæ is that it contains a large and peculiar group of beetles, the highly modified pachyrrhynchids, with eleven genera and about three hundred nine known species; that is, about 37 per cent of the Philippine Curculionidæ. Approximately ninety species of the pachyrrhynchids are confined to the Philippine Islands. A very few are found in adjacent regions; these will be discussed later. The pachyrrhynchids have attracted the attention of systematic entomologists for many years on account of their

* Iris, Dresden (1888) 273; (1889) 1.

peculiar and unique structure, their limited distribution, their rather striking coloration, and their mimetic relation to species of related genera, to each other, and to certain genera and species of entirely different families. Most species of this group are found in mountainous regions, many in rather inaccessible localities, and are widely scattered over the Islands; this accounts for the fact that it is only in the last ten years that any considerable progress in the knowledge of this group has been made.

HABITS OF THE PACHYRRHYNCHIDS

In order that the peculiarities of this group may be better understood, a more-detailed short description of the pachyrrhynchids is here given, setting forth some of the points on which they differ from other Curculionidæ. The snout beetles belong to the largest family known, the Curculionidæ. In these insects, the head is more or less prolonged into a beak which is used for boring. Ninety per cent of the snout beetles have the regular hard wing covers, or elytra, and also the regular transparent wings for flying well developed. The legs are mostly short and not particularly adapted for walking. In the pachyrrhynchids the rostrum is short and broad, the thorax mostly subspherical, the elytra subspherical to oval; the soft wings for flying are entirely absent. Furthermore, the elytra along the suture have degenerated to such a degree that they have actually grown together and cannot be separated. The whole structure of the body is extremely hard and solid. In fact, the body is so solid that one may step on these beetles lying on the ground in the forest without injuring them. The legs are rather long and are adapted for walking about on twigs and leaves of plants. The appearance of the beetles in walking about is spiderlike. This appearance is partially due to their peculiar markings. Very little is known concerning the life habits of this group. The following fragmentary account is the only record of its biology.

The species *Pachyrrhynchus venustus* Waterhouse was found on a fern, *Acrostichum aureum* Linnæus, in the swamp at the base of Mount Maquiling, Laguna Province, Luzon. This beetle has the same common behavior as have other species of the group; namely, in climbing about, on being approached, it tries to hide by crawling to the underside of a leaf or to the opposite side of the stem, but if approached closely it instantly drops to the ground, draws the legs up close to the body, and remains motionless for some time. In the dense undergrowth it is very

difficult to rediscover the beetle once it has dropped. Hardly any other curculionid group can equal this group in beauty of color, and very few in general scientific value. (Plate 33.)

DISTRIBUTION OF THE PACHYRRYNCHIDS

Concerning their importance, Prof. K. M. Heller of Dresden, eminent specialist on the Curculionidæ, made the following remarks about the pachyrrhynchids in 1912:

The scientific value which has been neglected by the systematic entomologist and speculative zoölogists, particularly as regards geographic distribution, as they did not know what to make of the group can only be brought forward gradually through knowledge of the different species involved. It seems that hardly any other group offers so many problems as the one in question.

The geographic distribution of the group is strikingly peculiar and interesting in view of the fact that all the species are wingless and, therefore, have extremely limited qualifications for traveling.

The pachyrrhynchids are represented by 14 genera and 344 species, distributed as follows: In the Riu Kiu Islands, 1 genus and 1 species; Borneo, 1 genus and 1 species, the genus endemic; New Guinea region, 2 genera and 27 species, 1 of the species reaching to Australia; Moluccas, 3 genera and 6 species; the Philippines, 11 genera and 309 species, of which 9 genera are endemic and 5 genera endemic to Luzon; 1 genus endemic to Panay; 1 genus endemic to Negros.

Table 28 shows clearly that Luzon is the probable center of dispersal of the pachyrrhynchids in the Philippine Islands. More-detailed information on this group of beetles is given in a monograph by Schultze.*

Near the northeastern part of Australia, in the Solomon Island-Bismarck Archipelago-New Guinea region (with at least one species extending to Australia) is the genus *Pantorhytes* Faust, represented by four species; this genus is most closely related to *Pachyrrhynchus* and may be considered its ancestral form or vice versa. Another genus of the pachyrrhynchids found outside the Philippine Islands, *Sphenomorpha* Behrens, contains about nine species and is found from New Guinea to the Moluccas. Another genus of this group, *Apocyrtidius* Heller, with one species only, is found in Borneo. Aside from the three genera mentioned, with about thirty species, there are in

* Philip. Journ. Sci. 23 (1923) 609-673, pls. 1-6; 24 (1924) 309-366, pls. 7-9; 25 (1924) 356-390, pls. 1, 2; 26 (1925) 131-309, pls. 1-12.

TABLE 28.—Showing the distribution of the pachyrrhynchids (subfamily Brachyderinæ, family Curculionidæ), June 10, 1925.

Genus.	Philippine Islands, 309 species and 23 subspecies.																									
	Riu Kiu Islands.	Babuyanes.	Batanes.	Luzon.	Pollilo.	Catanduanes.	Mindoro.	Romblon.	Sibuyan.	Masbate.	Ticao.	Leyte.	Biliran.	Samar.	Panay.	Negros.	Cebu.	Bohol.	Dinagat.	Sitargao.	Bucas.	Mindanao.	Basilan.	Palawan.	Busuanga.	Sulu Islands.
<i>Pachyrrhynchus</i>	1	2	2	55	4	4	2					2		8	1	1		2	1	3	4	14	1			
<i>Eupachyrrhynchus</i>				1																						
<i>Macrocyrus</i>				12																						
<i>Eumacrocyrtus</i>																1										
<i>Prospocyrtus</i>															1											
<i>Apocyrtus</i>				2																						
<i>Pseudapocyrtus</i>				6	1	1																				
<i>Nothapocyrtus</i>				1																						
<i>Ezanolhapocyrtus</i>				5																						
<i>Metapocyrtus</i>		2	3	74	5	2	5	2	3		1	8	4	12	5	11		7	3	6	4	25		1	1	2
<i>Homalocyrtus</i>				3	1	1		1	1		1	2		2				1	1	1	1	2				
<i>Pantorhytes</i>																										
<i>Sphenomorpha</i>																										
<i>Apocritidius</i>																										
Total.....	1	4	5	159	11	8	7	3	4		2	12	4	22	7	13		10	5	10	9	41	1	1	1	2

Genus.	Moluccas, 6 species.						New Guinea to Australia, 27 species.							Total species.	Total subspecies.		
	Borneo.	Sangi.	Talaut.	Ternate.	Halmahera.	Batchian.	New Guinea.	Southeast.	Celebes.	Morty.	Fiji.	Woodlark.	Solomon.			New Britain.	Australia.
<i>Pachyrhynchus</i>		1		1	1											87	13
<i>Eupachyrhynchus</i>																1	
<i>Macrocyrtus</i>																12	
<i>Eumacrocyrtus</i>																1	
<i>Proapocyrthus</i>																1	
<i>Apocyrthus</i>																2	
<i>Pseudapocyrthus</i>																8	
<i>Nothapocyrthus</i>																1	
<i>Exnothapocyrthus</i>																5	
<i>Metapocyrthus</i>																180	10
<i>Homalocyrtus</i> ^a			1				15	1			1	2	2	1	1	16	
<i>Pantorhytes</i>							5		1	1						20	
<i>Sphenomorpha</i>																9	
<i>Apocrytidius</i>	1															1	
Total.....	1	1	1	1	2	1	20	1	1	1	1	2	2	1	1	344	23

^a The species of *Homatocyrtus* are imperfectly known, and some specimens of this genus have not been identified; the numbers in the table indicate the species that have been determined.

the regions indicated outside the Philippine Islands, three species of the genus *Pachyrrhynchus*, in Sangi, Ternate, and Morotai Islands, and one species of *Homalocyrtus* in Talaut. Thus, the pachyrrhynchids are represented in Borneo and to the southeast of the Philippines by thirty-four species in five genera and only two of those genera extend to the Philippine Islands (see fig. 57).

The pachyrrhynchids are represented in the Philippines by eleven genera and about three hundred nine species. Nine genera are endemic to the Islands, five are found only in Luzon, one only in Panay, and one only in Negros. Three genera seem to be rather evenly distributed over all of the islands except Luzon (see Table 28), which has by far the greatest number of species; namely, one hundred fifty-nine of the three hundred nine Philippine species. Mindanao contains the second best representation, with forty-one species. The outstanding feature of the distribution of pachyrrhynchids is that about 64 per cent of the species are found in Luzon. Comparison of the species of the Philippine Islands with those found outside the Islands, to the south, shows three hundred nine Philippine species against thirty-four extra-Philippine species, or only about 11 per cent extra-Philippine. Table 28 shows another peculiarity of distribution; three species of *Pachyrrhynchus* are found south of the Philippine Islands and eighty-three in the Philippine Islands, fifty-five of which are found in Luzon and one is found north of the Philippine Islands in the Riu Kiu group (Ishigakishima) (see fig. 59).

The Riu Kiu species is of extraordinary importance because it is difficult to account for its presence in the Riu Kiu Islands, the fauna of which is Formosan in character, yet no species of this group of beetles is known to occur in Formosa.

Other significant facts are that the monotypic genus *Eumacrocyrtus* of Negros is most closely allied to the endemic Luzon genus *Macrocyrtus*, and the monotypic genus *Proapocyrtus* of Panay is most closely related to the endemic Luzon genus *Apocyrtus*. The monotypic Bornean genus *Apocyrtidius* seems to have characters intermediate between *Pachyrrhynchus* and *Metapocyrtus*, the two largest Philippine genera.

What conclusions can be based on the above outlined facts? Heller * makes the following statement in this respect:

Probably the expansion of the pachyrrhynchids reached the Philippine Islands only in the most recent geological period and through the large

* Philip. Journ. Sci. § D 7 (1912) 297.

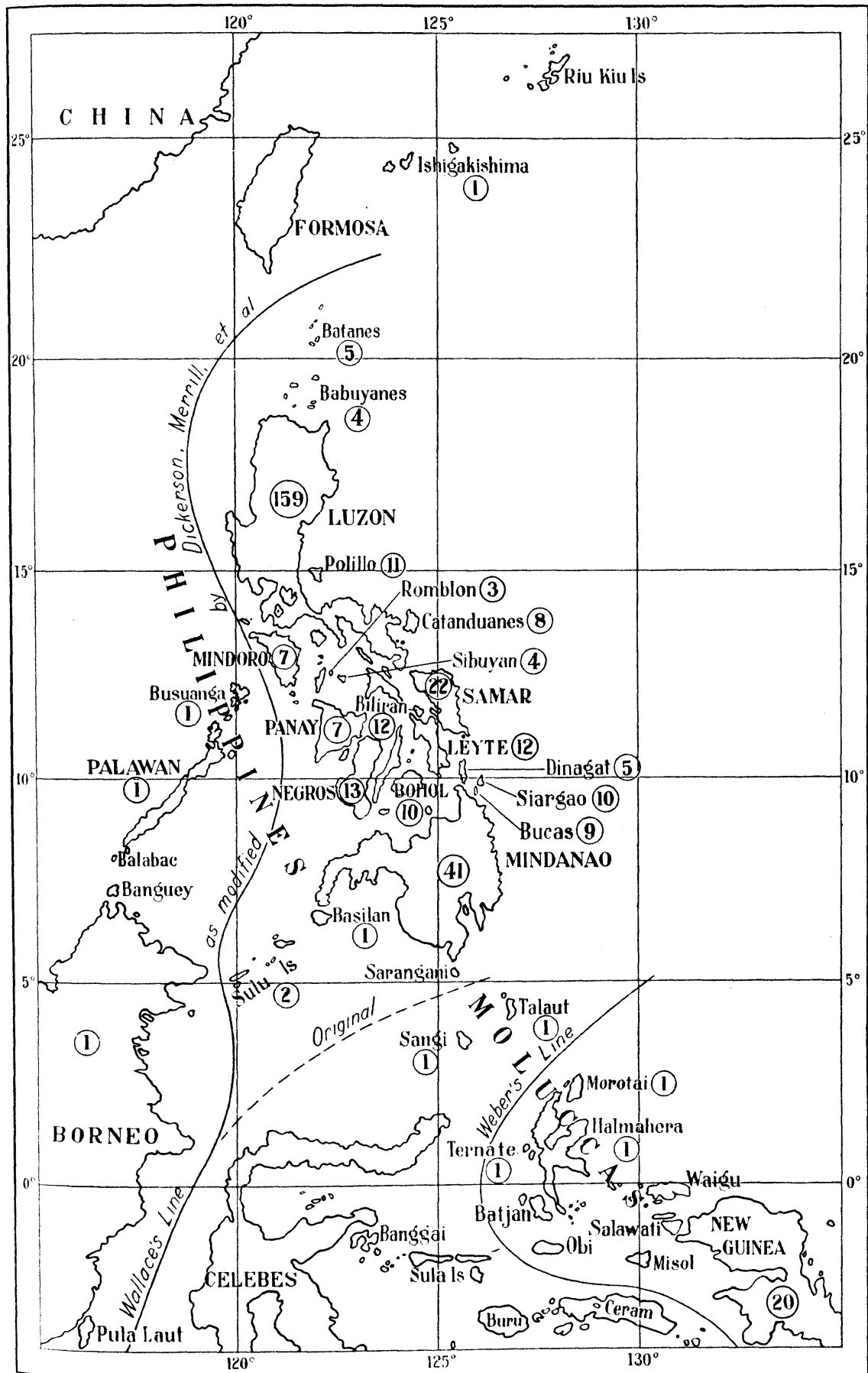


FIG. 59. Distribution of the pachyrrhynchids in the Philippine Islands and adjacent regions. The southern part of Weber's Line should have been drawn between Sula and Buru, as in fig. 4.

territorial extension across 15 degrees of latitude led to the development of a large number of species.

According to Heller the Sarasins make the statement, as a result of their studies, that a direct connection never existed between the Moluccas and the Philippines, but that the Moluccan-Papuan elements reached the Philippines only by way of Celebes. With this statement I do not concur. Reasons for dissenting from the views of Heller and of the Sarasins are given on another page.

Wallace * makes the following statement:

The Philippines are almost surrounded by deep sea, but are connected with Borneo by means of two narrow submarine banks, on the northern of which is situated Palawan, and on the southern the Sulu Islands. Two small groups of Islands, the Bashees and Babuyanes, have also afforded a partial connection with the continent by way of Formosa. It is evident that the Philippines once formed part of the great Malayan extension of Asia, but that they were separated considerably earlier than Java; * * *. They have also received a few Chinese types by the route already indicated, and a few Australian forms owing to their proximity to the Moluccas. * * * Beginning in late Miocene times when the deposits on the south coast of Java were upraised, we suppose a general elevation of the whole of the extreme shallow seas uniting what are now Sumatra, Java, Borneo, and the Philippines with the Asiatic continent, and forming that extended equatorial area in which the typical Malayan fauna was developed. After a long period of stability, giving ample time for the specialisation of so many peculiar types, the Philippines were first separated; then at a considerably later period Java; a little later Sumatra and Borneo; * * *.

CONCLUSIONS BASED ON THE DISTRIBUTION OF PHILIPPINE INSECTS

My conclusions based on the study of insects are as follows: The Philippines were connected with the mainland of Asia (possibly through Formosa, possibly through a now completely obliterated formation) at a very early period. During this time indigenous species now found in the uplands entered Luzon. Then a separation occurred, between Luzon and the land north of it at least. After the first break the Philippine Islands still were connected with each other, with the exception of Palawan. The Philippine Islands, through the eastern chain by way of Mindanao, were connected with the Moluccas, Celebes, and probably New Guinea and some of its nearby islands. During the same period the invasion and distribution of Papuan-Malaysian elements, such as the ancestral derivative forms of Lepidoptera and pachyrrhynchids, as mentioned before took place. This invasion

* Island Life, ed. 3 (1902) 389.

must have extended over a long period of time during which some of the Papuan forms reached as far as northern Luzon, the Riu Kius being at that time, together with the Babuyanes, probably connected with Luzon. After that long period of stability the Philippines were the first to be separated from the rest of the Malay region, the break occurring at the junction near the Moluccas. At that time also it seems that the Philippine Islands became isolated from one another and assumed practically the island character of to-day. At the period when the Philippines were isolated from the rest of the Malay region, probably Celebes, Java, Sumatra, Borneo, and Palawan were still connected with each other. During the last period the various endemic genera developed, particularly in the pachyrrhynchids.

Heller's statement that the pachyrrhynchids reached the Philippine Islands in the most recent period from the south is not sustained by my study. If his statement were correct, such highly modified and specialized forms should also be found in Celebes, Sumatra, Java, or Borneo in somewhat relative abundance. Furthermore, it is an accepted fact that all forms which exhibit mimicry of their surroundings or of some other insect or object are considered very old species, since such tendencies can only be produced very slowly through natural selection and the survival of the fittest. Furthermore, the model, being the protected and more-abundant species, is older than the mimetic, rarer, and more-recent species. Upon these various grounds it is apparent that Luzon was at least the secondary center of development and distribution of the pachyrrhynchids and from there they extended their range over land connections north and south as opportunity offered, during the Tertiary and the Quaternary.

In general, the Philippine insect fauna presents the same series of alliances as do the flora and other elements of the fauna. In certain groups, the alliances are stronger with the islands to the south and southeast of the Archipelago, while in other groups the alliances are stronger with western Malaysia. In the mountains of northern Luzon there is a striking representation of Asiatic types of insects, corresponding to the rather striking floral elements and certain representatives of our avifauna. The insect distribution, in itself, indicates previous land connection to the north or northwest, but this must have been very early; to the south and southeast, with Celebes, the Moluccas, and New Guinea; and to the southwest, with western Malaysia. Conclusions drawn from the known geographic dis-

tribution of insects are essentially the same as those derived from the distribution of plants, mammals, birds, reptiles, batrachians, and fresh-water fishes. As in the other groups, the data clearly show that the Palawan-Calamian islands were long a part of Borneo after direct connection with the more-eastern part of the Philippines was broken at Mindoro Strait.

LAND MOLLUSKS OF THE PHILIPPINES

The importance of a study of Philippine land snails has not been underestimated, but unfortunately no one has been found who was able to improve upon the last-published discussion of this subject, the excellent work of A. H. Cooke.*

In order to make essential additions it would be necessary not only to reëxamine available collections but also to make new collections and habitat studies at the same time. Cooke inferentially regarded former land connections as the prime essential for the spreading of land snails within the Philippines. The importance of such connections is great indeed, but other factors no doubt enter and a knowledge of them is necessary before many puzzling cases can be explained. The distribution of limestone formations is probably a limiting factor in some cases. The distribution of certain plants which provide the food of some of these land snails should be studied in connection with other ecological conditions. Again, several species of land snails are used for food and the possibility of transportation by man must be considered. The closet scientist can help in this work, but the future well-trained exploring naturalist has the major task yet to do.

According to Cooke, the land-snail fauna of the Philippines is derived from what we call in this book Sundaland and Papualand. The earlier migration into this region was from Papualand, and a later and now more-dominant Sundaland migration has largely overwhelmed the former. The dominance of the latter invasion is seen by Table 29 which was prepared from Cooke's data.

Cooke, following other workers, divides the Philippine Islands into provinces and subprovinces, based upon the distribution of the genus *Cochlostyla*. The center of dispersal of this genus is Luzon. According to Cooke this genus is a recent development but his supporting arguments are far from convincing. Is it not possible that this genus developed from temperate-zone ancestors which invaded northern Luzon during early Tertiary time from Formosa? As Luzon is very clearly the center of

* Proc. Zool. Soc. London (1892) 447-469.

TABLE 29.—*Showing distribution of characteristic Sundaland genera of land snails in the Philippine Islands.*

Genus.	Sumatra	Java.	Borneo.	Celebes.	Philippines.
<i>Sitala</i>		1	5		2
<i>Amphidomus</i>	5	15	6	6	4
<i>Clausilia</i>	4	8	3	1	1
<i>Kaliella</i>		1	1		5
<i>Glessula</i>	1	2	1		1
<i>Plectotropis</i>	1	3			1
<i>Lagochilus</i>	1	4	4	2	9
<i>Opisthaporus</i>	3	3	7	7	1
<i>Alycæus</i>	1	2	8	2	2
<i>Coptochilus</i>	2		2		1

origin of this genus and, at the same time, the only island in which evidence for postulating a long-continued upland has been recognized, an investigation of the land snails of Formosa may throw some light upon this hypothesis. It is also possible that in the plateau region of Mindanao an upland area was maintained for a considerable portion of the Tertiary.

The recognition of an essential unity of the whole Philippine land-snail fauna is noteworthy. As in several of the groups of plants and animals that are considered in this book, the land-snail fauna of Palawan has Bornean affinities, but the recognition of several species of *Cochlostyla* upon that island or its dependencies ties it faunally to the rest of the Philippines.

Table 30 and fig. 60 have been prepared from Cooke's data upon the distribution of the subgenera of *Cochlostyla*, a very characteristic Philippine land-snail genus. The map may in a sense be too conclusive, in that the lines are fixed. This is particularly true for the subprovince the Cuyos, which has been tied to Mindoro Province on the slender evidence that Cooke presents with only tentative conclusions. The table and the map indicate that Luzon is clearly the metropolis of the genus *Cochlostyla*. The possibility that this genus may have been derived from an early Tertiary form which entered from the north must be entertained. That such a form and its derivatives could spread southward over dry land appears probable. A hypothetical elongate island (or islands) during Vigo-Miocene time provided a land bridge over which these forms could spread to Mindanao and, in turn, to Celebes and New Guinea. The possibility will be discussed at length in the next chapter in connection with the faunal relations of a temperate-zone mammalian fauna of northern Luzon.

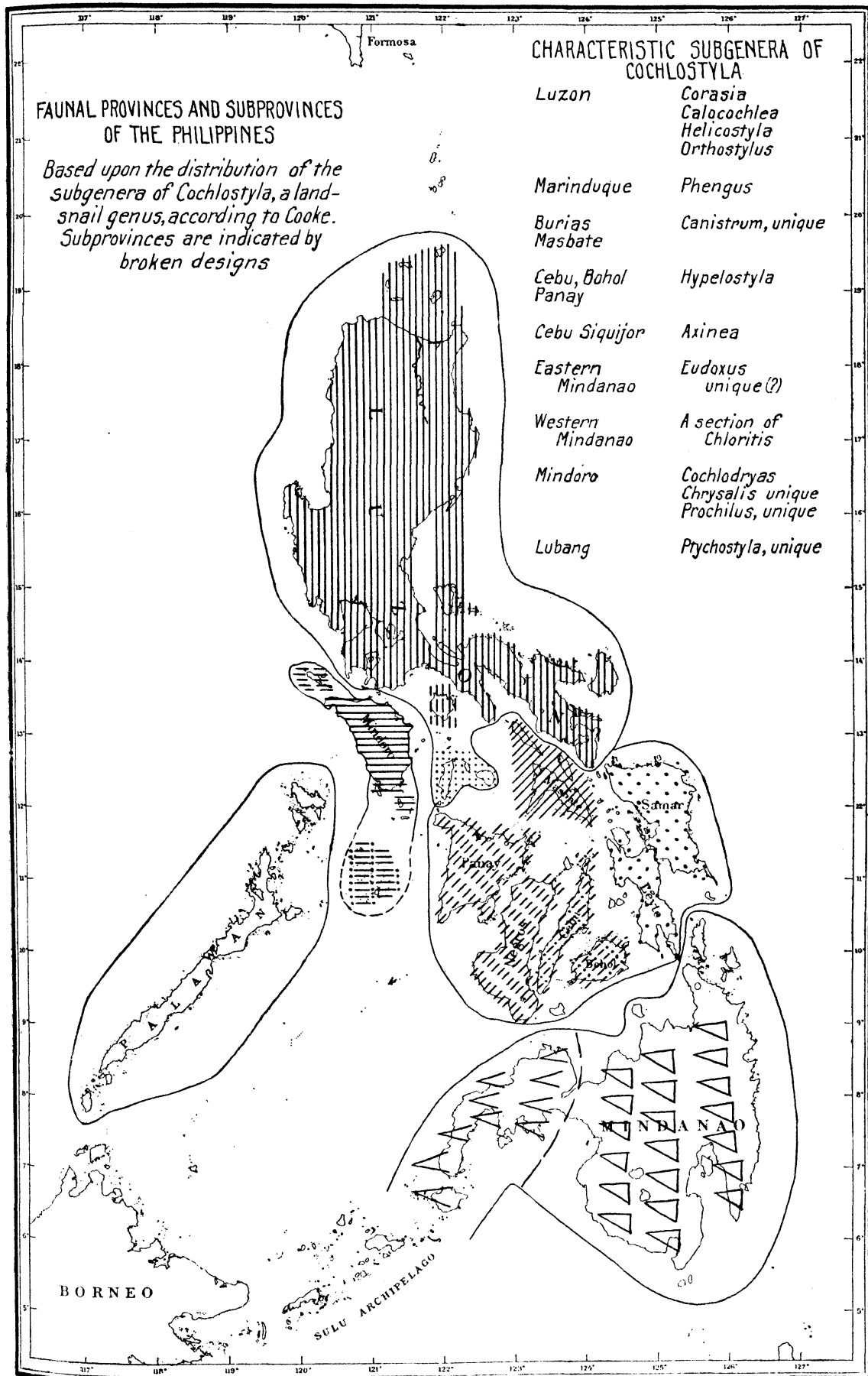


FIG. 60. Faunal provinces and subprovinces of the Philippines according to Cooke.

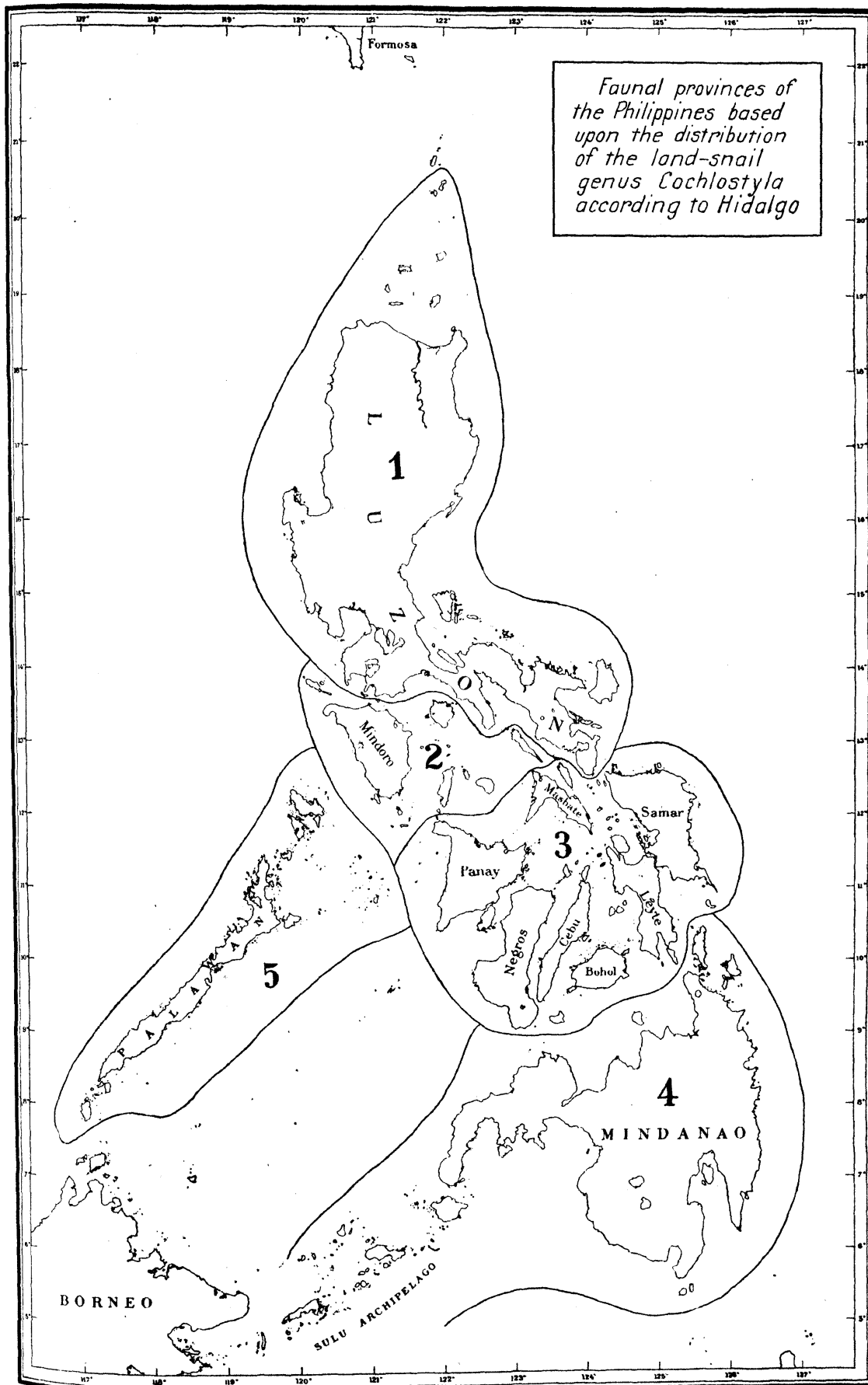


FIG. 61. Faunal provinces of the Philippines according to Hidalgo.

The general agreement among various workers upon the distribution of the species of the genus *Cochlostyla* is well demonstrated by fig. 61 which throws into map form Hidalgo's* conclusions. The greatest discrepancies between the two maps presented are shown in Marinduque, the Cuyos, and Burias. Hidalgo showed that Ticao is faunally tied to Masbate and the Cuyos to Palawan, but his evidence for tying Marinduque, Tablas, Romblon, Sibuyan, and Burias to Mindoro is far less convincing than Cooke's. A comparison of these maps and Plates 1 and 2 indicates that the major factor in the distribution of Philippine land snails was the former land connections between land masses now separated by seas.

* Obras Malacológicas. Madrid (1890) 578-584.

MAMMALS OF THE PHILIPPINES

Among the mammals the horse, cattle, carabao, sheep, goat, domestic cat, and dog have been introduced into the Archipelago by man. The largest indigenous (and endemic) mammal found in the Philippines is the timarau (*Bubalus mindorensis* Heude), which is confined to Mindoro and apparently finds its closest ally in Borneo.* According to Hollister it is strictly congeneric with a species found in Sarawak, and the *Anoa* of Celebes, which has been claimed by some authorities to be closely allied to the Mindoro species, belongs in another genus. There are several shrews, one flying lemur, numerous bats, two so-called skunks (*Mydaus*), one clawless otter (*Aonyx*), one civet, three palm civets, one binturong, one cat (other than the domestic cat), a few squirrels, three flying squirrels, numerous rats and mice in various genera, and one porcupine (Plate 35, fig. 1). There also occur one pangolin, or scaly anteater (Plate 36), two slow lemurs, three tarsiers, a few monkeys, several pigs, one mouse deer (the chevrotain) (Plate 35, fig. 2), several deer, and the dugong.

MAMMALIAN FAMILIES

The assumptions made and the conclusions reached in this book, with respect to the Mammalia, are based largely on the lists of Philippine mammals published by Hollister.† This author attempted no revisionary work on the mammals. His list is wholly based on previously published work by himself and others. He included a bibliography of about one hundred fifty titles, not all of which however deal specifically with Philippine species. In short, it must be appreciated that present knowledge of the occurrence, distribution, and identity of Philippine mammals is imperfect. There is no doubt that the literature contains some spurious species, and that there are many unknown species. However, there are many of which our knowledge may be said to rest upon an established basis, and these

* Dammerman notes that "the Bornean *Bubalus* is a form of carabao and perhaps introduced."

† Philip. Journ. Sci. § D 7 (1912) 1-64; Proc. U. S. Nat. Mus. 46 (1913) 299-341, 3 pls.

are the forms that will be cited in the advancement of our argument.

The mammals listed by Hollister are included in nine orders, of which the Chiroptera, or bats, are the most numerous. The more prominent families are represented as follows:

Order Insectivora; the shrews, fairly abundant.

Erinaceidæ.

Soricidæ.

Tupaiidæ.

Order Dermoptera; the flying lemur.

Galeopteridæ.

Order Chiroptera; the bats, numerous.

Pteropidæ.

Emballoruridæ.

Megadermidæ.

Rhinolophidæ.

Hipposideridæ.

Vespertilionidæ.

Molossidæ.

Order Carnivora.

Mustelidæ (the skunk *Mydaus*; the clawless otter *Aonyx*).

Viverridæ (civet, palm civets, and the binturong *Arctictis*).

Felidæ (wild cats).

Order Rodentia.

Sciuridæ (squirrels).

Petauristidæ (flying squirrels).

Muridæ (rats and mice, numerous genera).

Hystriidæ (porcupine).

Order Pholidota.

Manidæ (scaly anteater, pangolin).

Order Primates.

Lemuridæ (slow lemurs).

Tarsiidæ (tarsiers).

Cercopithecidæ (monkeys).

Hylobatidæ (monkeys).

Order Artiodactyla.

Suidæ (pigs, several species).

Tragulidæ (mouse deer, chevrotain).

Cervidæ (deer, several genera and species).

Bovidæ (timarao, carabao).

Order Sirenia.

Dugongidæ (dugong).

ALLIANCES AND PROBABLE MIGRATION ROUTES OF PHILIPPINE MAMMALS

While knowledge of Philippine mammals is incomplete, certain alliances are evident. The Philippine pigs (*Sus*), deer (*Rusa*), monkeys (*Pithecus*), tarsiers (*Tarsius*), some rodents (*Rattus*), some squirrels (*Sciurus*), cat (*Felis*), civet (*Viver-*

ra), flying lemur (*Cynocephalus*), and some shrews (*Pachyura*, *Crocidura*, etc.) doubtless reached the Islands when land connections were continuous with what is now Borneo, these types in general being of wide Malaysian distribution, although some representatives in certain genera may have come from Celebes.

There was unquestionably a later migration of Bornean and western Malaysian types into Balabac, Palawan, and the Calamian Islands, and into the Sulu Archipelago, as indicated by the following data: The mouse deer (*Tragulus*) occurs in the Philippines only in Balabac; the pangolin, or scaly anteater (*Manis*), only in Palawan and Culion; the slow porcupine (*Theromys*), only in the Calamian Islands, Palawan, and Balabac; at least half of the few squirrels (*Sciurus* and *Nannosciurus*), only in Palawan, Culion, the Sulu Archipelago, and Basilan; the mongooses (*Mungos*), only in Palawan and Culion; the binturong (*Arctictis*), only in Palawan; the weasel (*Mustela*), only in Palawan and Sulu; the clawless otter (*Aonyx*), only in Palawan; and the so-called skunks (*Mydaus*), only in Balabac, Palawan, and the Calamian Islands. There are thus two distinct series of western Malaysian types extending into the Philippines, one an early migration when land connections were continuous between Borneo and the Philippines proper, and a distinctly evident later migration through Borneo and Palawan only as far as the Calamian Islands to the north, and as far as Basilan and possibly the Zamboanga Peninsula to the south, indicating that at the time of this migration the Philippines proper were separated from the Calamian-Palawan and the Sulu groups.

MAMMALS OF NORTHERN LUZON

The alliances with eastern Malaysia are chiefly shown in a very interesting series of rodents collected by John Whitehead on Mount Data, northern Luzon, and studied by Thomas.

Whitehead collected the following species from this small plateau:

Crocidura grayi Dobson.
Felis domestica Linnæus (feral).
Paradoxurus philippinensis Jourdain.
Celænomys silaceus Thomas.
Chrotomys whiteheadi Thomas.
Rhynchomys soricoides Thomas.
Phlæomys pallidus Nehring.
Mus everetti Günther.

Mus luzonicus Thomas.
Mus decumanus Pallas (feral).
Mus chrysocomus Hoffman.
Mus ephippium negrinus Thomas.
Batomys granti Thomas.
Carpomys phæurus Thomas.
Carpomys melanurus Thomas.
Crateromys schadenbergi Meyer.

Regarding Whitehead's material Thomas writes:*

In addition to these, *Crunomys fallax*, a new genus and species, was obtained in the district of Isabella, east of Monte Data.

Therefore no less than six new genera and eight new species were discovered in the island, a proportion of novelty that has perhaps never been equalled in the history of Mammal-collecting.

What are the true affinities of the isolated fauna of Luzon is a question that is not easy to answer, for the representative forms are mostly so peculiar as to render their zoological relationships more or less doubtful. On the whole, the connections, such as they are, seem to be partly with Celebes and partly with the Australian region. Thus *Rhynchomys* seems to have its nearest ally (*Echiothrix*) in Celebes; *Mus chrysocomus* is actually a Celebean species; while *Chrotomys*, *Celænomys*, and *Crunomys* belong to a subfamily, the Hydromyinae, hitherto known only from Australia and New Guinea. Finally, *Crateromys* seems to have its nearest ally in *Lenomys* from Celebes, and in another new genus not yet described that occurs in New Guinea.

On the other hand, *Phlæomys* is so isolated that I can make no suggestions as to what is its nearest ally, and *Carpomys* and *Batomys* belong to a group of arboreal genera scattered over the oriental part of the East Indian Archipelago. This group of genera may possibly either have a definite alliance one to the other, independent of *Mus*, or may be isolated survivors of an older murine fauna, of which *Mus* has now gained the dominant position, or finally may all be independent offshoots of the same central genus. Probably the second of these hypotheses approaches nearest to the truth, although one or two of the less differentiated genera, such as *Vandeleuria*, may have arisen in the third way.

Doctor Hollister states that, in working up the large mammal collection made by Raven in Celebes, he was constantly impressed with the relationships in many groups with Philippine species. Thus, two of the six species of small shrews (*Crocidura*) found in Celebes, a genus hitherto not known from that island, are close to Mindanao forms, while the bat genus *Harpyionycteris*, hitherto known from a single species occurring in Mindoro, proves to have a second species in Celebes.

The close relationship between the mammalian fauna of the Philippines and Celebes indicates that this affinity is probably due, at least in part, to a former land connection now submerged.

POSSIBLE ORIGINS OF THE NORTHERN LUZON MAMMALIAN FAUNA

LAND BRIDGES

Unfortunately, owing to the scarcity of large mammals in the Philippines, a study of mammals does not give any positive evidence of mammalian forms that could enter the Philippines only through an Eocene or Oligocene Formosan connection, but

* Trans. Zool. Soc. London 14 (1899) 378.

the presence of temperate-zone types of mammals confined to northern Luzon is somewhat intelligible, if such a northern migration route is conceived.

The existence of an elongate island (or closely linked islands) during Vigo-Miocene time along the site of the present eastern Philippine coast indicates that mountain-building movements along one of the dominant tectonic lines of the Philippines, the northwest-southeast axis, gave rise to such an island. Some of the Celebesian life forms probably entered the Philippines upon this high mountainous passage, and some of the northern mammals may have migrated southward as well. Possibly some of the unique mammals now present in northern Luzon entered Celebes at that time. Thomas has already pointed out their affinities with forms from Celebes. If this is a true explanation, then certain of these forms could have entered northern Celebes only when the Celebesian mountain elevations formed a continuous high range or nearly continuous range with northern Luzon. No evidence of the existence of a continuous high range of mountains appears in the Pliocene record nor, for that matter, in the Pleistocene record. Since some of these mammals of northern Luzon are not lowland forms, it is highly probable that they could not have gained a foothold in this region through a Matthew's raft, since these rafts are typical lowland features and in general would only transmit a lowland fauna. At the same stage certain amphibians and reptiles of Celebesian and of New Guinean affinities possibly penetrated northern Luzon.

RAFTS AND OCEAN CURRENTS

The mammalian fauna from the highlands of northern Luzon is uniquely endemic, but all of the species collected there are of small size and on this account some of them could have been the results of accidental transport in the Japan Current by natural rafts or even in some cases by some of the early settlers of northern Luzon who traveled northward from New Guinea in canoes. Many zoölogists scoff at the raft hypothesis but Matthew, who has made a splendid study of this problem, concludes that it is quite possible for rafts to transport mammals.

According to this careful investigator natural rafts have been reported during the past three centuries several hundred miles off the mouths of large tropical rivers such as the Ganges, Amazon, Congo, and Orinoco, and occasionally living mammals have been reported upon them. Matthew has estimated the chances of successful colonization as follows:

Three hundred miles drift would readily reach any of the larger oceanic islands except New Zealand. Assume as one in ten the probability that the raft drifted in such a direction as to reach dry land within three hundred miles.

In case such animals reached the island shores and the environment afforded them a favorable opening, the propagation of the race would require either two individuals of different sex or a gravid female. Assume the probability of any of the passengers surviving the dangers of landing as one in three (by being drawn in at the mouth of some tidal river or protected inlet), of landing at a point where the environment was sufficiently favorable as one in ten, the chances of two individuals of different sexes being together might be assumed as one in ten, the alternate of a gravid female as one in five. The chance of one of the two happening would be $\frac{1}{10}$ plus $\frac{1}{5} = \frac{3}{10}$. The chance of the species obtaining a foothold would then be $\frac{3}{10}$ times $\frac{1}{3}$ times $\frac{1}{10}$ equals one in a hundred.

If then we allow that ten such cases of natural rafts far out at sea have been reported, we may concede that 1,000 have probably occurred in three centuries and 30,000,000 during the Cenozoic. Of these rafts, only 3,000,000 will have had living mammals upon them, of these only 30,000 will have reached land, and in only 300 of these cases will the species have established a foothold. This is quite sufficient to cover the dozen or two cases of Mammalia on the larger oceanic islands.*

In Matthew's opinion these assumptions do not overstate the case but are quite sufficient to explain the differences between the comparatively greater wealth of the mammalian fauna upon large oceanic islands near continental masses than on small islands far removed. The greater length of coast line on large islands is obviously a favorable factor. The greater the distance, the greater the time required for a given journey and the greater the probability of the raft's destruction with the consequent drowning of its passengers. Neglecting current direction and wind Matthew makes the following comparison:

Comparing Saint Helena, 1100 miles from Africa and 10 miles in diameter, with Madagascar, 200 miles from Africa and 1000 miles in length, we see that the probabilities of effecting a colonization would be 100 times $3\frac{1}{2}$ times $5\frac{1}{2}$, or 3025 times greater in the case of Madagascar. New Zealand, 800 miles long and 1200 miles from the Australian coast, will receive $\frac{8}{10}$ times $\frac{1}{6}$ times $\frac{1}{6}$, or $\frac{1}{45}$ as many colonizations as Madagascar, but 80 times $\frac{11}{12} \times \frac{11}{12}$ or 67 times as many as Saint Helena.

I believe that it is to their small size rather than to unfavorable conditions for survival that the poverty of fauna, especially of higher vertebrates, in the smaller oceanic islands is due.

The oceanic currents and prevalent winds do, of course, profoundly modify the above generalities in each individual instance. They have prevented the populating of Cuba from North America, while facilitating invasions from South and Central America. The present set of currents reduces

* Climate and Evolution, N. Y. Ann. Acad. Sci. 24 (1915) 203-209.

the probability of mammals reaching Madagascar from the African mainland, while increasing the chances of Oriental animals reaching it. It reduces materially the opportunities for Australian fauna to reach New Zealand.*

In the chapter on the biologic aspects of Philippine geography (p. 42), the northward direction of the prevailing ocean currents in Philippine waters is described and in the chapter on Tertiary and Quaternary climates of the Philippines it is shown that the Kuro-Siwo was a dominant factor in oceanic circulation during the Pleistocene. These various factors indicate clearly that the rafting of small mammals from New Guinea to Luzon is possible, since New Guinea has several large tropical rivers on its eastern coast from which rafts could be launched into the northwestward-flowing current shown upon the pilot charts of the south Pacific Ocean for the summer quarter. Since this current has probably been constant, at least during the Pleistocene and the Recent, sufficient time is provided for the landing on and colonization of northern Luzon by the ancestors of some of the small mammals described above. Sufficient time together with the somewhat different environment of Luzon may have produced the marked endemism noted by Thomas.†

Light reports that, as far as he could find from the literature, there are no mammalian species common to Luzon and Formosa. This absence of common species is explained, in part at least, by the prevailing northward currents and the lack of large rivers on the mountainous eastern coast of Luzon from which rafts might be launched and in part by long-continued separation of the two island masses. Some of the ancestors of the mammalian species of northern Luzon may have entered that island from the north during early Tertiary times, but present knowledge does not enable us to determine with definiteness any Asian forms that must have arrived via Formosa rather than from the south.

* Many small, low, oceanic islands are flooded by tidal waves or typhoons at intervals. If this occurs but once in a century or even in several centuries it will impoverish the fauna.—A. W. HERRE.

† The same argument applies with equal or greater force to the distribution of snakes and lizards. The data presented by these three groups of vertebrates are comparatively scanty; in the case of mammals, especially, the known species are few and information concerning their distribution, both in the Philippines and in neighboring land areas, is too fragmentary to be of much use in a study of geographic distribution.

SUMMARY OF THE MAMMALS OF THE PHILIPPINES

From present knowledge of Philippine mammals the following tentative conclusions may be drawn: The fauna as a whole is dominantly western Malaysian. The latest invasion came from Borneo when Palawan and its dependent islands and the Sulu Archipelago were definitely land-tied to it.

The ancestor of the timarau (*Bubalus mindorensis* Heude) probably reached Mindoro during the early Pleistocene via a Palawan peninsula from Borneo. Certain mammalian elements entered from Celebes upon a narrow isthmian passage to Mindanao. Certain elements in the mammalian fauna of northern Luzon may have arrived from New Guinea upon rafts and succeeded in colonizing. The forms with New Guinean affinities are all small and hence could make the journey on rafts. The absence of small marsupials, such as *Cuscus*, from northern Luzon is puzzling. It is quite probable that such may have landed, but were exterminated by the more-powerful carnivorous animals already natives of the Philippines. Formosan mammals may have entered the Philippines from the north during early Tertiary times by an overland route, but the probability that any Formosan forms drifted by rafts to the Philippine shores is very slight.

An element in the Philippine mammalian fauna showing distinct affinities with the mammalian fauna of Celebes, New Guinea, and Australia corresponds to the rather conspicuous floral elements in the Philippine flora. The mammalian fauna of the Philippines corresponds with the flora in its alliances both with eastern and western Malaysia, the faunal elements from both regions doubtless having reached the Philippines through channels similar to those by which the floral elements reached the Islands.

REVIEW OF THE ORIGINS OF THE BIOLOGIC PROVINCES OF THE PHILIPPINES

In the preceding chapters the many lines of evidence dealing with the distribution of life in the Philippines have been followed. In this, the concluding chapter, an attempt is made to gather the loose strands and weave as far as possible a complete fabric. The warp of this fabric is composed of the inorganic geologic events of Tertiary time, and interwoven in this warp are the variegated threads of life in its various aspects. As a result of the shifting pattern in the Philippine life loom, the fabric design is highly complicated, beautiful, and varied.

GEOLOGIC INFLUENCES DETERMINING BIOLOGIC PROVINCES AND SUBPROVINCES OF THE PHILIPPINES

An understanding of the groundwork of Philippine life may be had only through a general knowledge of the geology of the region and its environs together with the indirect changes induced by climatic isolation.

Geologically, the same formations occur in the Philippines as have been recognized in the neighboring islands, Formosa to the north, and Borneo, Java, and Sumatra to the south; but these formations during the Tertiary were in part deposited under decidedly different conditions. The Philippine sequence, as at present known, is by no means so complete as is that of Sumatra, Java, and Borneo, or even Formosa, a part of which island has not been explored in detail. The life story in the Philippines begins, as far as we know, in early Tertiary; that is, probably during Eocene and Oligocene time. At this time, the site of the Philippines was, in all probability in part at least, land directly connected with the present site of Formosa which, in turn, was tied to the Asiatic continent. How far this early Tertiary land mass extended southward is not known. Because of the absence of a lithologic record of the early Tertiary in the Philippines, the history is fragmentary. However, this old and faded palimpsest yields a logical interpretation of the existent upland flora of northern Luzon. As an accompaniment to this flora is an insect fauna, particularly characterized

by its Lepidoptera, and a bird species, the crossbill, dependent upon the distribution of the pine. Such are the biologic reflections of this early Tertiary time. Unfortunately, owing to the scarcity of large mammals in the Philippines, a study of mammals does not give any positive evidence of forms that could enter the Philippines only through the northern connection, but a peculiar highland fauna may have descended from forms that entered this region from the north. The presence, then, of Himalayan and northern Asiatic types, which are now chiefly confined to northern Luzon, is somewhat intelligible.

A much clearer picture of the later Tertiary is had, since the sediments of the Vigo group of probably middle and upper Miocene age are widespread not only throughout the Philippine Archipelago but also in Formosa, Borneo, and Celebes. At this stage, an archipelagic condition prevailed throughout the entire terrane from Formosa to Java and Borneo. A part of this condition was due to structural changes that took place just before the beginning of Vigo time. At this stage probably the Formosan rift system was formed, and movements within this great rifting zone have been so frequent that no direct land connections between Formosa and the Philippines have since existed.

The probable existence of an elongate island (or an elongate chain of closely linked islands) along the site of the present eastern Philippine coast indicates mountain-building movements along one of the dominant tectonic lines of the Philippines, the northwest and southeast axis. Some of the Celebesian plants and animals probably entered the Philippines upon this high mountainous passage and some of the northern species adapted to a temperate climate migrated southward as well. Possibly some of the unique mammals now present in northern Luzon entered Celebes at that time. Thomas has pointed out their affinities with forms from Celebes. If this is a true explanation, then certain of these forms could have entered northern Celebes only when the Celebesian mountain elevations formed a continuous high range with northern Luzon. No evidences of the existence of a continuous high range of mountains appear in the Pliocene record or, for that matter, in the Pleistocene record. Since the mammals of northern Luzon are not lowland forms, it is highly probable that they could not have gained a foothold in this region through a Matthew's raft, because rafts of that class are typical lowland features and in general would transmit only a lowland fauna. At the same stage certain am-

phibians and reptiles of Celebesian and of New Guinean affinities possibly penetrated northern Luzon. Many of the tropical Australian floral types that Merrill has recognized from Mindanao to northern Luzon were probably dispersed at that time as well. According to the Sarasins, at that stage Celebes was connected to the south with Java and there was also an isthmian connection with New Guinea via Halmahera. In this way certain Papuan forms as well as early Malaysian types could have entered. A Sulu bridge may have existed during a portion of the Vigo-Miocene, and over such an isthmian connection the characteristic Malaysian forest trees, the dipterocarps, may have been spread, since a well-developed dipterocarp flora occurs in Pliocene deposits in northern Luzon at Sagada. This flora was probably introduced into Luzon during the preceding Vigo-Miocene time.

Such are the mere sketch lines of Vigo time. Much work remains to be done in clarifying this rough sketch and putting in a vast mass of detail for a complete drawing. Far greater fossils collections should be obtained from the beds of Vigo-Miocene age, and the desirability of securing a good fossil flora of this age is exceedingly great. Vertebrate fossils are as yet unknown from these beds.

Philippine islands of Pliocene age were somewhat different in character from those of Vigo-Miocene. The existence of an elongate island or a chain of eastern elongate islands at that stage is probable; but, if such did exist, the elevations were by no means as great as those of Vigo-Miocene time, since the Malumbang formation of Pliocene age is notably a shallow deposit and contains but little material derived from the wear of high-standing land except in the vicinity of Baguio, northern Luzon.

During the Pliocene, according to the Sarasins, Celebes was connected by its northern arm with Mindanao in the vicinity of Sarangani Island, and it was chiefly at that period, that the Celebes-Mindanao interchange occurred. According to these students of that "anomalous" island, the continued lifting of Celebes and its surrounding archipelago, beginning in the Miocene and increasing in the Pliocene, led to a long period of land formation, which is inferred from the study of the island fauna. From a faunal study and from geologic research they conclude that northern Celebes was connected by a land bridge through Sangi with Mindanao (that is, the Philippines) while southern Celebes was connected with east Java and the Sunda

Islands, more particularly Flores. During the same geologic period Celebes had a Moluccan connection which in turn was united with New Guinea and Australia. Animal and plant migrations took place to and from Celebes over all of these connections. Javanese animals wandered to Celebes and, in turn, Philippine animals traveled southward over Celebes to, possibly, Flores or New Guinea, and in turn New Guinean forms traveled over the Moluccan bridge to Celebes. The Sarasins think that many of these forms stopped in Celebes and did not spread farther. From the species that arrived in Celebes new species were formed and in time even new genera, whose origin can only be inferred from the distribution of the nearest related form, while the other part remained unchanged as still living evidence of previous land connections.

The Sarasins' statement of the relation of Celebes to its neighbor Borneo is, in connection with Pliocene species, particularly interesting. They show that numerous animal species that are common to Borneo and Celebes occur also in Java or the Philippines and might have reached Celebes from either of these two sources. Since no animal species is exclusively peculiar to Borneo and Celebes they conclude that no direct land connection has existed and their statement in substance is: No mammal, no bird, no reptile, no amphibian or fish, no snail, no crab, no bug, no ant is exclusively characteristic of Borneo and Celebes. Therefore, the migration of an Asiatic Sunda fauna to Celebes did not go out direct from Borneo, but did go from Java to southern Celebes or from Borneo to the Philippines and from there to northern Celebes. Nevertheless, the narrow Strait of Macassar, which separates Borneo and Celebes, is a sea boundary of great significance. The period of the land connections described above may be very likely designated as Pliocene. At the end of the Pliocene or at the beginning of the Pleistocene began the slow disappearance of the land connections through eruption or invasion of the water.

The Sarasins think that the four land bridges noted above have contributed to the Celebesian fauna about as follows: The Javan bridge, 28.3 per cent; the Philippine bridge, 21.9; the Moluccan bridge, 15.3; the Flores bridge, 8.9. This gives a ratio for the four bridges of, approximately, 4:3:2:1; and from this they conclude that the Celebesian fauna is dominantly Asiatic in relationship rather than Moluccan-Australian.

Judging from certain common faunal and floral elements and the apparent absence of marine Pliocene from Batangas Prov-

ince, Luzon, probably Mindoro was connected with northern Luzon during the Pliocene. From a geologic point of view little is known concerning the Pliocene of Palawan, but it seems probable that Palawan may have been a land mass during a portion of that time.

Mindanao was probably divided into several Pliocene islands during a portion of the Pliocene. The coarse sediments or coral limestones that occur in Mindanao indicate neighboring land in all phases thus studied, so that connection and disconnection of these different islands over the present site of Mindanao was highly probable. From the characteristic Malaysian dipterocarp flora at Sagada, which has been referred to the Pliocene epoch, we conclude that northern Luzon was in a somewhat similar archipelagic condition and that considerable land masses existed in that region. The present-day existence of a relict Himalayan flora, which is adapted to present-day altitudes of 1,500 meters or more, indicates that these land masses attained considerable elevation but were bordered by a coral strand and low-lying land covered by a tropical forest similar to that of to-day.

Other and greater complications are discernible in the Pleistocene. Not only were these changes of the Pleistocene due to the different diastrophic movements, but the withdrawals and restorals of tropical waters as the result of widespread glaciation and deglaciation in the temperate zones during this period caused a uniting and a separating of island masses several times during the period. The high specific endemism in the Philippines probably developed during that period, since the minor environmental changes were frequent. Such specific differences as McGregor describes in detail in the chapter on birds probably occurred during that period from a common stock introduced during Miocene or Pliocene time throughout the Philippines. McGregor's description of hornbills and their distribution may well be reviewed in this connection.

During that period Luzon, Polillo, Marinduque, and Burias formed at times one large island, judging from hydrographic studies. These studies coincide in a remarkable fashion with the distribution of birds. In the same way the hydrographic unit Samar, Leyte, Bohol, and Surigao corresponds to one of McGregor's hornbill species, while another hydrographic unit, Negros, Panay, Masbate, and Ticao, is sharply contrasted with its neighbor to the east. Cebu, on the other hand, was until probably late Pleistocene time a string of coral islands which

had but little connection with either the "Visayan" island to the west or the large "Surigao" island on the east. The relationship of the avifauna of Palawan-Borneo to Mindoro is definitely recognizable. The avifauna of Mindanao exhibits, as one would expect, definite affinities with that of the neighboring Sulu Archipelago and Celebes. The ability of birds to travel rapidly over a land mass is great, except for the forms that are markedly restricted by food and peculiar life habits. The recognition of definite areas within these land masses is hardly to be expected. According to McGregor, such examples do occur, however, notably in the case of the crossbill, whose bill is peculiarly adapted for opening pine cones the seeds of which furnish its principal food. On this account this species is found only in the regions of northern Luzon where a pine forest flourishes.

During the Pleistocene, some of the minor floral subdivisions were probably formed. Thus, Merrill recognizes a marked distinction between the flora of Zambales Mountains and that of the major portion of Luzon. As was indicated in the chapter on hydrography, the existence of a Pleistocene Zambales island is highly probable and its union to Luzon in late Pleistocene or very recent time has been brought about in large part by a process of filling in the separating strait and converting it into a portion of the central plain of central Luzon.

According to Merrill, Mindoro constitutes a somewhat intermediate region between Palawan on the one hand and Luzon on the other. This explanation seems reasonable when one remembers that Luzon was probably connected with Mindoro during the Pliocene and Mindoro was linked to Palawan in the Pleistocene.

Taylor's interesting studies on the herpetology of the Islands yield somewhat similar evidence during the Pleistocene, as will be seen by a comparison of his map with McGregor's. His suggestions concerning the recency of Mindanao in its present form coincide with Mr. Moody's picture of a Mindanao archipelago during certain stages of the Pleistocene.

In connection with mammalian forms, it appears highly probable that Palawan was united with Borneo and with Mindoro during the Pleistocene. The timarau is a large mammal, too heavy to be transported by a Matthew's raft. The scaly anteater of Palawan and Calamianes and the chevrotain of Balabac are characteristic Bornean forms that also occur on Palawan or its

dependencies. In the absence of any of the species of deer Palawan contrasts strikingly with the eastern Philippines.

The mammalian fauna in northern Luzon is unique and, like the plants and some of the Himalayan Lepidoptera, indicates the persistence of an upland region in northern Luzon during the Pleistocene. Otherwise, the mammalian fauna of the Philippines in connection with its Pleistocene distribution is not notable, as it largely consists of widespread Asiatic genera characteristic of the Tropics.

Herre's studies of fresh-water fishes of the Philippines indicate that during early or middle Pleistocene time the westward-flowing streams of Palawan and some of the streams of Mindoro probably emptied into a large master stream of Sundaland, the mouth of which was probably located somewhere in the China Sea between central Luzon and the Asiatic mainland, since the cyprinids of Mindoro and those of Palawan are closely related and in some cases are identical with those of Borneo. During the same period, Cagayan Sulu beyond much doubt formed the outer part of a vastly extended Borneo, as is shown by the fresh-water fishes found in one of its lakes. The relationship between the fishes of eastern Borneo and those of the Zamboanga Peninsula indicates a probable land connection during that time, although the occurrence of Cyprinidæ in the Agusan drainage shows that their distribution probably dates to some stage in the Pliocene or very early Pleistocene. The absence from Celebes of Mindanao fresh-water fishes indicates that Celebes and Mindanao were probably separated by water during middle and late Pleistocene.

That most interesting of mammals, man, geologically considered, was probably influenced greatly by the shifting of land and sea that occurred in the Philippines during Pleistocene time. A glance at Beyer's map of the distribution of races indicates such influence in connection with the Negrito distribution (fig. 62). According to Beyer, the Negritos of Palawan are closely related to those of the Malay Peninsula but are distinct from those of Zambales. The Zambales Negritos are, in turn, differentiated from those of eastern Luzon. Beyer also notes minor differences between those of Ambos Camarines and those of northern Luzon. The Negrito stock of Surigao is, however, related to the Camarines stock which, in turn, is related to the

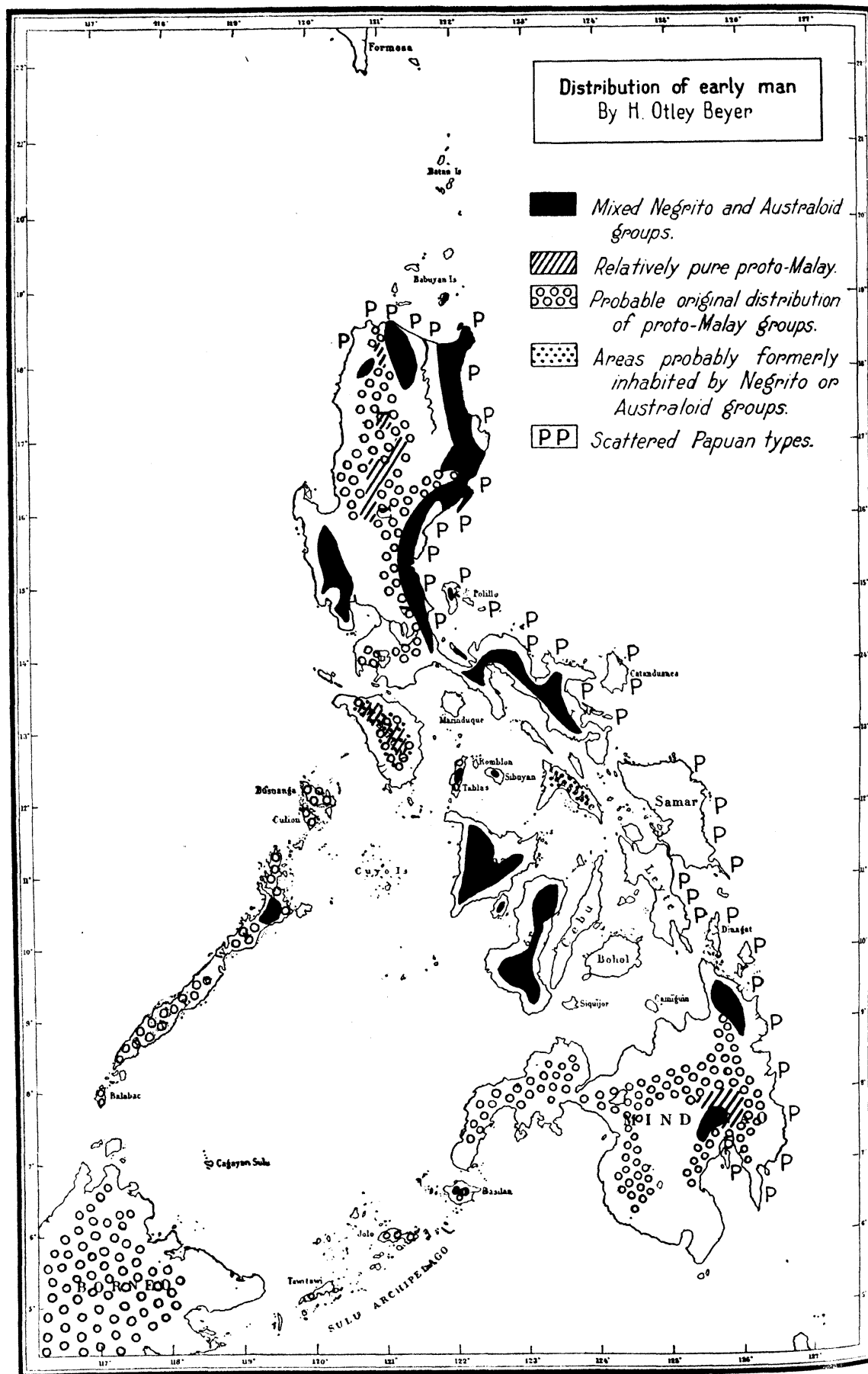


FIG. 62. Distribution of early man in the Philippines, by H. Otley Beyer.

Negrito of Negros and Panay. In terms of Pleistocene geology, this may be interpreted to indicate that Palawan was firmly united with Borneo during early Pleistocene. Likewise at this stage a well-defined Sulu isthmus existed over which the Negritos penetrated from the large southern connection in Mindanao, spread eastward and northward overland across Samar and Leyte to Camarines Peninsula, northward to Luzon and to Zambales, which was later isolated by sea invasion. Another branch of the Negrito race spread across a land connection between Camarines Peninsula, Ticao, Masbate, Panay, Negros, Sibuyan, and Tablas, that existed during early Pleistocene time. During middle or late Pleistocene time most of Samar was submerged. Leyte and Bohol were likewise largely covered by the Pleistocene sea and were broken up into many small islands. Through such restriction of habitat the Negritos disappeared from the intervening area. Through different environmental conditions in middle and late Pleistocene time, differences among the variously separated Negrito groups occurred. If the maps of hydrography and palæogeography in the previous chapters are reviewed the possibilities of this explanation will appear greater, and the place of early man in the natural history of the Philippines will then be seen to be conditioned by the same environmental pressures and conditions as is that of the other mammals.

A later proto-Malay migration tended to crowd the Negritos to the northern portions of the islands. The restricted Negrito distribution in Palawan is a notable example of a concentration due to the pressure of peoples of a higher type.

FLORAL PROVINCES AND SUBPROVINCES OF THE PHILIPPINES

The discussion of the floristic provinces is contributed by Elmer D. Merrill.

The accompanying map, fig. 63, indicates a tentative scheme of floral provinces and subprovinces. The main provinces recognized are the Bornean, represented by horizontal rulings; the Formosan, represented by diagonal rulings; and the Philippine, represented by vertical rulings. The various subprovinces are represented by the intersections of the various major rulings. Thus, Palawan is marked by solid, vertical, and horizontal lines crossed, which indicates that the flora of a region so marked is composed of both Bornean and Philippine floral elements. The vertical pattern crossed by diagonal lines in northern Luzon marks the elevated region which contains a mixture of Formosan and Philippine floral types. The various vertical pat-

terns mark the floristic subprovinces of the strictly Philippine affinities where specific Philippine endemism is high.

The general alliances of the Philippine flora have been indicated (p. 154). There are, of course, striking differences in floras of different parts of the Archipelago; but, generally speaking, with the exception of a few areas, botanical subregions within the Archipelago are not sharply defined. The types of vegetation are strongly delimited by the seasonal distribution of the rainfall, by the resulting high humidity, by altitude, and by previous geologic conditions. In relation to the seasonal distribution of the rainfall there is a very striking tendency for numerous species to follow the general line of distribution from Mindanao northward through Leyte, Samar, the Provinces of Sorsogon, Albay, and Camarines in Luzon, and through the eastern parts of Tayabas Province of the same island even to the Pacific coast range of Cagayan and Isabel. The regions just mentioned are those characterized by no pronounced dry season, the rainfall being more or less uniform throughout all months of the year.

Local endemism is highly developed in the Archipelago, and every large island presents many species that have not been found elsewhere. Moreover, endemism may be strictly localized within certain parts of the same island. However, in most large genera that present a high percentage of endemic species there are usually a few widely distributed forms which occur in most islands of the Archipelago. Many of them are widely distributed species that are confined to the Philippines, others have a wide distribution in the Tropics of the Old World or in the Indo-Malaysian region. This applies to both low- and high-altitude species.

Owing to the position of the Batan and Babuyan Islands, between Luzon and Formosa, there are naturally found in these groups certain Formosan species which do not extend southward to the mainland of Luzon. So far as present knowledge of the floras of these two groups is concerned, the Babuyan Islands are botanically much more closely allied to Luzon than are the Batan Islands. Balabac, Cagayan Sulu, Palawan, Busuanga, Culion, and Cuyo present a series of Bornean types that do not extend into the Archipelago proper, although in a few cases the western Malaysian types that extend into Palawan reach Mindoro and western Panay. There are a few genera and a few striking species that have a general distribution in

the Malay Peninsula, Sumatra, Borneo, Palawan, and the Calamian group, in a few cases extending as far as Mindoro. A rough estimate of the Palawan-Calamian special alliances may be indicated by 50 per cent Philippine and 50 per cent Bornean affinities. Likewise to the south, the Sulu Archipelago presents certain Bornean elements that are absent from the main part of the Archipelago, some of which extend into the Zamboanga Peninsula of western Mindanao. The Bornean elements probably represent the later migration into the parts of the Philippines indicated, further migrations into the Archipelago proper having been inhibited by sea channels.

The one sharply defined botanical subregion in the Philippines is that approximately delimited by the political subdivision known as the Mountain Province, a region in northern Luzon characterized by high mountains and by the dominance of the pine *Pinus insularis* Endlicher. This region presents a very large number of Asiatic types that do not occur elsewhere in the Philippines. Mountain Province presents the most southeastern extension of range of a fairly large number of Himalayan types. As already noted (p. 161), nearly all of the Himalayan types that occur in the mountains of northern Luzon also occur in Formosa. Doubtless they reached northern Luzon and Formosa at approximately the same time and through the same channels. Some species otherwise known only from Formosa also occur here, as well as a few otherwise known only from Japan. It has already been indicated (p. 62) that in the early Tertiary there were apparently land connections between northern Luzon and Formosa and that Formosa itself was then a part of the Asiatic continent. A land flora must exist before many of the faunal elements and even of some floral elements can enter. The floral elements which may be dated geologically in an approximate manner are those found at the present day in the higher mountains of northern Luzon. These floral elements were probably present even in early Tertiary time only in the higher and consequently colder upland region of that time. A lowland flora of tropical Asian derivation (that is, an Asiatic flora such as occurs in Indo-China to-day) may have occupied the lowland portion of the Philippine land of Eocene and Oligocene time. This theory is supported by the well-recognized broadening of the Torrid Zone during the Eocene and the Oligocene, which resulted in the northern migration of many plant forms far beyond the present-day limits of those tropical or warm-temperate plants. Through an inten-

sive study of the dipterocarps it has been found that for the establishment of the dipterocarp forests a previous forest is necessary, for the dipterocarp seeds will only germinate and produce young plants when shaded by other forest trees. Later, after some of the dipterocarps have attained an age of seventy years, they succeed in the struggle for their place in the sun and then become dominant and overshadow the primeval trees under whose shelter their early life was spent. The absence of the dipterocarps from the present Formosan flora indicates that these forms did not enter with the rest of the tropical Asian lowland flora but were a later development. The geologist and the palæobotanist will, it is hoped, test this hypothesis more fully.

In Zambales Province, Luzon, some rather characteristic species have been found that are not known to occur elsewhere. The physical and geological features of that part of Luzon, especially the presence of the great central plain extending northward from Manila Bay to Lingayen Gulf west of the Zambales Range, clearly indicate that Zambales was formerly an island. Mindoro presents a flora in general similar to that of its neighbors Luzon and Panay; but, as with most other individual islands in the Philippines, it also presents a large number of endemic species and a certain admixture of forms that are otherwise known in the Philippines only in the Calamian-Palawan group, and outside of the Philippines in Borneo, Sumatra, and the Malay Peninsula. Samar and Leyte present much in common in their floras, but the rest of the Visayan Islands—Panay, Negros, Cebu, Bohol, and Masbate—seem to present a fairly uniform flora with local endemism in each island. Botanical exploration has been at most superficial in these islands, and hence data are not available on which to base any conclusions as to their previous conditions of insularity, or their connections with each other or with other islands. In very many respects their floras resemble those of the western parts of Luzon.

The highlands of Bukidnon, Mindanao, present some herbaceous plants of northern affinities, which flourish in this open region in the temperate climate provided by the greater altitudes. The exact significance of such temperate elements is not as yet known. Possibly the dispersal of seeds by wind or by birds may account for the development of those plants in that region where, upon accidentally finding their suitable life conditions, they became established. Another explanation is that these

temperate plants represent a relict flora which reached Mindanao via an elongate elevated ridge that may have extended from Luzon to Celebes during Miocene time. Again, they may have been introduced in both ways. Future collecting in that comparatively little known island will probably answer this question more definitely.

The provinces and subprovinces here set forth are only tentative, but the broader divisions will probably stand the test of time. Modifications must come and, if future workers are stimulated to collect with the object of testing the ideas set forth and of elaborating or modifying them, the present work will have been worth while.

FAUNAL PROVINCES AND SUBPROVINCES OF THE PHILIPPINES

In fig. 64, showing the faunal provinces and subprovinces of the Philippines, the horizontal rulings indicate the Bornean province; the varying types of vertical rulings, the Philippine province; and the diagonal rulings, the Formosan province. Where the rulings intersect, transitional subprovinces are indicated.

As was indicated above, the Philippines have been faunally and florally supplied from at least four different directions. An old relict flora with an accompanying fauna now exists in northern Luzon. This flora was established there in the early Tertiary, when the Philippine land mass was directly connected to Formosa. Later, a strong, dominant, western Malaysian flora and fauna probably entered the Philippines in Vigo-Miocene and Pliocene time. In part these dominant western Malaysian species entered by way of Borneo and in part by an indirect route from Celebes. At that same time by the latter route, slight Papuan elements also entered Mindanao over a Sangi isthmus. In early or middle Pleistocene time, a definite Sulu bridge connected Borneo with the Zamboanga Peninsula. During the same portion of Pleistocene time, Borneo was firmly united with Palawan; and, through the Calamian Islands, a temporary connection at least existed between Palawan and Mindoro. A slight temporary connection may have existed between the Cuyo Islands and eastern Panay. A glance at the map of Philippine faunal provinces will indicate the two dominant provinces—a southwestern Bornean province and an eastern Philippine province. A Formosan province may be recognized on the higher peaks of northern Luzon above the elevation of 1,500 meters as a dominant temperate fauna and flora. These three provinces, then, indicate that the fundamentals of Philippine

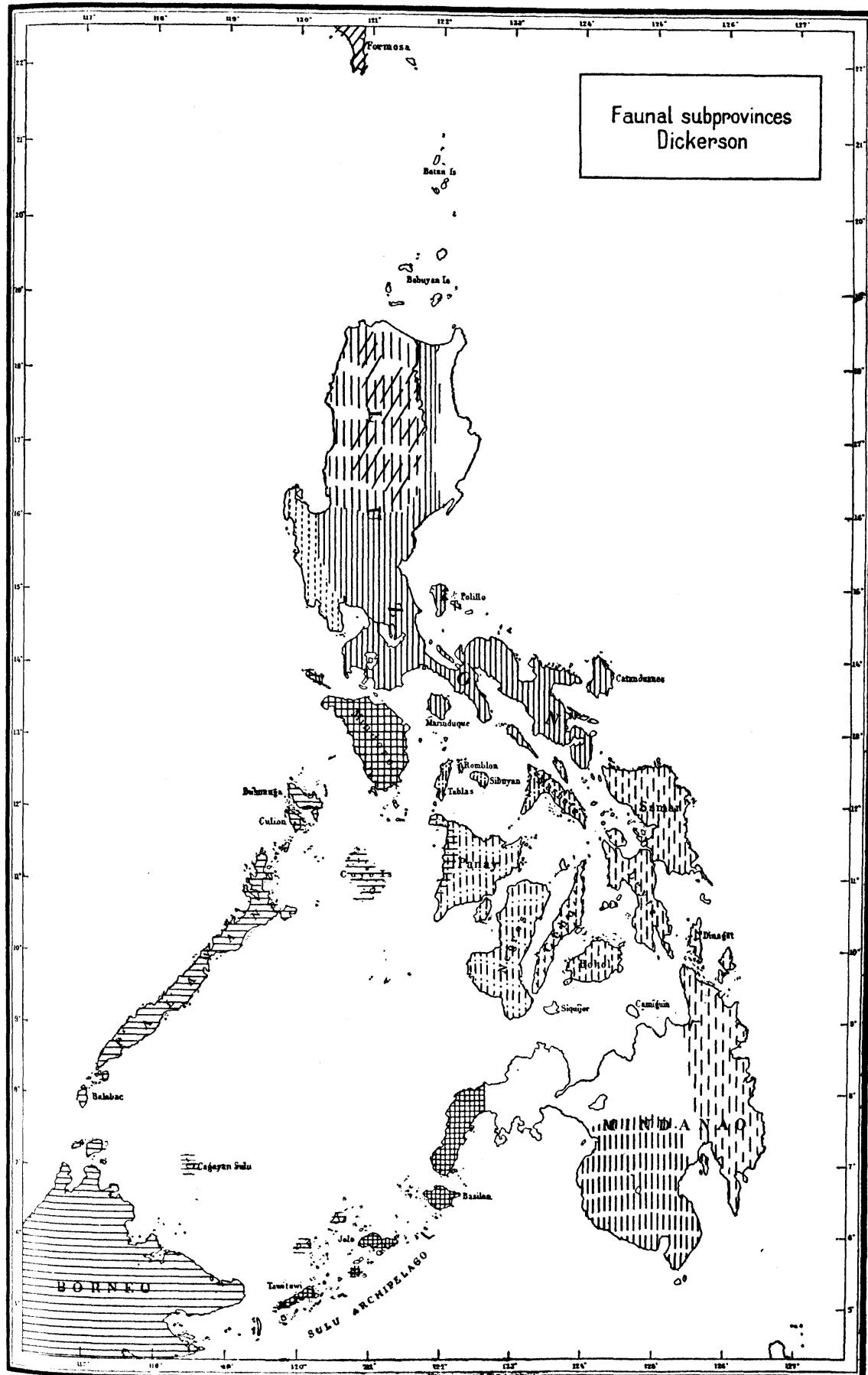


FIG. 64. Philippine faunal subprovinces, by Dickerson.

life as shown above are due to basic geologic changes in the form of the land. Some of the subdivisions of these provinces are also due in part to geologic changes, in part to the indirect influences of climatic changes during the Pleistocene in the temperate regions which resulted in successive withdrawals and restorals of oceanic waters in the tropical regions of the earth, in part to temperature and humidity conditions and, finally, in part to ecologic and symbiotic relations. Such then is the complex with which we are dealing. The insufficiency of our knowledge of many of these factors renders a complete exposition impossible. Much remains to be learned concerning both the inorganic and the organic bases of life in the Islands—the meeting place of many diverse elements and the scene of rapid geologic action. The most-striking biologic unit, and at the same time probably the oldest, in the Philippines is in the highlands of northern Luzon. This subprovince is essentially the same for both fauna and flora.

Along with the temperate Himalayan-Asian flora described above, certain characteristic faunal elements entered the Philippines from the north. With the pine came the crossbill; with certain of the plants certain butterflies and other Lepidoptera characteristic of the northern Himalayan region extended their ranges southward. Possibly at the same time, the ancestors of the temperate mammalian fauna of the Mount Data region became established in the higher altitudes and, traveling down the elevated elongate range which probably existed during pre-Vigo and Vigo time, reached the higher mountains of Celebes. As far as known, the hypothesis that small mammals are adapted to a temperate zone is more probable than that they are of Celebesian origin, as Thomas indirectly indicates. There are, in nature, biologic “rat traps” through which species can pass in one direction only and this apparently is one of them. The only difficulty of maintaining this idea is that we are apt to apply it in far too many cases!

Schultze has shown that the probable center of dispersal of the pachyrrhynchids is northern Luzon. That subprovince is the region inhabited by a most unusual assemblage of small endemic mammals, originally described by Thomas. Taylor has shown that northern Luzon has a distinctive amphibian and reptilian fauna. The distinctive features of the subprovince are thus strongly marked by the many different biologic groups.

Of all the zoölogical groups, birds and their distribution are best known. On this account, the generalized faunal map of provinces and subprovinces is largely based upon McGregor's distributional studies. A comparison of his map (fig. 50) with Taylor's map (fig. 56) brings out at once certain well-marked features that are identical. Both recognize the Bornean features of Palawan and the transitional character of Mindoro and the Sulu Archipelago. The geographic distributional studies of insects, of fresh-water fishes, and of mammals lead to the same conclusions. The essential unity of all the eastern Philippines is likewise emphasized by these studies.

The subprovinces of Mindanao are based upon Taylor's work, while the distinctiveness of the Cebuan subprovince is the result of McGregor's careful research. Although there is not exact correspondence in the boundaries of these faunal provinces with the floral, yet certain fundamentals are present in both, and in some cases all or portions of the subprovinces are identical. Again, it must be remembered that much work remains to be done upon distributional studies in the Philippines. For clearness, maps such as those here presented are necessary, but the reader must not expect that the limits here fixed will be definite although in certain cases the shore line of these tropic seas have set limits far more fixed than zoölogical provinces within continental land masses.

WALLACEA

Wallacea is outlined sharply by Wallace's Line (as modified) on the west and Weber's Line upon the east, as fig. 4 shows. This area is in a biologic sense far more sharply set off than are similar areas within the land masses of Eurasia, Africa, North America, and South America. Even so, these sharply drawn map lines will be found in certain cases far less distinct in Nature. Botanically and zoölogically this terrane may be described as being fundamentally Asian, with Papuan and Australian overtones.

Wallacea is fundamentally delimited from the neighboring regions by great differences in geologic history. In particular, the area in question is a stress area dominated by great movements, some of which were initiated during mid-Tertiary time and have continued to the Recent. Other and later mountain-building forces have been operative in mid-Pleistocene and

Recent times. Weber's Line and Wallace's Line, as modified, are in both cases fundamentally geological. Likewise the two lines in their entire length have in various parts varying values. Some portions of both these fundamental geologic lines are at least as old as Miocene and, in all likelihood, probably as old as Eocene.

Wallace's Line was originally named by Huxley, who regarded it as the line of separation between two distinct faunal regions, the Oriental and the Australian. Huxley's data were based upon Wallace's work. In this connection it is important to point out that Wallace regarded the fauna of Celebes as a mixture of Australian and Asian types, and he thought that, faunally, it was dominantly Australian and, in a more restrictive sense, Papuan. His recognition of the Asian characters in the Celebesian fauna is, however, quite clear.

WALLACE'S LINE

Wallace's Line as modified in this book will now be traced from the south to the north. Starting between the two islands Lombok and Bali, this line extends northward through Macassar Strait, thence through Sibutu Channel, thence northwesterly through Mindoro Strait, thence northerly along the west coast of Luzon, making a final turn through Bashi Channel into the Pacific. Weber, Molengraaff, and others have shown that Lombok Strait is of Pleistocene origin and that some of the faunal changes between Bali and islands immediately to the east in certain cases (as in Sumbawa) are due to an unfavorable habitat created by vast outpourings of volcanic ash and lava which, in the case of the last-mentioned island, happened even during historic time. The pauperitic character of the Sumbawa fauna is thus explained.

The Sarasins have shown that Celebes was connected to the south with Java by way of a land bridge now largely removed, but such remnants as Paternoster Islands and Postilion Islands remain. These authors also indicate a southward connection between Celebes and Flores. Through the work of these two naturalists, Macassar Strait is shown to be a sharp dividing line between Borneo and Celebes, which is at least as old as Miocene and probably even as old as Eocene. Sibutu Channel is far later in origin than Macassar Strait immediately to the south and, as our work shows, is of early Pleistocene origin. Sulu Sea is in all likelihood an older feature than is Sibutu Channel, but the evidence presented in this book indicates that

Mindoro Strait is of early or mid-Pleistocene age. Bashi Channel, however, as was shown in the discussion in the chapter on Hydrography, was initiated in all probability during the early portion of the Tertiary by fault movements along one of the dominant lines of the Formosan rift system. Thus it will be seen that Philippine connections with Borneo by way of a Sulu isthmus were probably had during early Pleistocene or late Pliocene, so that certain forms were enabled to pass from Borneo via Mindanao into Celebes and vice versa.

WEBER'S LINE

Weber's Line, as described and delimited by Pelseneer, passes through Timor Sea on the southeastern side of Timor, thence between Arafura and Kei Islands, thence it swings northwesterly through Ceram Sea, and northerly through Molucca Strait to the Pacific. This line, like Wallace's Line, varies in value from place to place. According to Molengraaff, that portion of it which he describes as the "circum-insular trough sea" is a very ancient portion, and he regards this as geologically the most important boundary. His circum-insular trough sea consists of Ceram Sea, the Ceram-Aru trough, the Kei trough, and Timor Sea, which he states separates geologically totally different structures from one another. He states that islands of this arc have come into existence as oceanic islands as anticlinal folding ridges appearing out of the sea, and yet they hang together with Asia as an extension of the eastern Himalayan system. According to this able geologist, geologically, they stand in close relationship with eastern Asia as a part of the Himalayan mountain system and even with the Alps, but in no connection at all with Australia. According to him, this absolutely sharp boundary is also, zoögeographically speaking, a very important dividing line. Concerning this he quotes Weber, who has made a study of the fresh-water fishes, to the effect that the fresh-water fishes of Kei Islands are throughout of Indian character and completely different from those of the Aru Islands, which have pronounced Australian or Papuan characters. These islands are, in this respect, a part of the continent of Australia. This is just what we might expect, because in Pleistocene time New Guinea, the Aru Islands, and Australia were connected as one continent. That portion of Weber's Line between Ceram Sea and Molucca Strait is in direct contrast with Molengraaff's circum-insular trough sea since, according to the Sarasins, it has been crossed by a strong

land bridge between Celebes and Halmahera, via the Sula * Islands and Obi Major. According to Molengraaff, Molucca Passage separates portions of the earth from each other. These portions exhibit very great structural differences and, so far as known, have never been strongly connected. According to Pelseneer, who drew the northern part of Weber's Line through Molucca Passage, this is likewise true biologically; that is to say, Halmahera has not been directly connected with Mindanao. In this connection, Molengraaff thinks that eastern Mindanao may have been connected through a now deeply submerged region with the middle arm of Celebes. This condition is easily seen by reference to Plate 40 and by tracing the 2,000-meter line. In Dickerson's opinion, the Mindanao rift system was in existence at least as early as Miocene, and movements along the various lines of this rift system have probably prevented a direct land connection between Halmahera and Mindanao. However, the possibility of a stepping-stone bridge by way of Talaut Island is not entirely eliminated.

The sharpness of these faunal and floral boundaries is now seen to be conditioned by the sharp geologic boundaries. West of Wallace's Line plants and animals have been able to migrate from the previously existing continental area to other parts, subject only to the limitations that are found in continental areas. East of Weber's Line, during middle and probably late Pleistocene time, Australian plants and animals likewise were enabled to migrate over New Guinea and even the Aru Islands. In the stress area between these two lines, migrations of Australian and Asian types of animals and plants have been somewhat interrupted by the nearly constant archipelagic conditions existing in Wallacea; and at times all or most intermigrations have been inhibited by impassable barriers in the form of separating arms of the sea. Among the various islands in this vast region and the previously existing continental area to the west and southeast, land connections during the Neocene and Pleistocene have never been more than narrow isthmuses. The distribution of birds, reptiles, lizards, fishes, mammals, and many groups of insects conforms to the distribution of plants in general. Many Asiatic types extend as far as Macassar Strait and, while some cross it, they appear in rapidly dwindling numbers toward New

* Lippincott's New Gazetteer (1913) and the Century Atlas give the spelling Xulla, although "Sula" is often used and may be confused with Sulu, of the Philippines.—R. C. MCGREGOR.

Guinea. Likewise, Australian types decrease with greater and greater rapidity westward and northward from New Guinea. In the Philippines there are distinct alliances with western Malaysia, not only in mammals, birds, amphibians, reptiles, and lizards, but in the flora as well. The Australian faunal and floral elements in eastern Malaysia are recognizable throughout Wallacea, but in general they are weaker than the Asian elements. While it is recognized that Wallacea differs from south to north, yet the broad characteristics throughout the area are the same; that is, Wallace's Line marks the limit of numerous Asiatic types and Weber's Line marks in a very similar manner the westward extension of Australian types. Weber's Line and Wallace's Line appear to be of approximately equal value as biologic lines of great importance. Fundamentally, these lines are geologic, thus illustrating the necessity of the coöperative efforts of geologists, hydrographers, biologists, and other scientists in the solution of the problems involved in studies of island life.

SIGNIFICANCE OF WALLACEA AND OF WALLACE'S AND WEBER'S LINES

Mr. Merrill supplied the following closing statement:

Wallacea, as herein delimited, is frankly an attempt to outline an unstable insular area between two more-stable, and at times, continental areas; namely, Sundaland and Papualand. The delimitation of Wallacea is based largely on the available hydrographic and geologic data. A general survey of the known distribution of various groups of plants and animals within the region has been made, with an attempt to correlate these data with geologic history.

Wallacea may be interpreted as a transition zone wherein Asiatic and Australian types mingle. For those who prefer a simple line of demarcation between the Asiatic and Australian faunas and floras, Wallacea's Line, as originally proposed or as we have modified it, or Weber's Line may be accepted. The general facts of geographic distribution within the region under discussion we believe point to a transition zone, rather than a simple separating line.

It is frankly admitted that the northern extension of Wallace's Line between the Philippines proper and Borneo does not so sharply separate the Asiatic and Australian bios as does the line as originally placed, or as perhaps does Weber's Line.

Asiatic and Sundaland types of both plants and animals are more strongly represented in the northern part of Wallacea (that is, in the Philippines outside of the Palawan-Calamianes area) than in the southern part of this terrane. This applies to the genera of plants, birds, fresh-water fishes, some groups of reptiles, some groups of insects, and perhaps to the mammals as a whole. We have, however, placed the boundaries of Wallacea in general conformity with the hydrography and geologic history of the region as approximately delimiting an unstable insular area lying between two more-stable and, until the more Recent, at times continental areas. The eastern boundary of this unstable area where it impinges on the more-stable Papualand is the approximate position of Weber's Line, and its western boundary where it impinges on the more-stable Sundaland is the approximate position of Wallace's Line as modified by its northern extension through the Philippine group and eastward between Luzon and Formosa.

The geographic distribution data at hand indicate with a fair degree of clearness that the present fauna and flora of Wallacea are composed of relict species and their descendants with infiltrations from both Sundaland and Papualand, exactly what would be expected if our assumption as to its geologic history be correct. Within the area Asiatic types decrease in number and importance as we proceed from the north and west to the south and east. Australian types similarly decrease in number and importance as we proceed from the south and east to the north and west.

There is much evidence to indicate lines of migration from Sundaland northward into the Philippines, thence southward into Papualand and vice versa, rather than much east and west migration across Wallacea; in other words, within Wallacea much of the migration has been in general north and south, rather than east and west. We might compare Wallacea to a narrow-based, elongated triangle lying between Sundaland and Papualand, the Lesser Sunda Islands and Timor forming its base, Luzon forming its apex. To a very considerable degree migrations within this triangular area have apparently been along the two longer sides, rather than directly east and west across it. The Philippine Islands forming its apex thus contain numerous Sundaland types that failed to reach Papualand; and a smaller but still striking series of Papualand and Australian types that failed to reach Sundaland. There are distinctly more Australian types of plants, birds, etc., in the Philippines than in

Sundaland. At the same time some eastern and western types apparently succeeded in negotiating both sides of this hypothetical triangle, as they are found in Sundaland, northern Wallacea (the Philippines), and in Papualand; some of these may have crossed the basal part of the triangular area indicated. A more-intensive exploration of the entire Malaysian region will supply the facts by which this hypothesis may be more thoroughly tested, than is possible at the present time. Vast areas exist in which biologic explorations have been superficial, and extensive regions have never been visited by any collector.

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Fig. 1. Banisilan, Cotabato Province, Mindanao.



Fig. 2. A marine terrace in central Bohol.



Fig. 3. Puerto Princesa, Palawan.

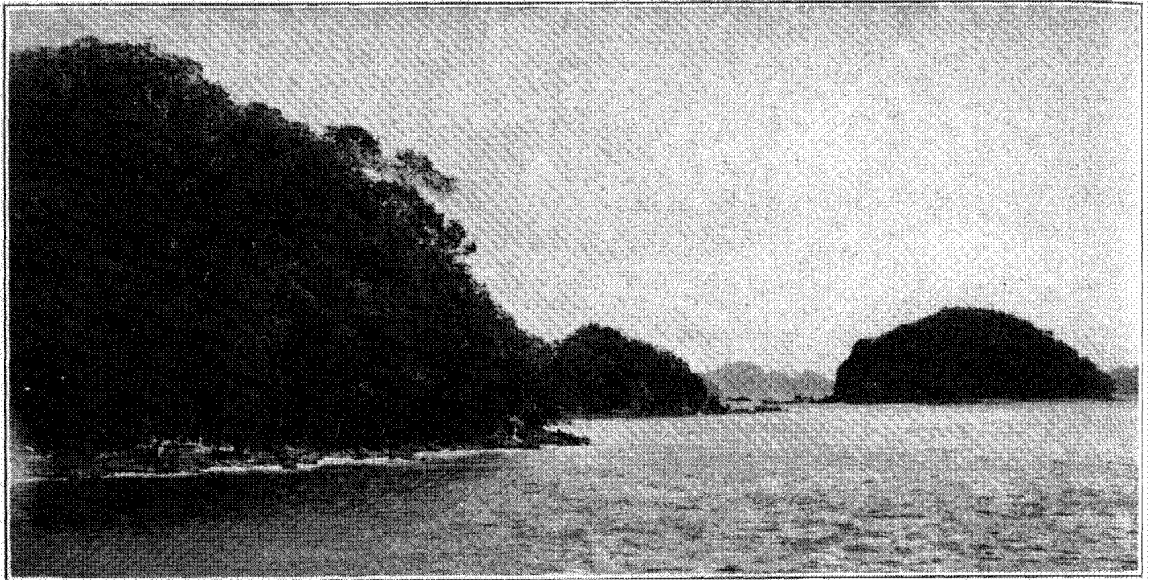


Fig. 1. Malampaya Sound, Palawan.

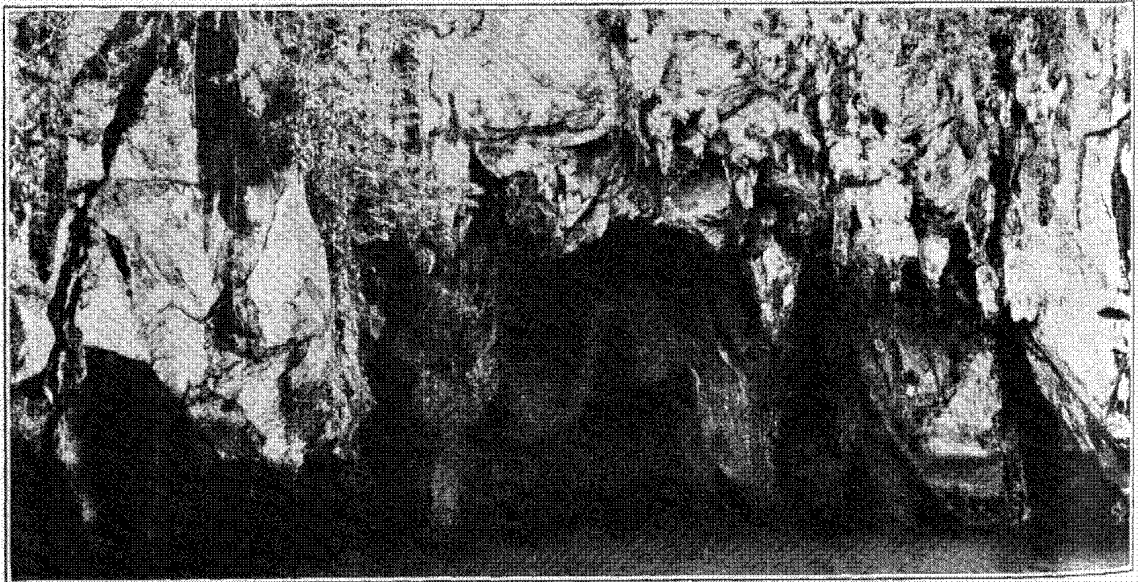


Fig. 2. Saint Paul River, Palawan. Entrance to cave.

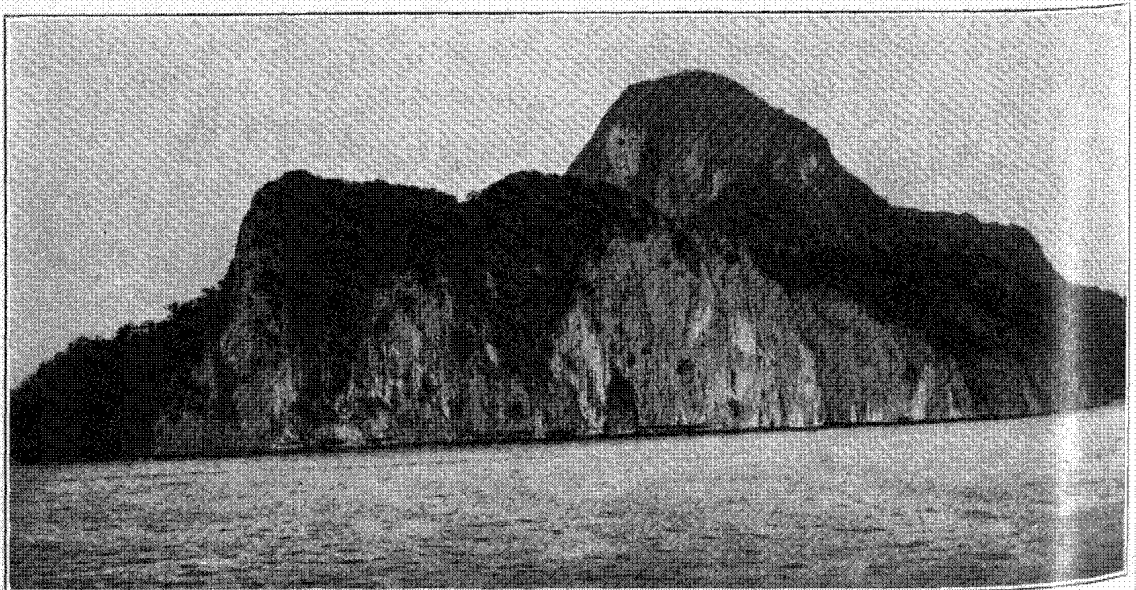


Fig. 3. Headlands of Saint Paul Bay, Palawan.

PLATE 2.

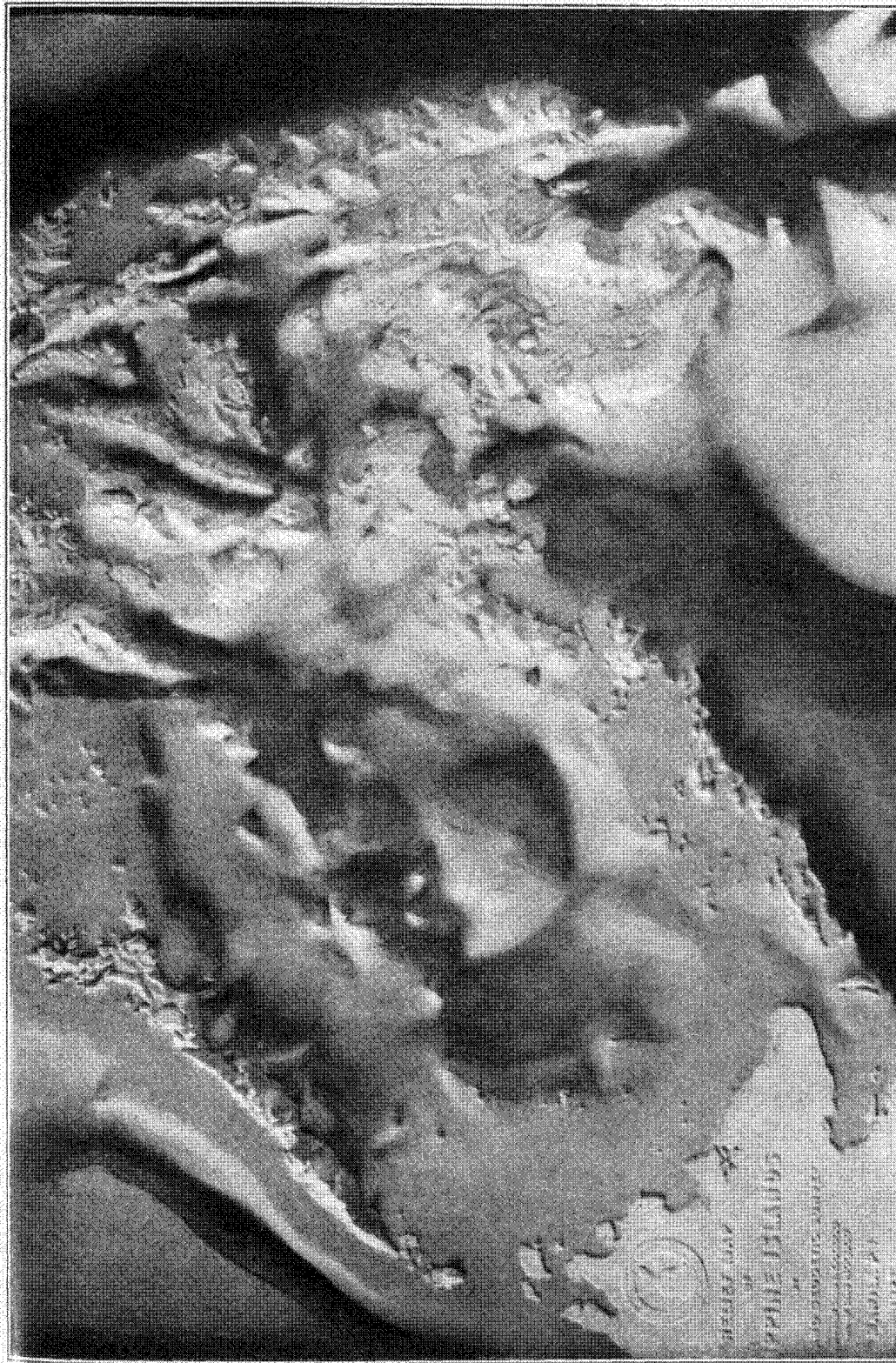


PLATE 3. THE SOUTHERN HALF OF THE PHILIPPINES.

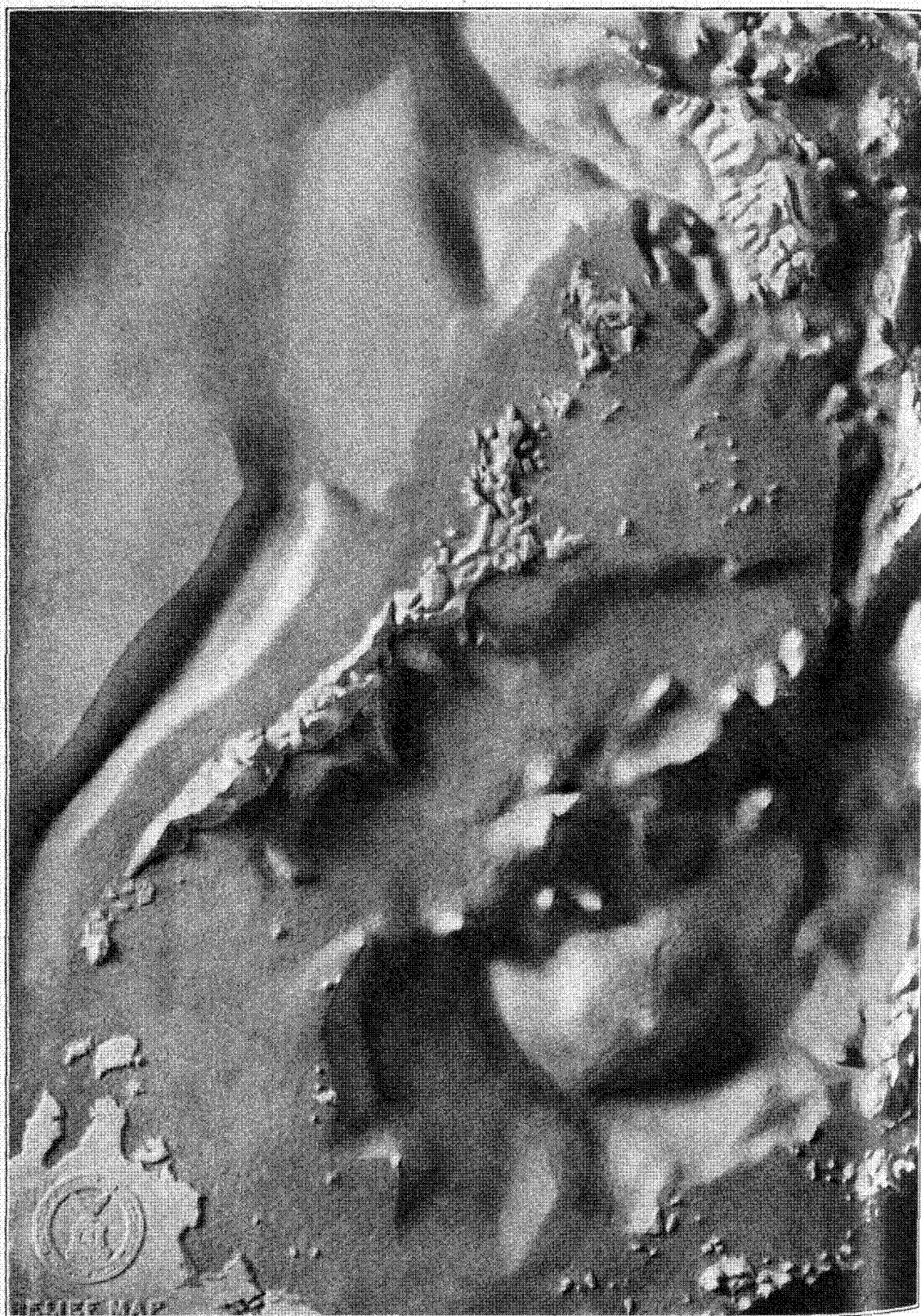


PLATE 4. THE PALAWAN TROUGH AND THE SULU SEA.

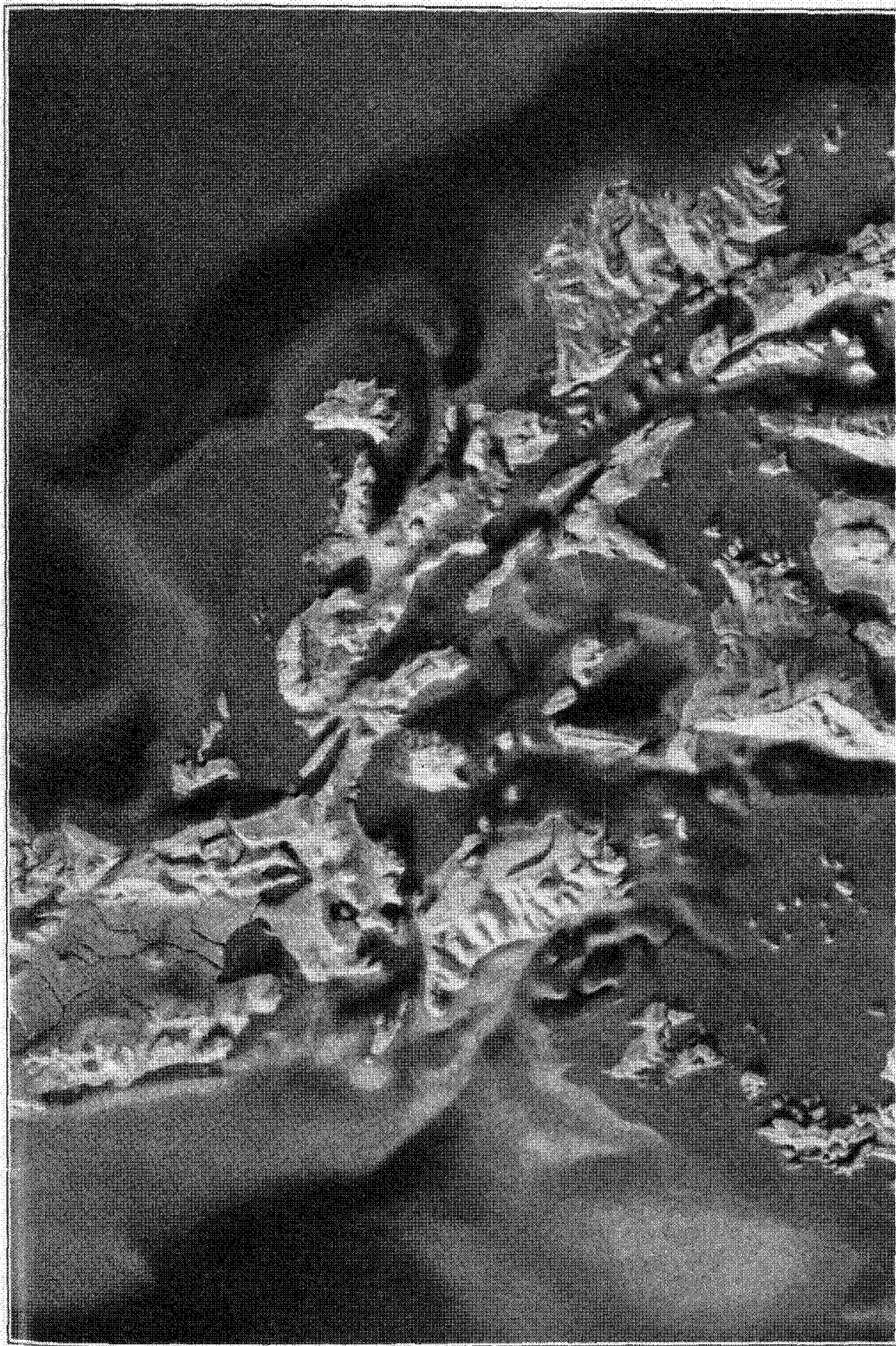


PLATE 5. THE PALAWAN TROUGH, THE TAAL RIFT, AND THE LUZON DEEP.

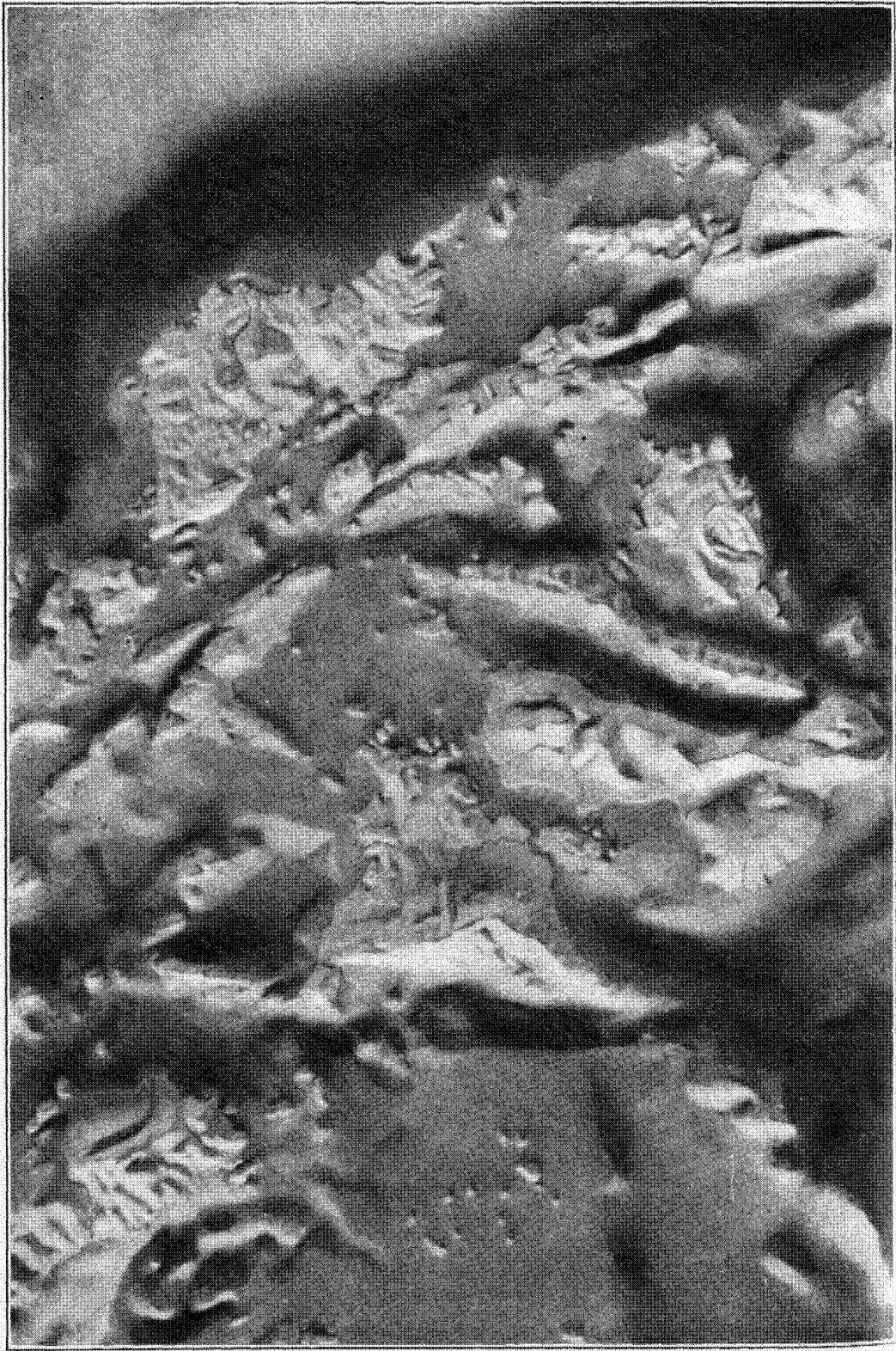


PLATE 6. THE VISAYAN SHELF SEA AND THE TABLAS DEEP.



PLATE 7. NORTHERN LUZON, THE BABUYANES, THE BATANES, AND FORMOSA.

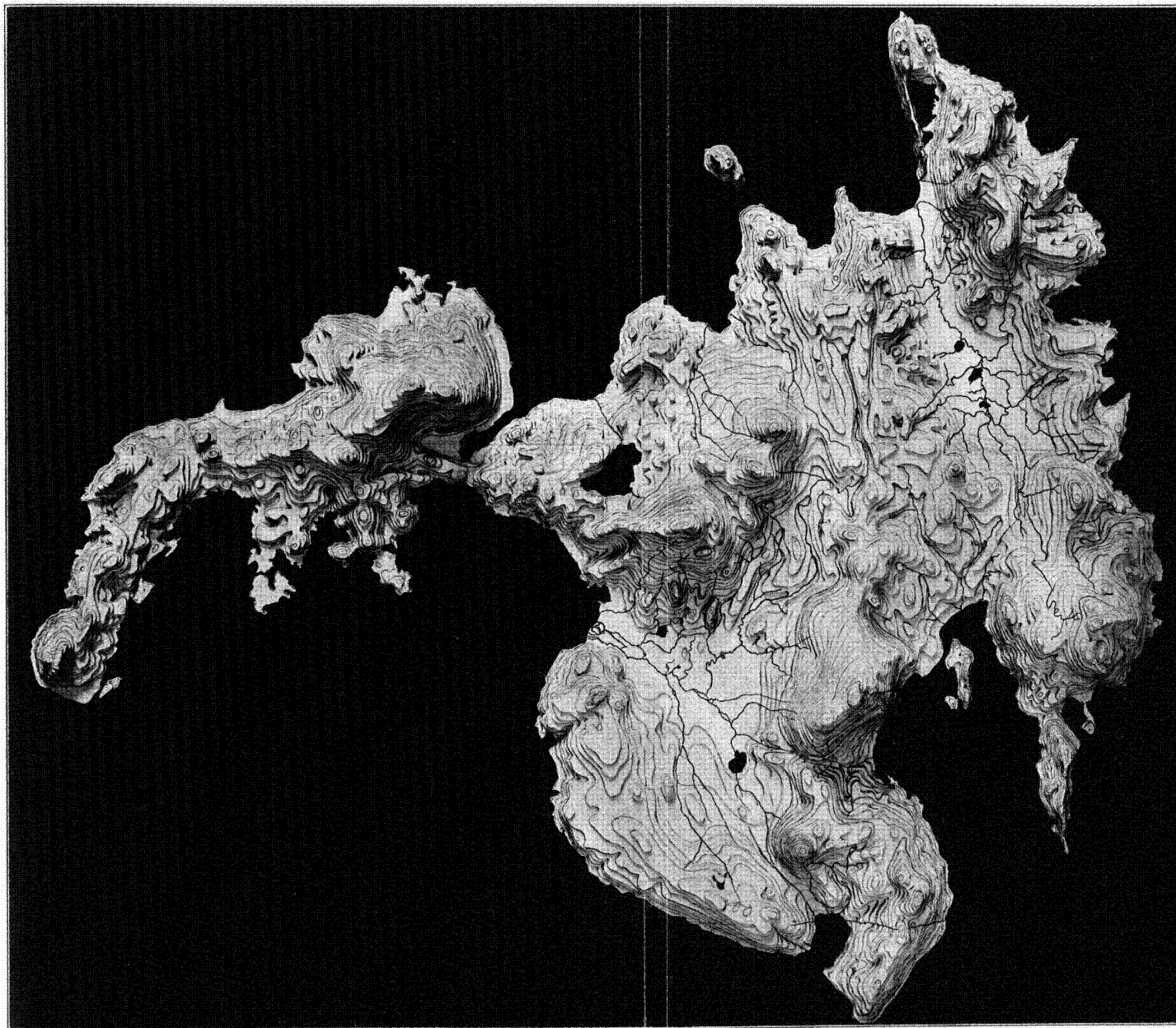


PLATE 8. MINDANAO; CONTOUR INTERVALS, 100 METERS.

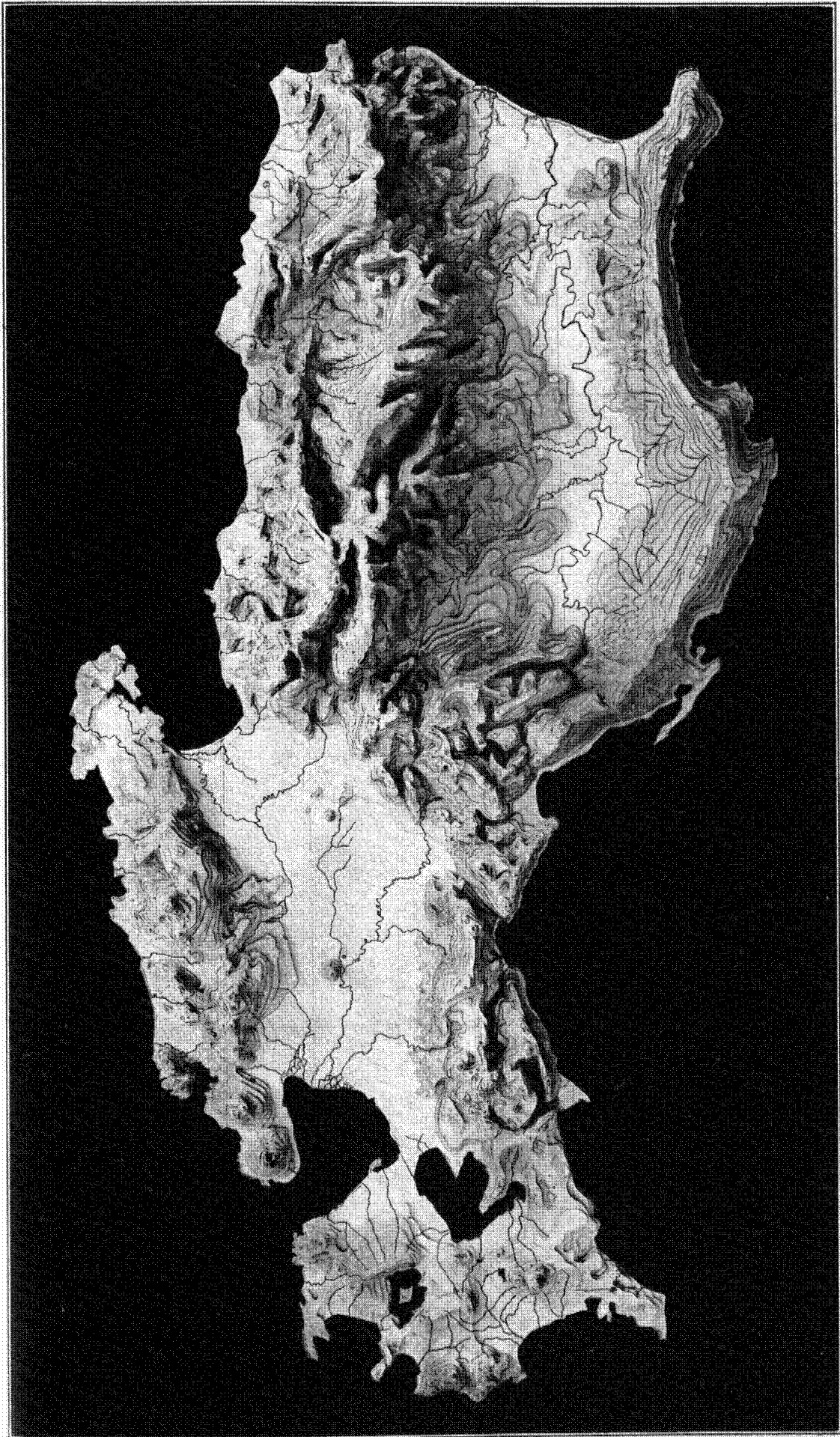


PLATE 9. NORTHERN AND CENTRAL LUZON; CONTOUR INTERVALS, 100 METERS.



Fig. 1. *Sonneratia caseolaris* (Linnæus) Engler, on an open coast.



Fig. 2. *Sonneratia caseolaris* (Linnæus) Engler, showing air roots.



Fig. 1. Interior of a mangrove swamp, Bongabon, Mindoro.



Fig. 2. Forest near Agusan River, Mindanao.

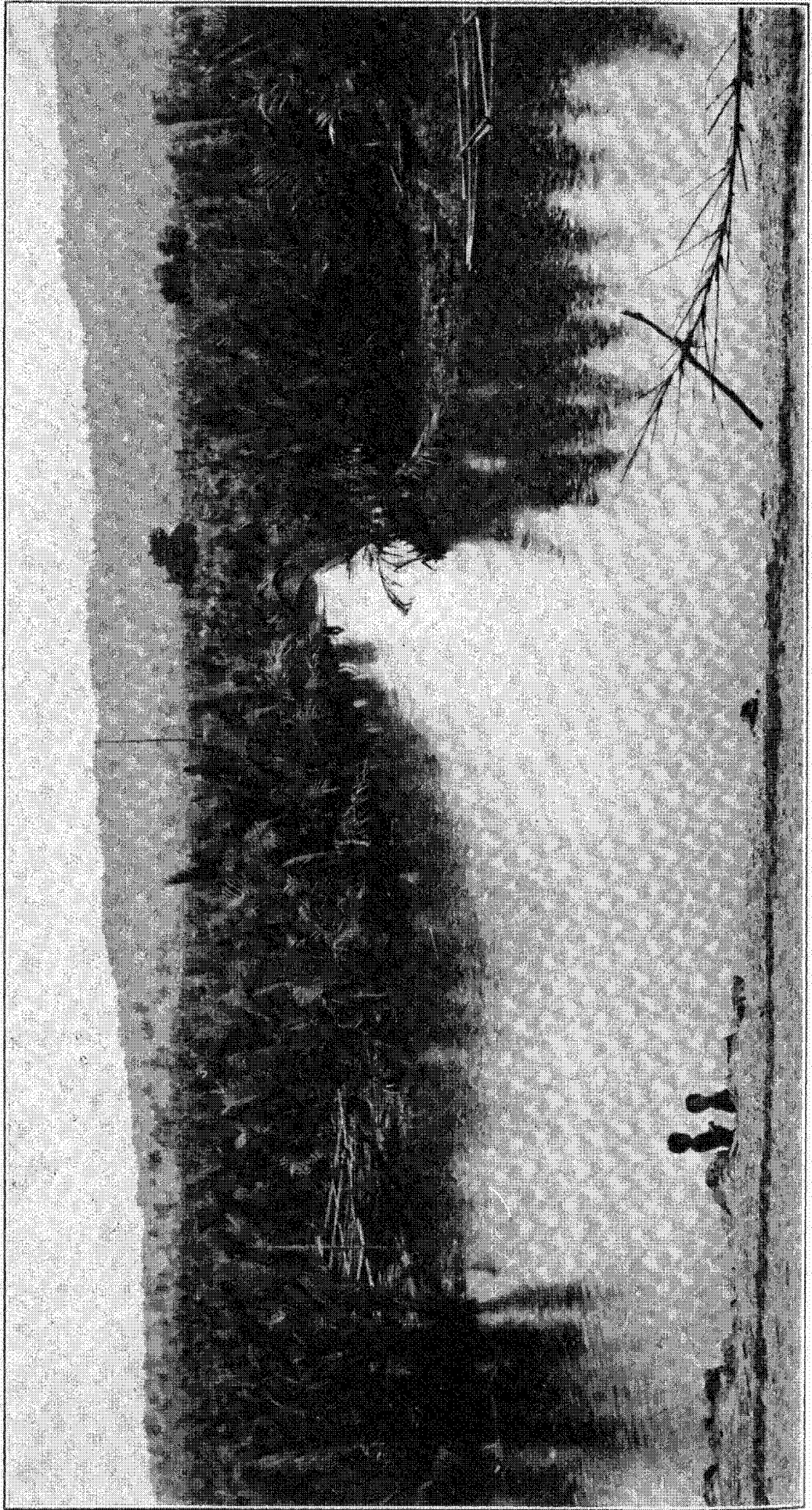


PLATE 12. NIPA PALM, *NYPA FRUTICANS* WURMB, SHOWING ITS HABIT.



PLATE 13. DIPTEROCARP FOREST AT THE EDGE OF A CLEARING.



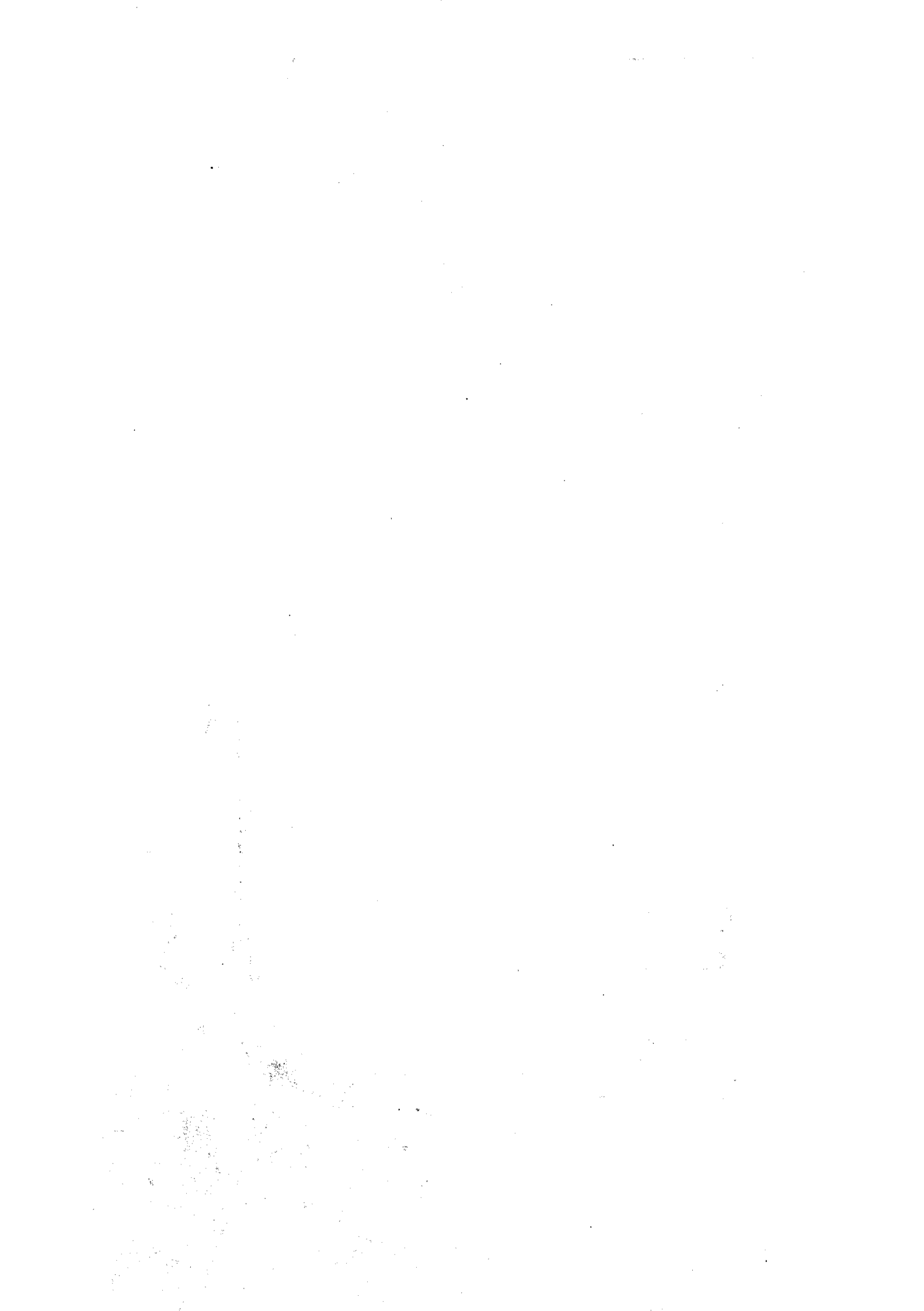
PLATE 14. LARGE DIPTEROCARPS IN NORTHERN NEGROS.



PLATE 15. PINE FOREST IN BENGUET, LUZON.



PLATE 16. A LEVEL AREA, NEAR THE LOWER LIMITS OF THE MOSSY FOREST, MOUNT MAQUILING, LUZON.



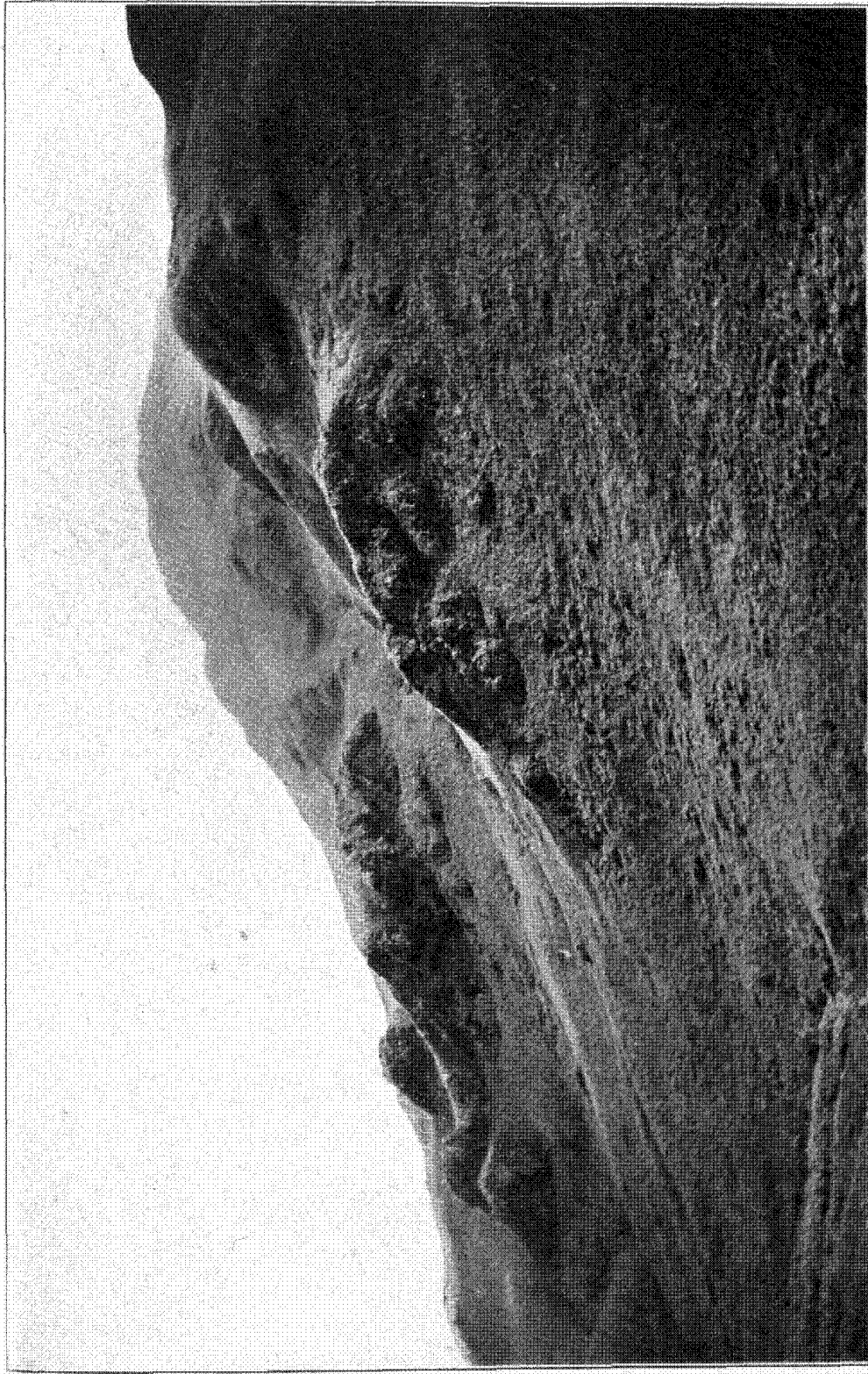


PLATE 17. THE SUMMIT OF MOUNT PULOG, LUZON.

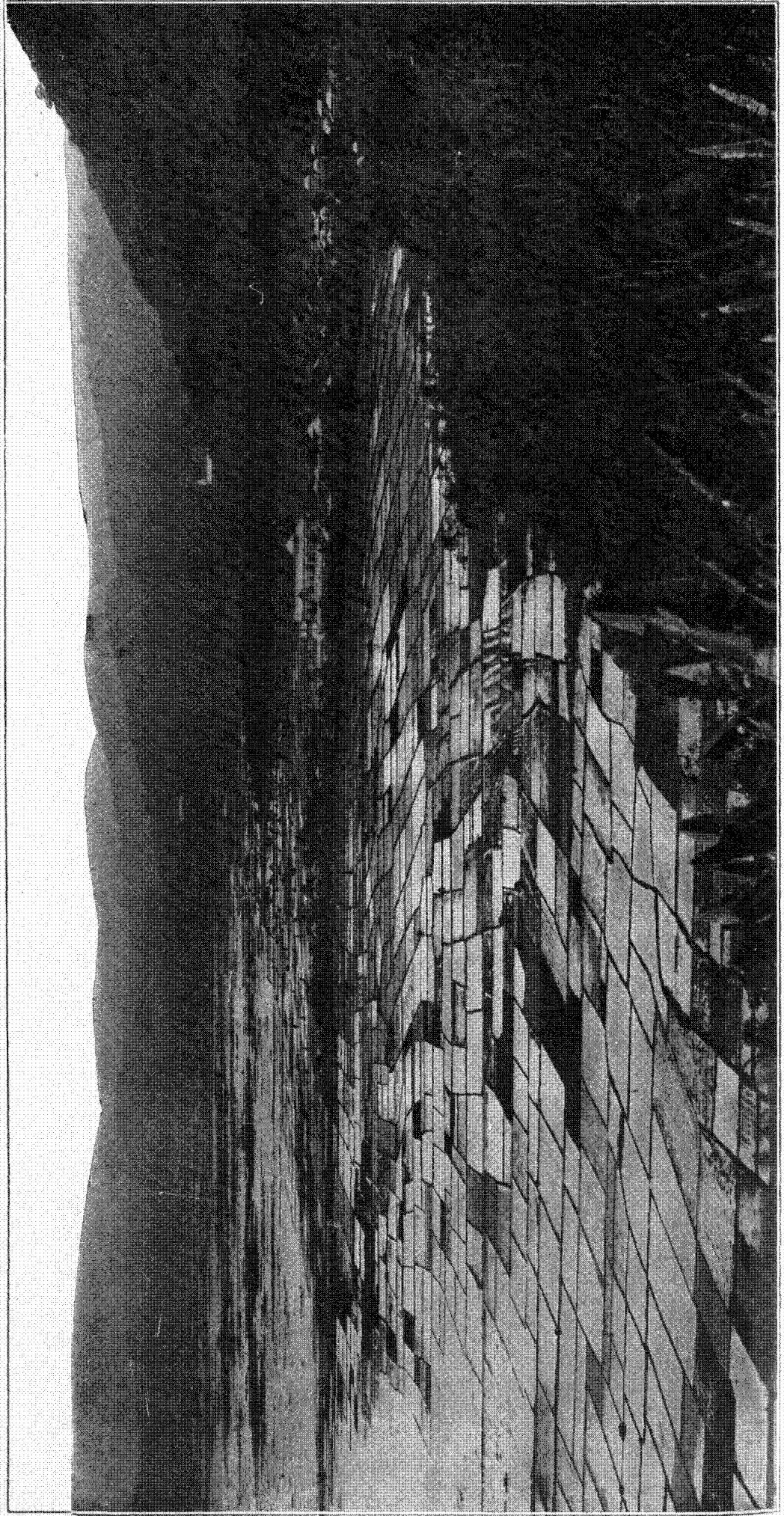


PLATE 18. A PART OF THE SHORE OF LAGUNA DE BAY, LUZON.

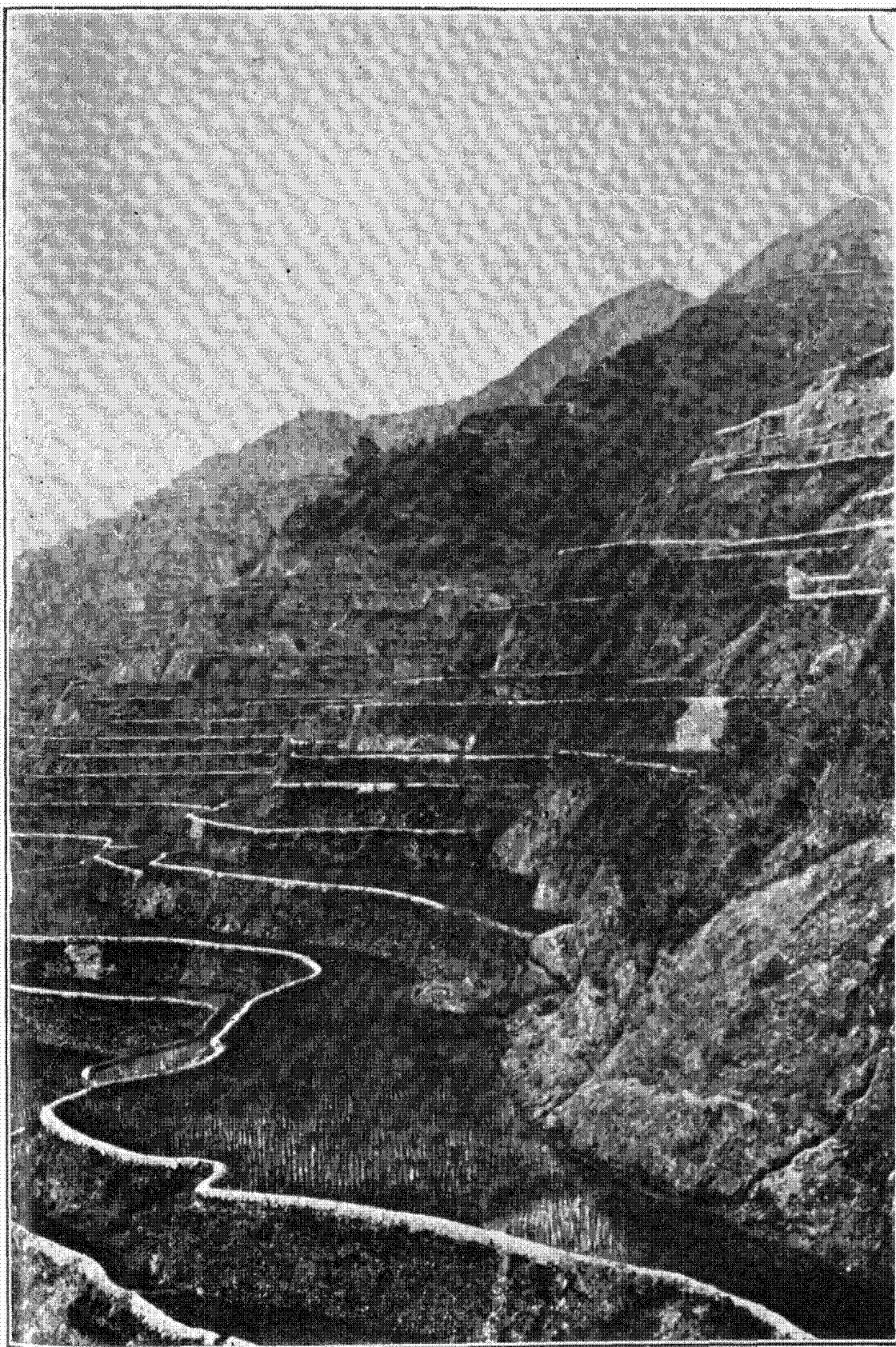


PLATE 19. RICE TERRACES IN IFUGAO SUBPROVINCE, LUZON.

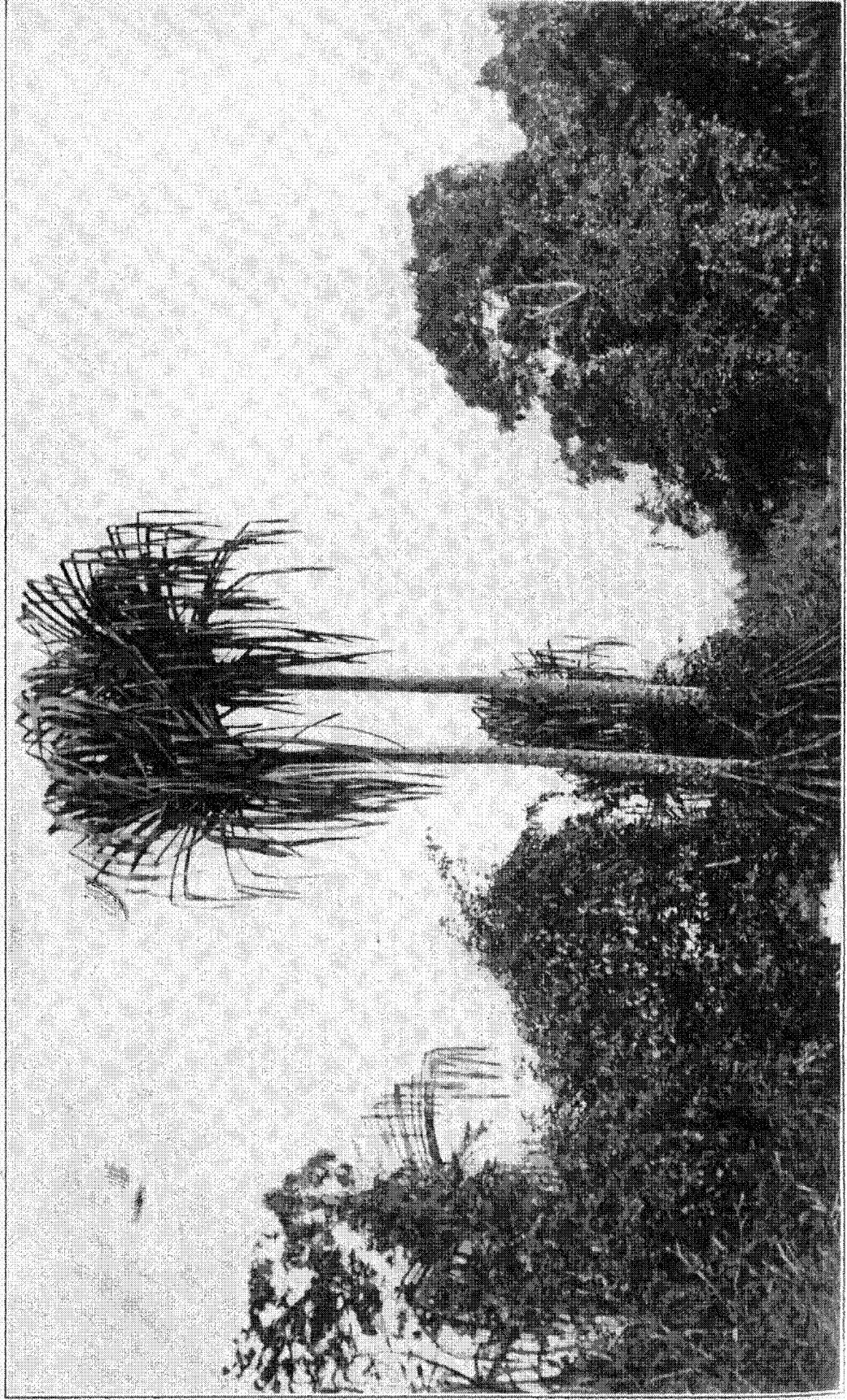


PLATE 20. A VIEW FROM AGUSAN RIVER, IN NORTHERN MINDANAO.

Address

DH

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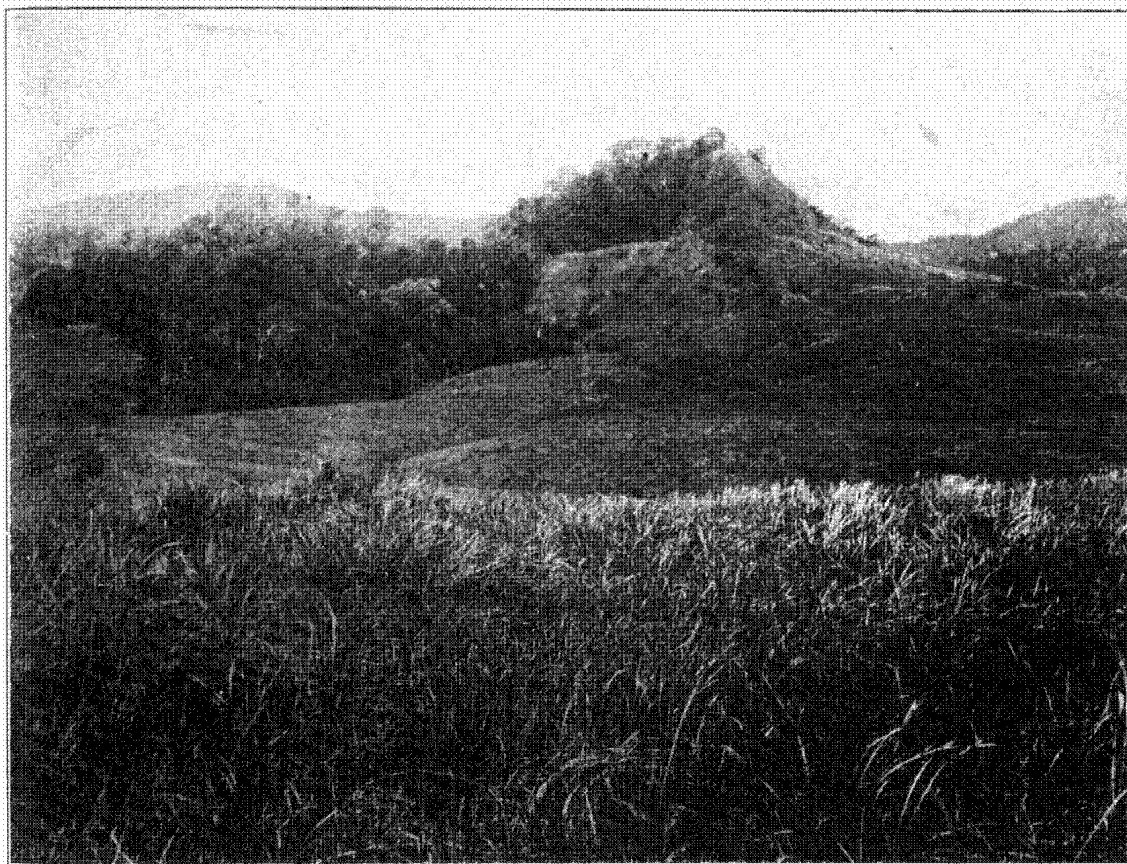


Fig. 1. Grassland near Port Banga, Mindanao.



Fig. 2. Grassland near Balagbag, Rizal Province, Luzon.

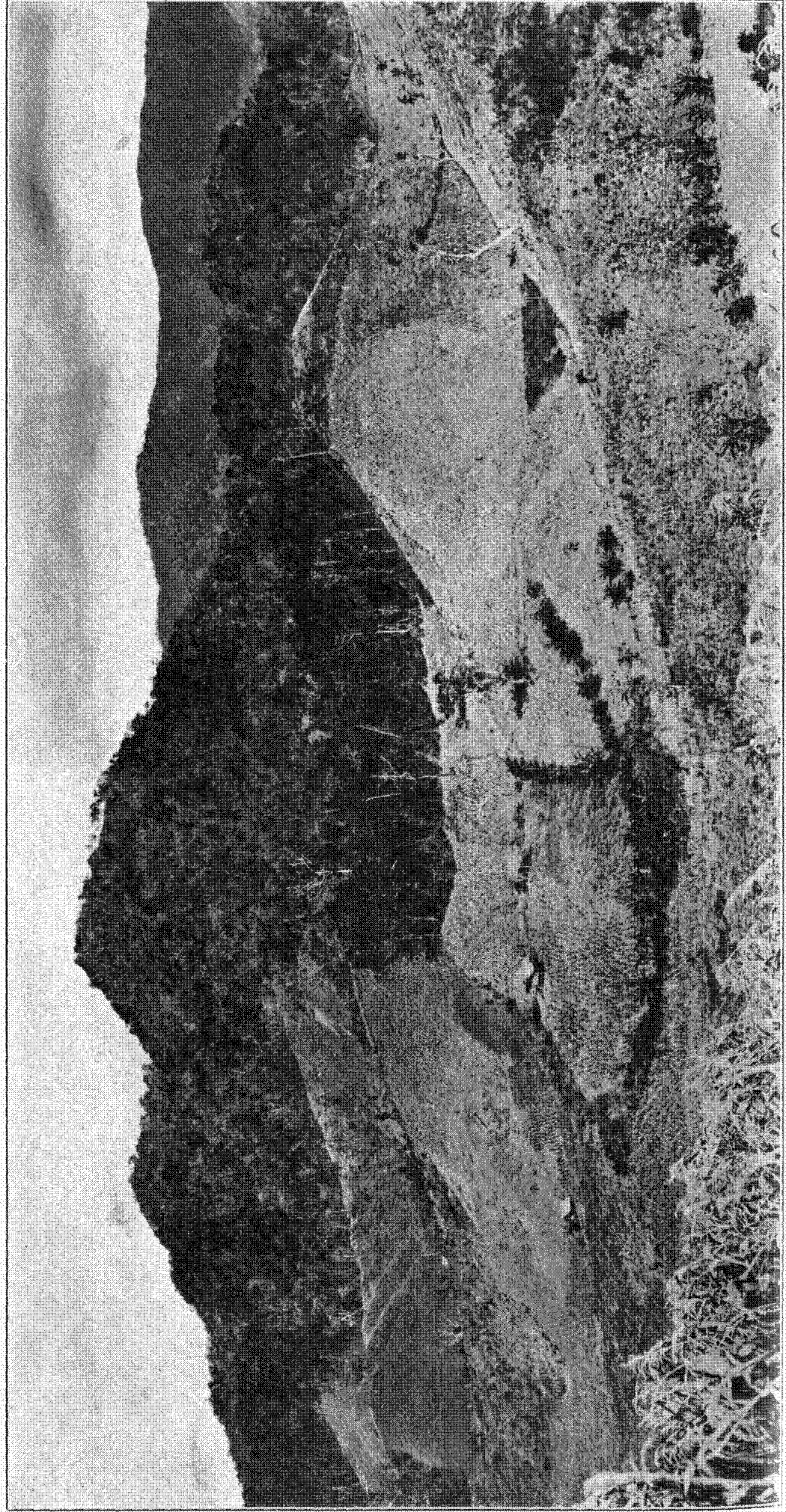


PLATE 22. CAINGINS IN THE MOUNTAINS OF NORTHERN NEGROS.

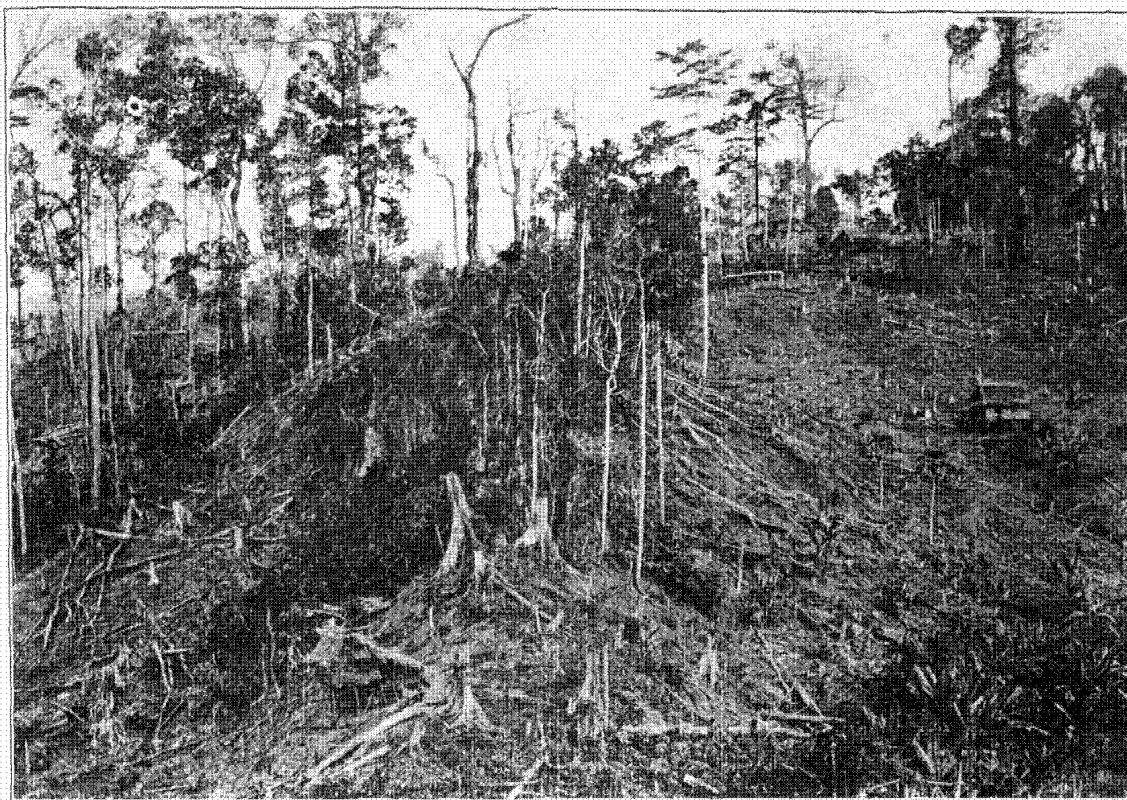


Fig. 1. A typical caiñgin in Occidental Negros.

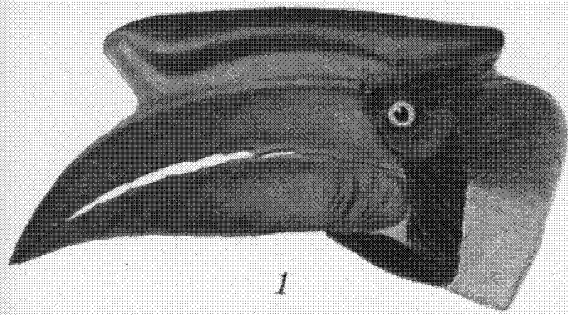


Fig 2. A clearing on level ground in Mindoro.

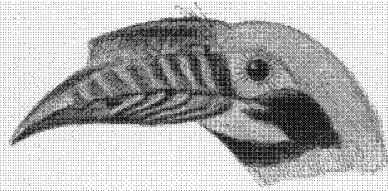
PLATE 23.



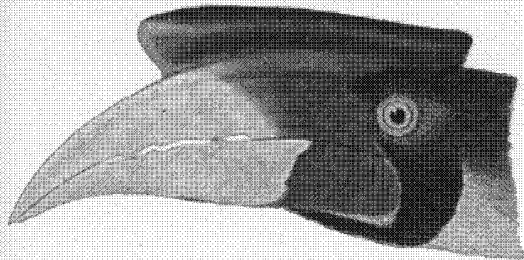
PLATE 24. A STAND OF SCHIZOSTACHYUM, A GREGARIOUS BAMBOO.



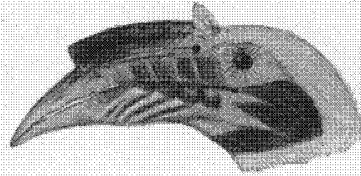
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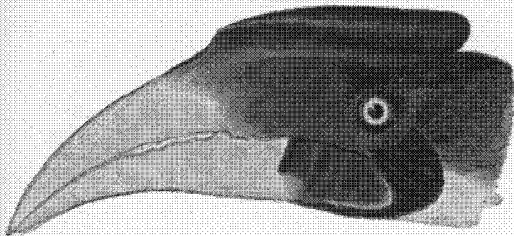
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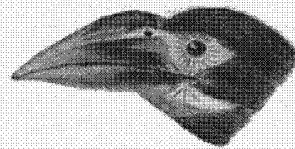
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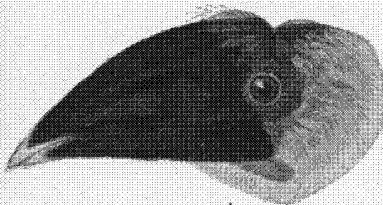
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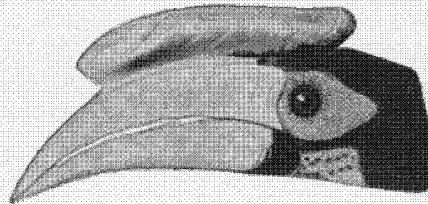
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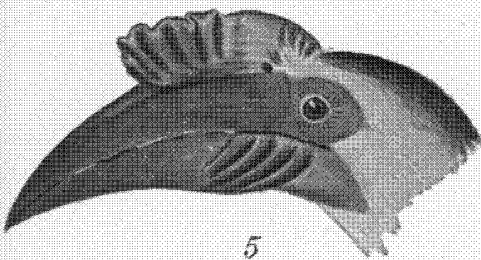
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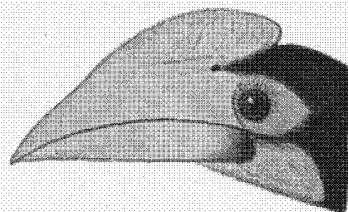
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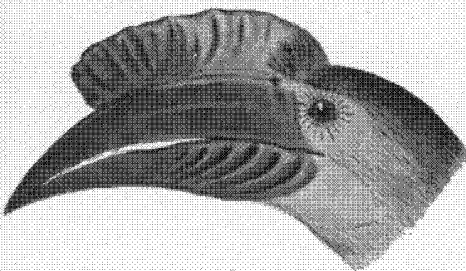
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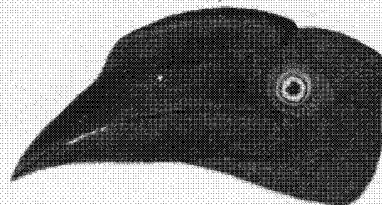
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PLATE 25. HEADS OF SOME PHILIPPINE HORNBILLS.

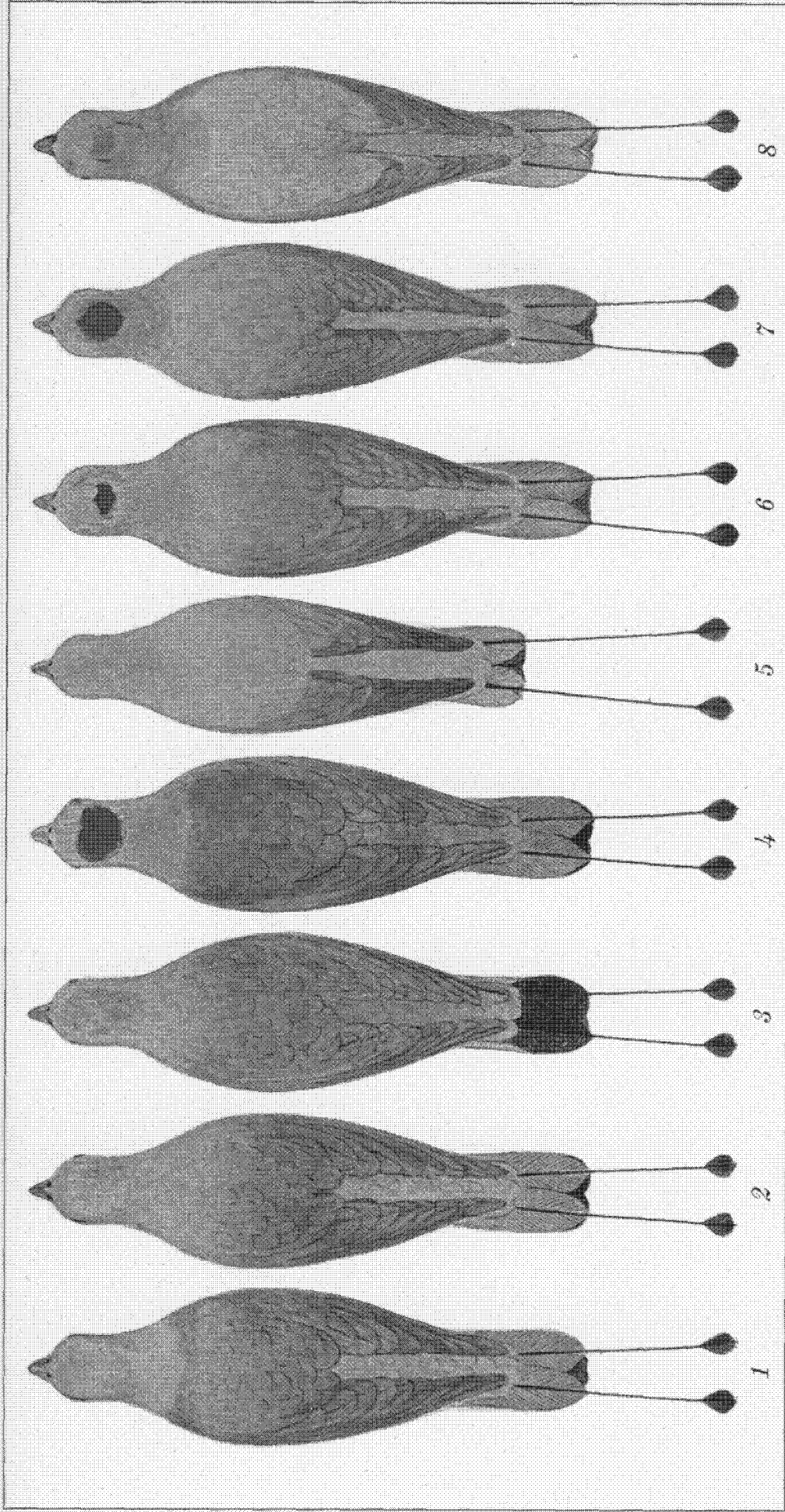


PLATE 26. PARRAKEETS OF THE GENUS PRIONITURUS. DORSAL ASPECT OF MALES.



Fig. 1. *Gekko monarchus* (Duméril and Bibron). 2. *Gymnodactylus agusanensis* Taylor.
PLATE 27.

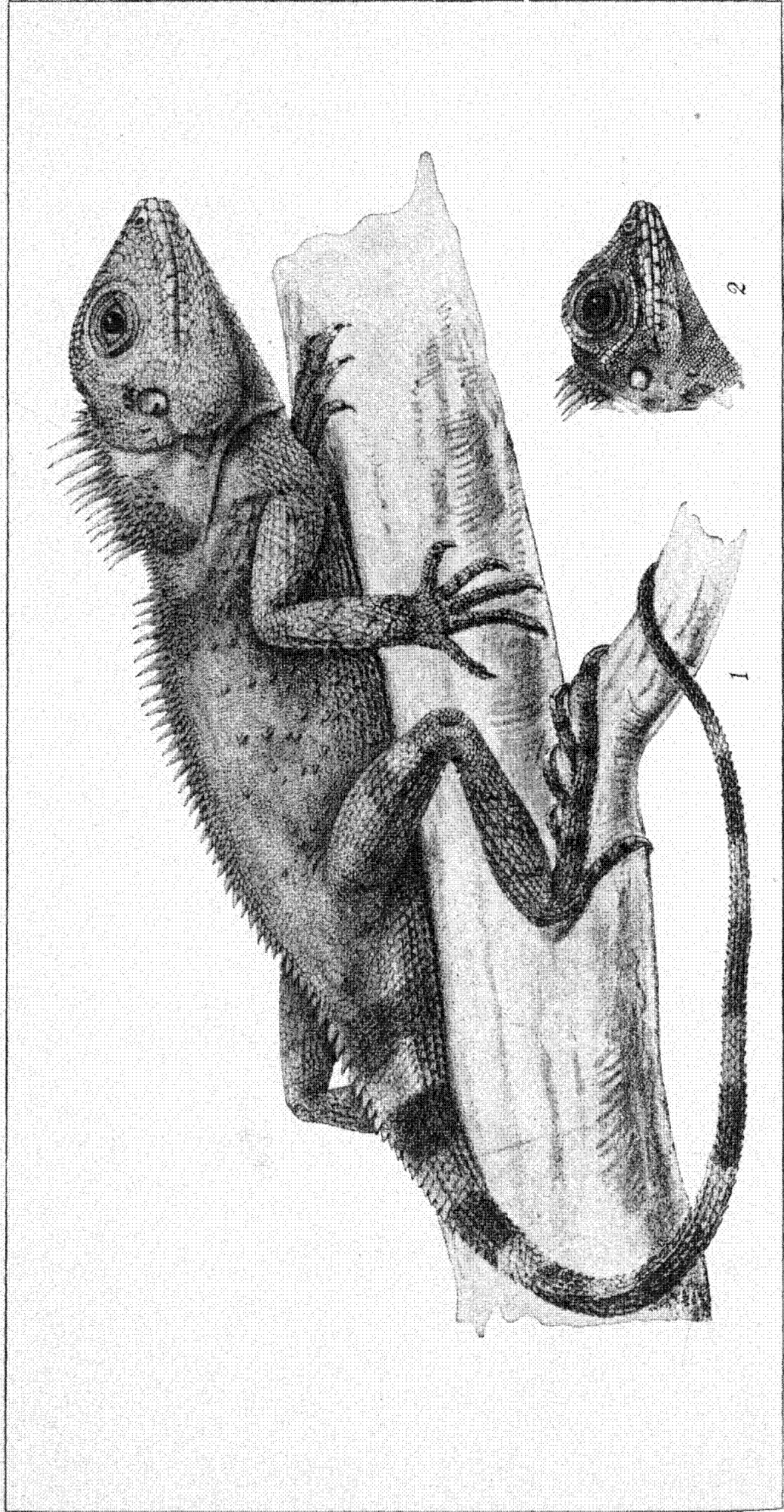


PLATE 28. GONYCEPHALUS INTERRUPTUS BOULENGER AND G. SOPHIE (GRAY).

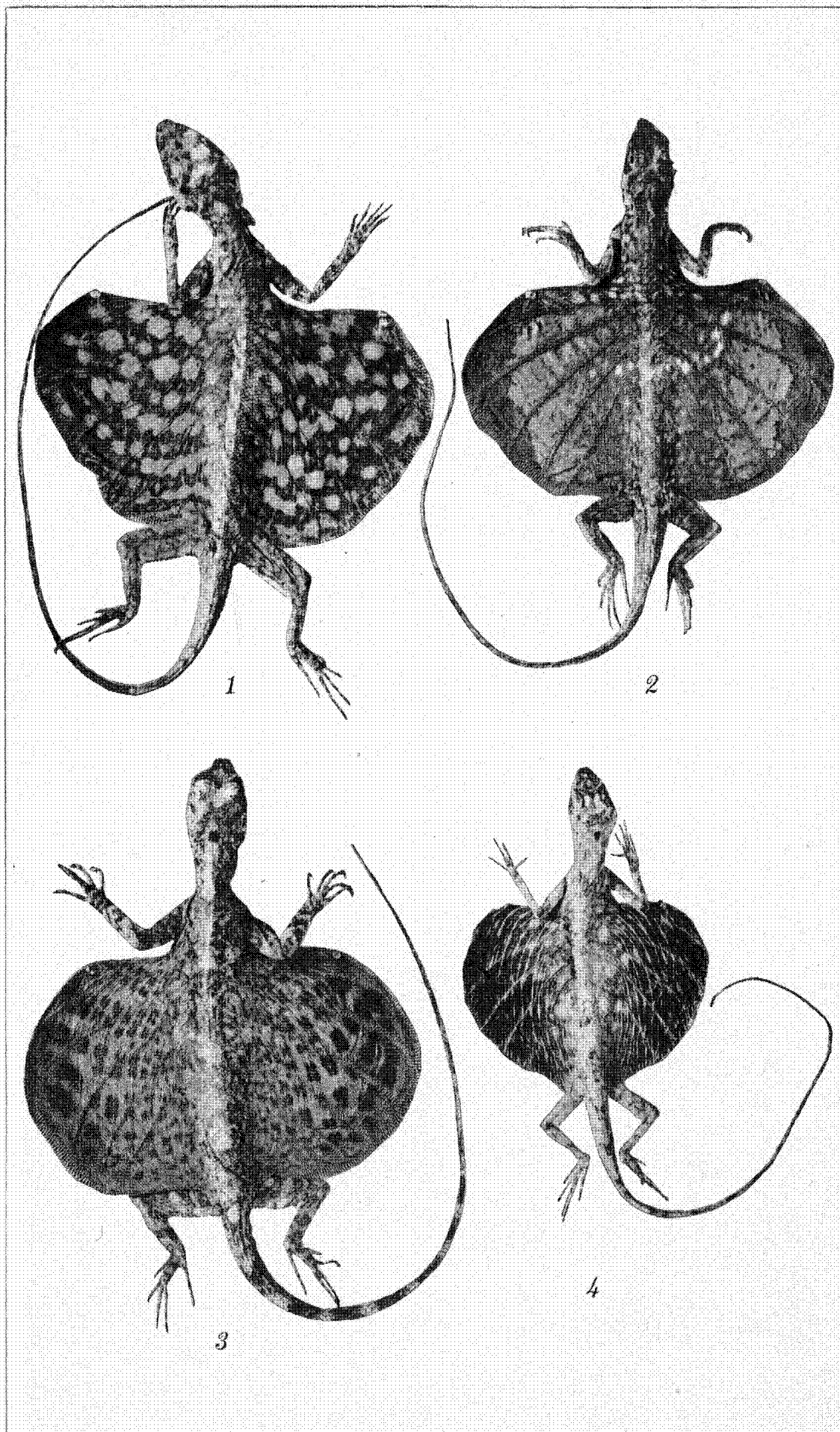
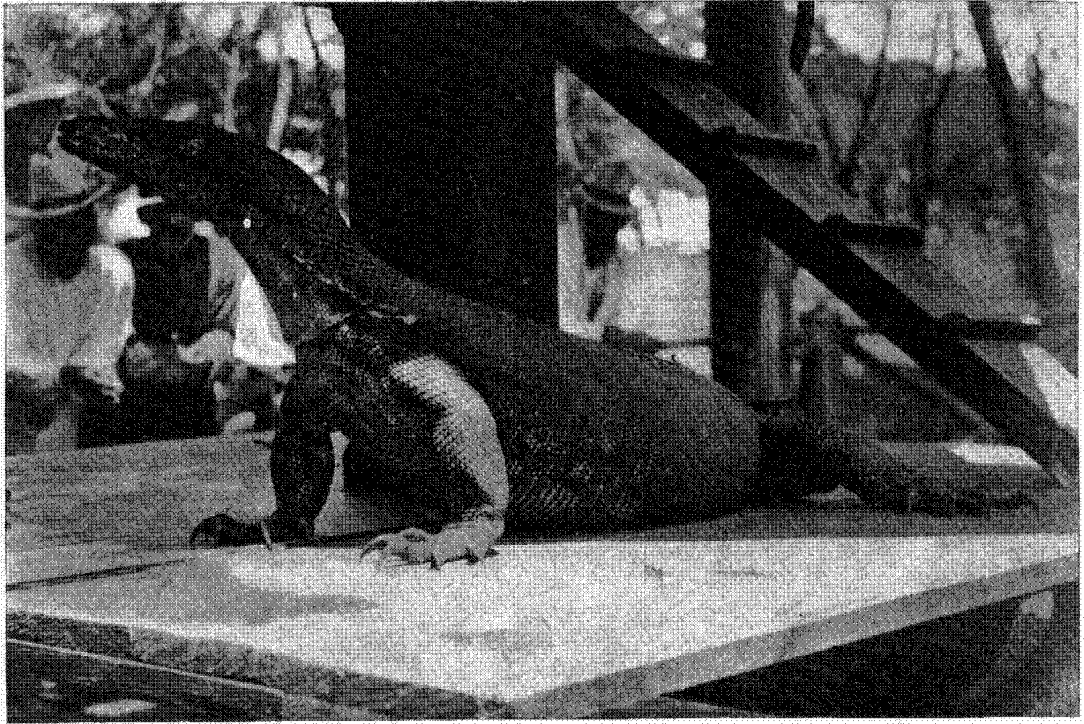
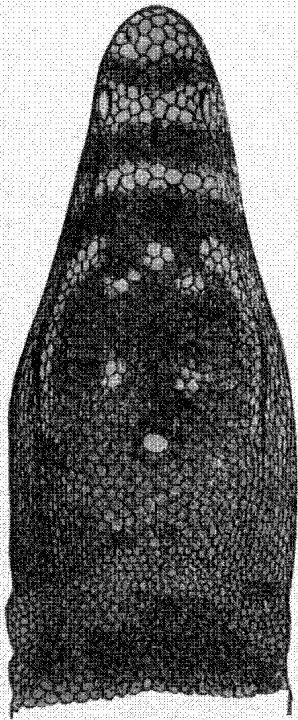


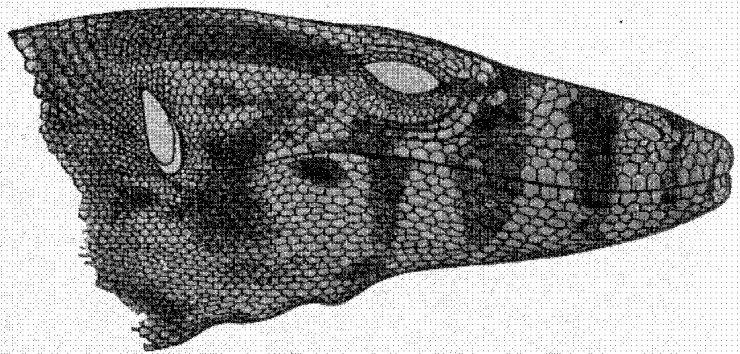
PLATE 29. PHILIPPINE FLYING LIZARDS.



1



2



3

PLATE 30. VARANUS SALVATOR (LAURENTI).



PLATE 31. PTYCHOZOOM INTERMEDIA TAYLOR.

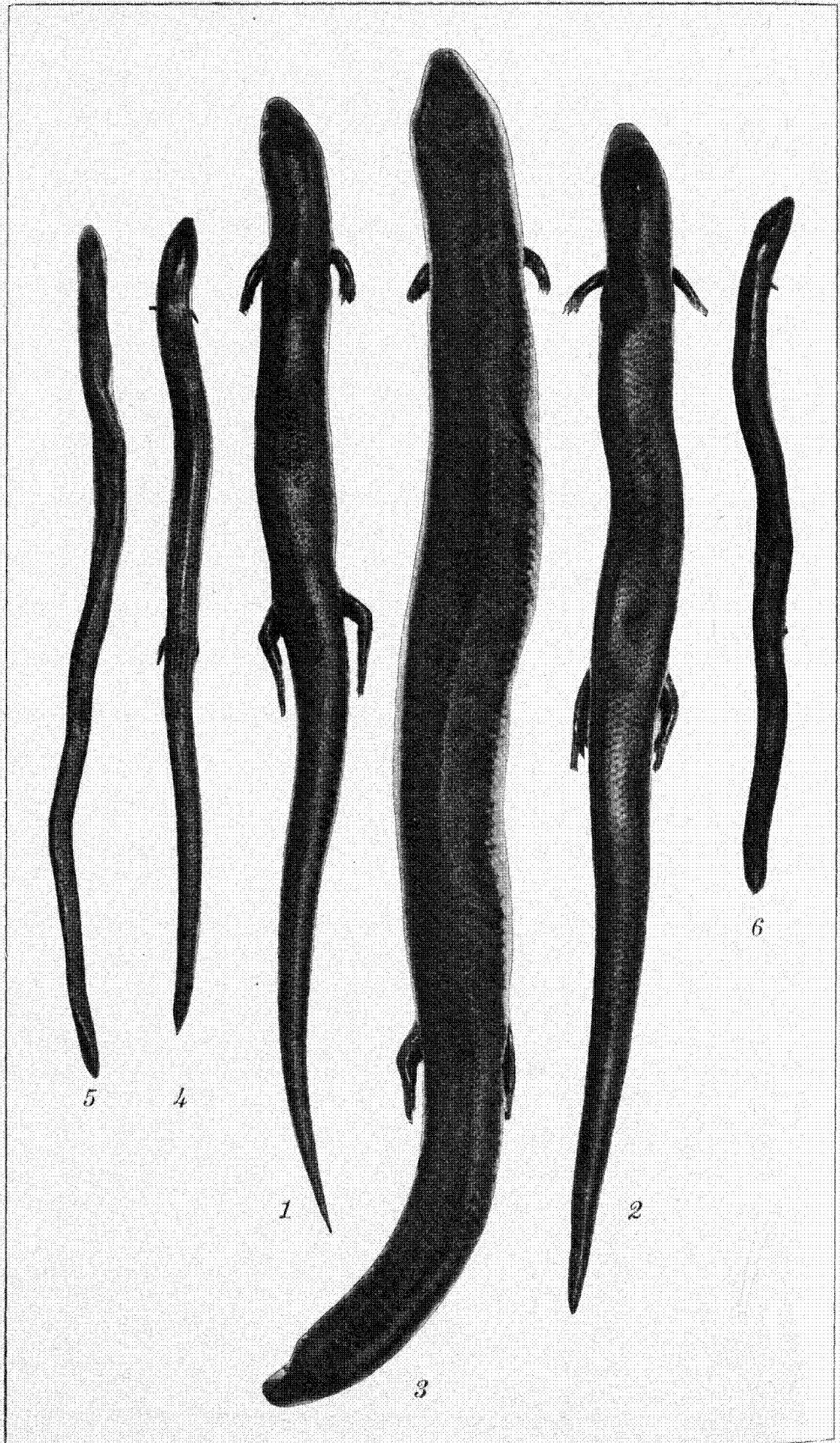


PLATE 32. SIX SPECIES OF THE GENUS BRACHYMELES.

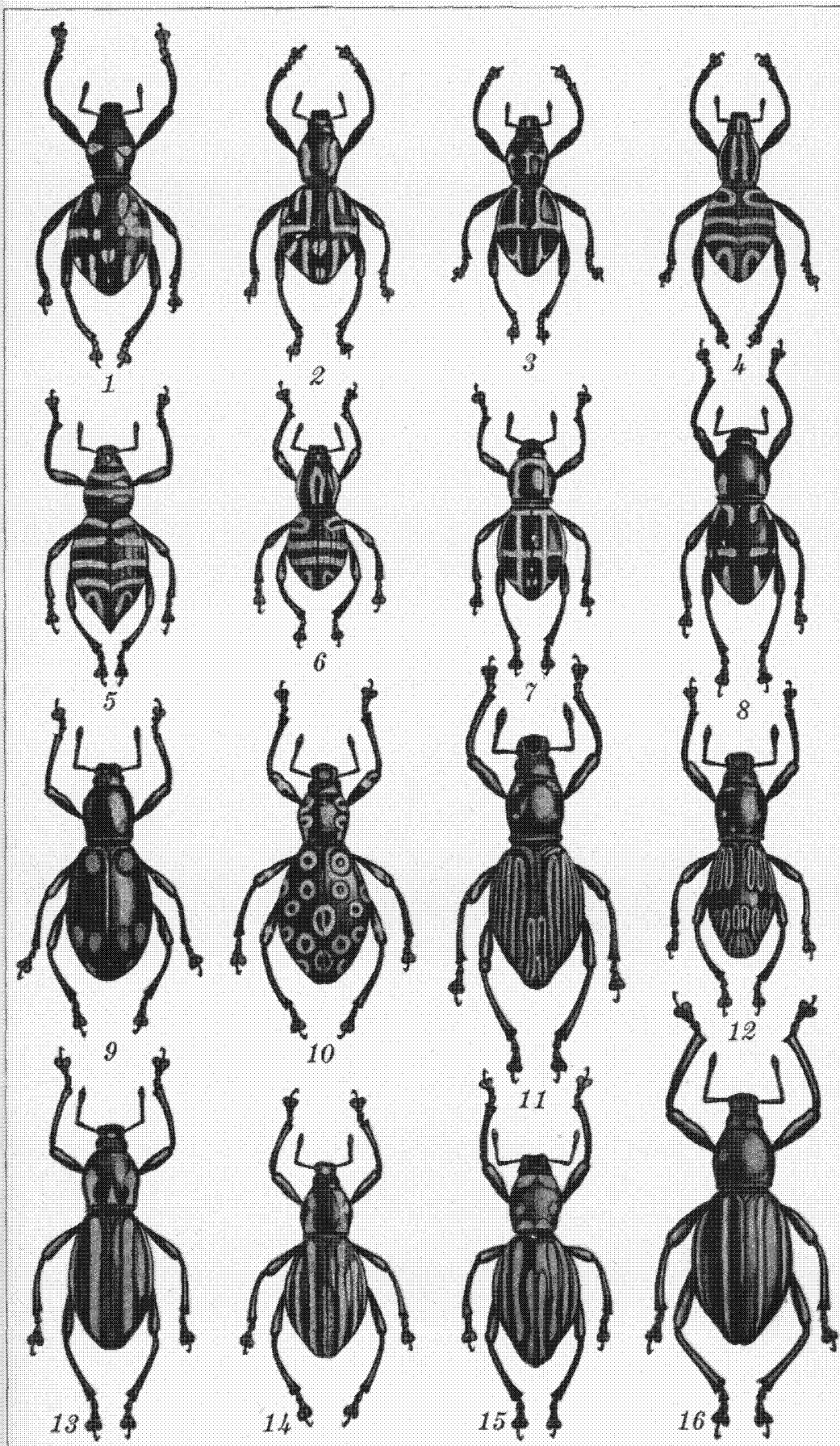
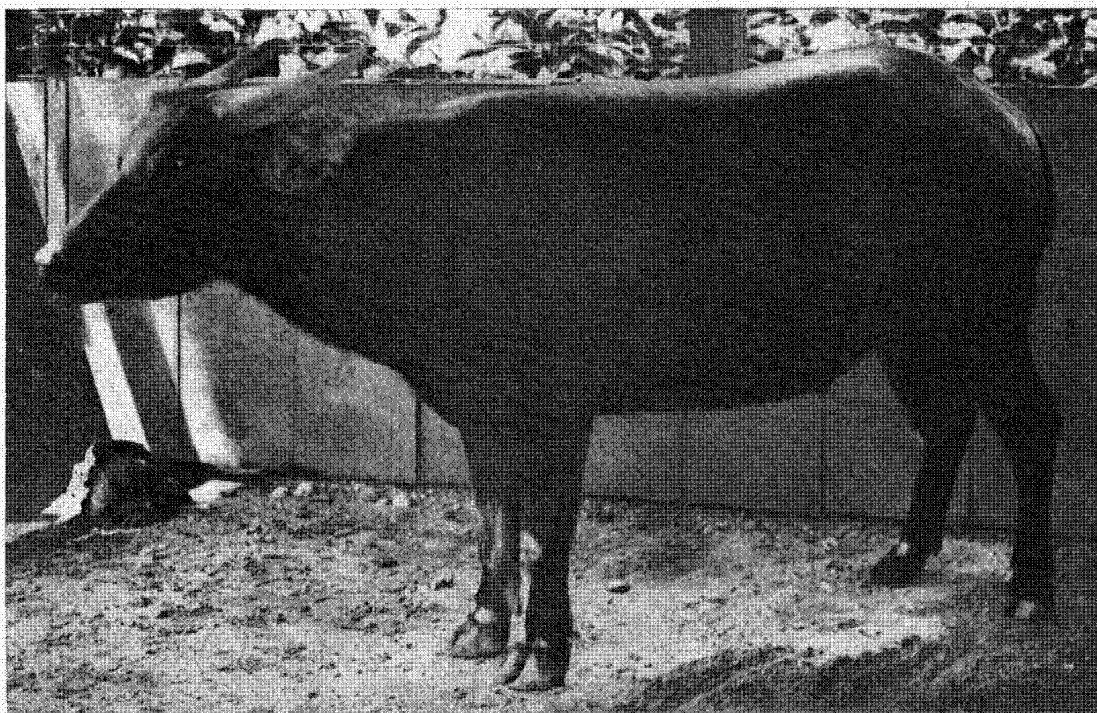


PLATE 33. CHARACTERISTIC SPECIES OF THE GENUS PACHYRRHYNCHUS.

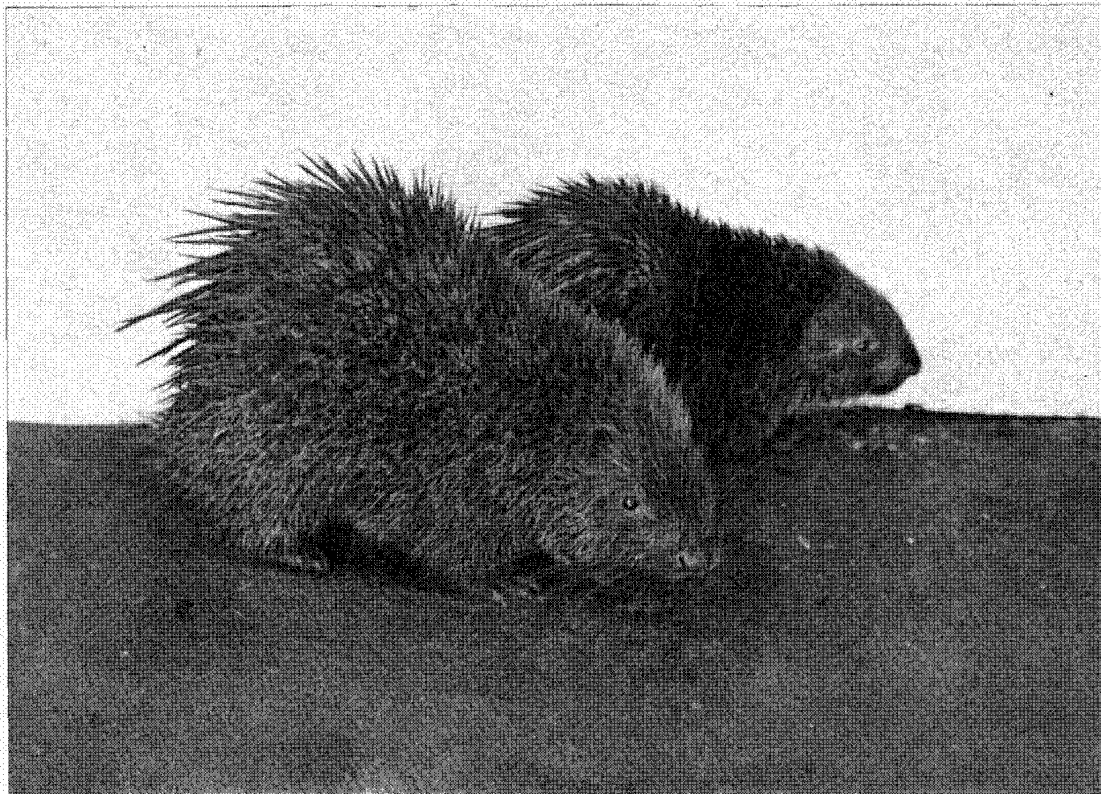


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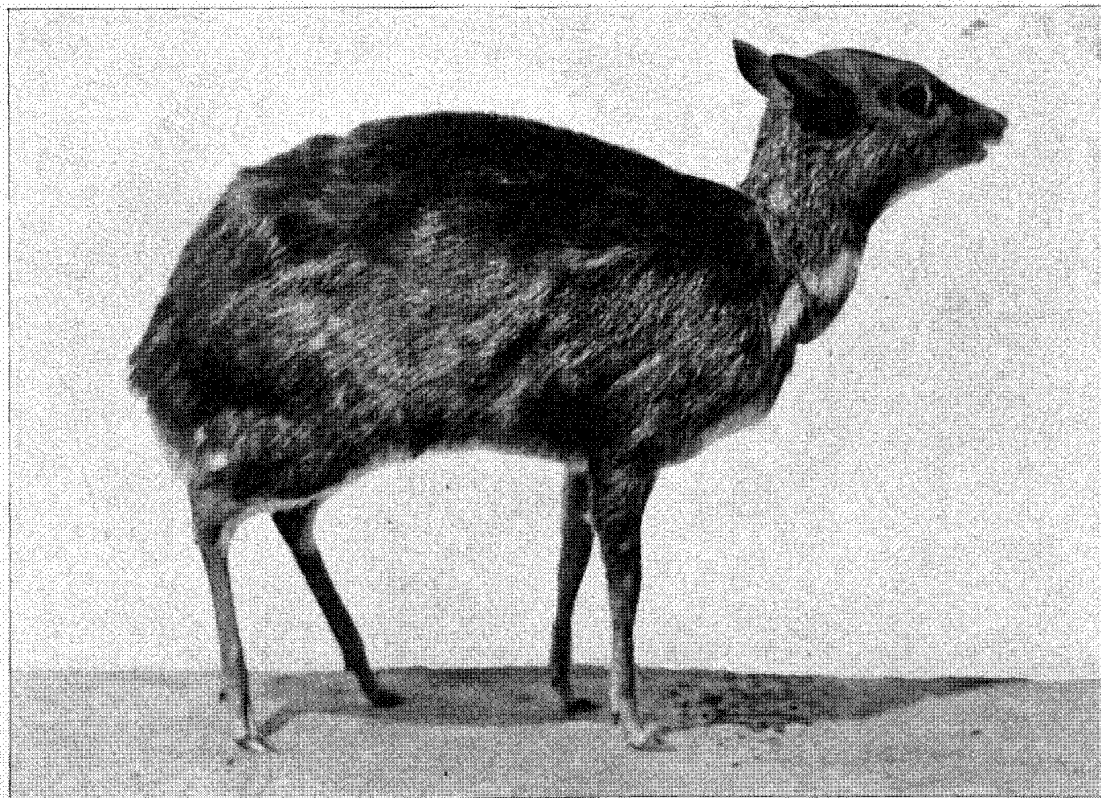


2

PLATE 34. TIMARAU, BUBALUS MINDORENSIS HEUDE.



1



2

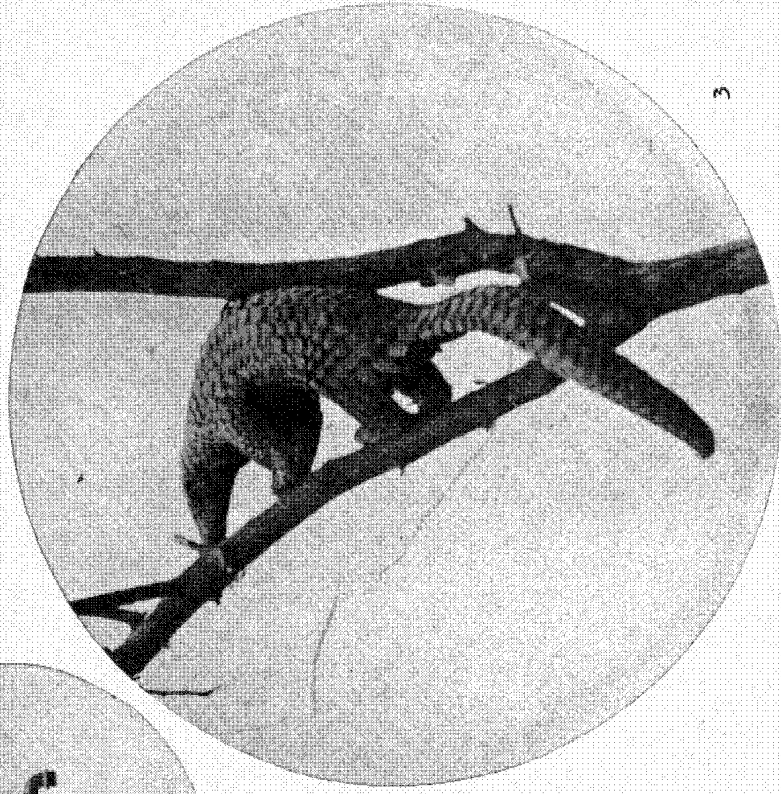
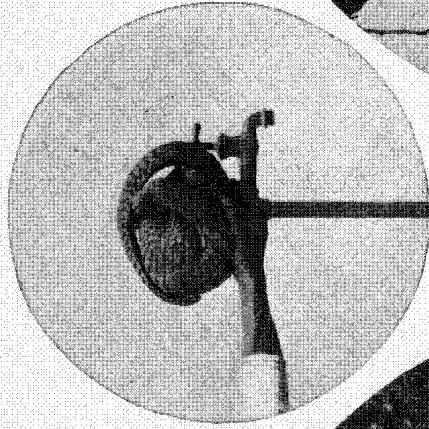
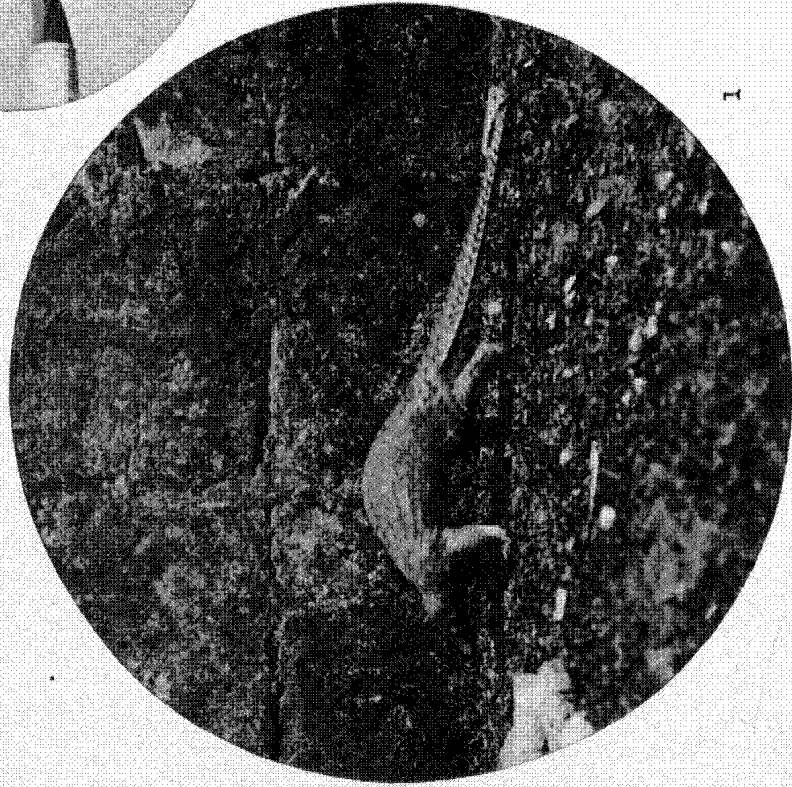


PLATE 36. PANGOLIN. *MANIS JAVANICA DESMAREST*.

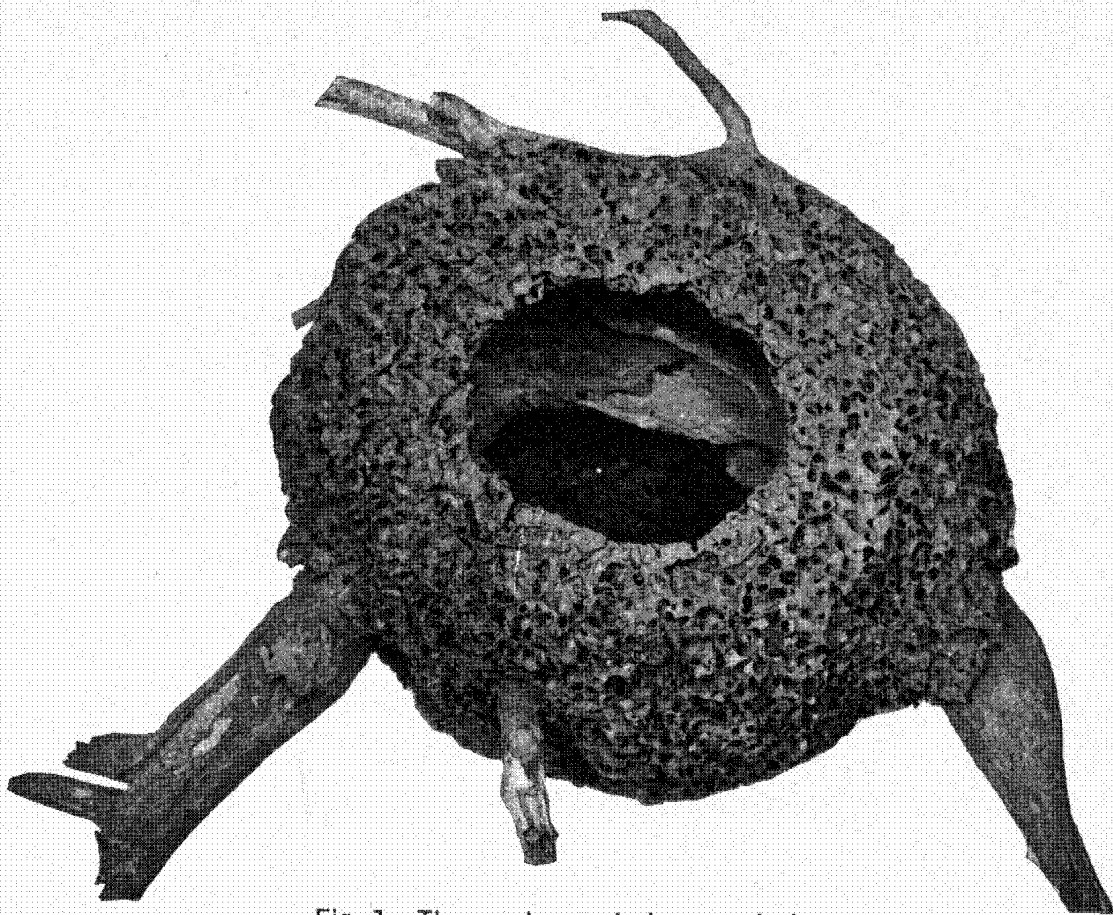


Fig. 1. The opening made by an anteater.

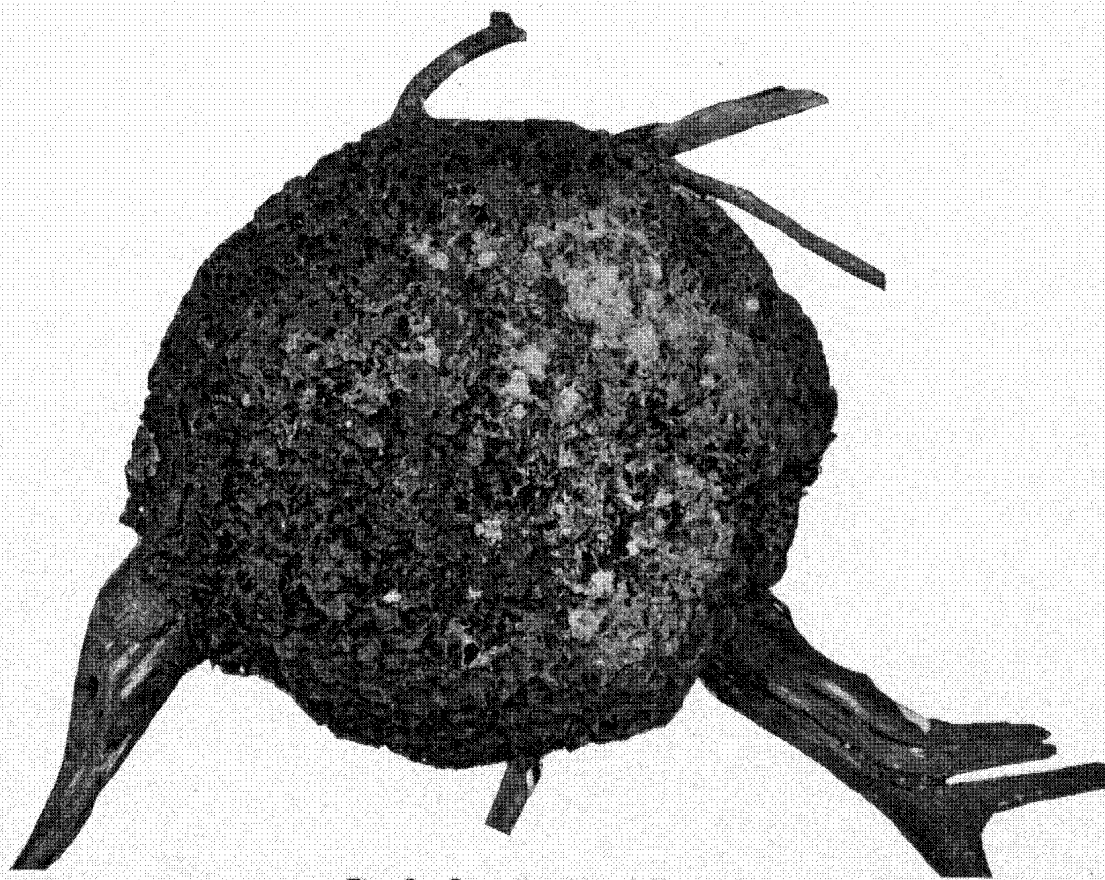


Fig. 2. Opposite side of the nest.

PLATE 37. ARBOREAL TERMITE NEST HOLLOWED OUT BY MANIS
JAVANICA DESMAREST.

CLIMATE MAP

OF THE
PHILIPPINE ISLANDS
SHOWING

SEASONS AND RAINFALL

Adapted from the Philippine Weather Bureau map
published in the Philippine Census, 1920.

Made in the Division of Mines
Bureau of Science, Manila, P.I.

SEASONS

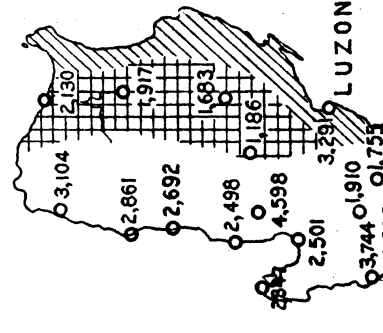
- 1st. Type—Two pronounced seasons, dry in winter and spring, wet in summer and autumn.
2d. Type—No dry season, with a very pronounced maximum rainfall in winter.
Intermediate A Type—No very pronounced maximum rain period; with a short dry season lasting only from one to three months.
Intermediate B Type—No very pronounced maximum rain period and no dry season.

RAINFALL

The numbers 01,963 indicate the stations
and the annual average in millimeters.

BATAVIA ISLANDS
3,083

BABUYAN ISLANDS



POLILLO

LUBANG

MINDORO

BUSUANGA

CULION

CUYO ISLANDS

PANAY

NEGROS

CEBU

BOHOL

CEBU

CEBU

CEBU

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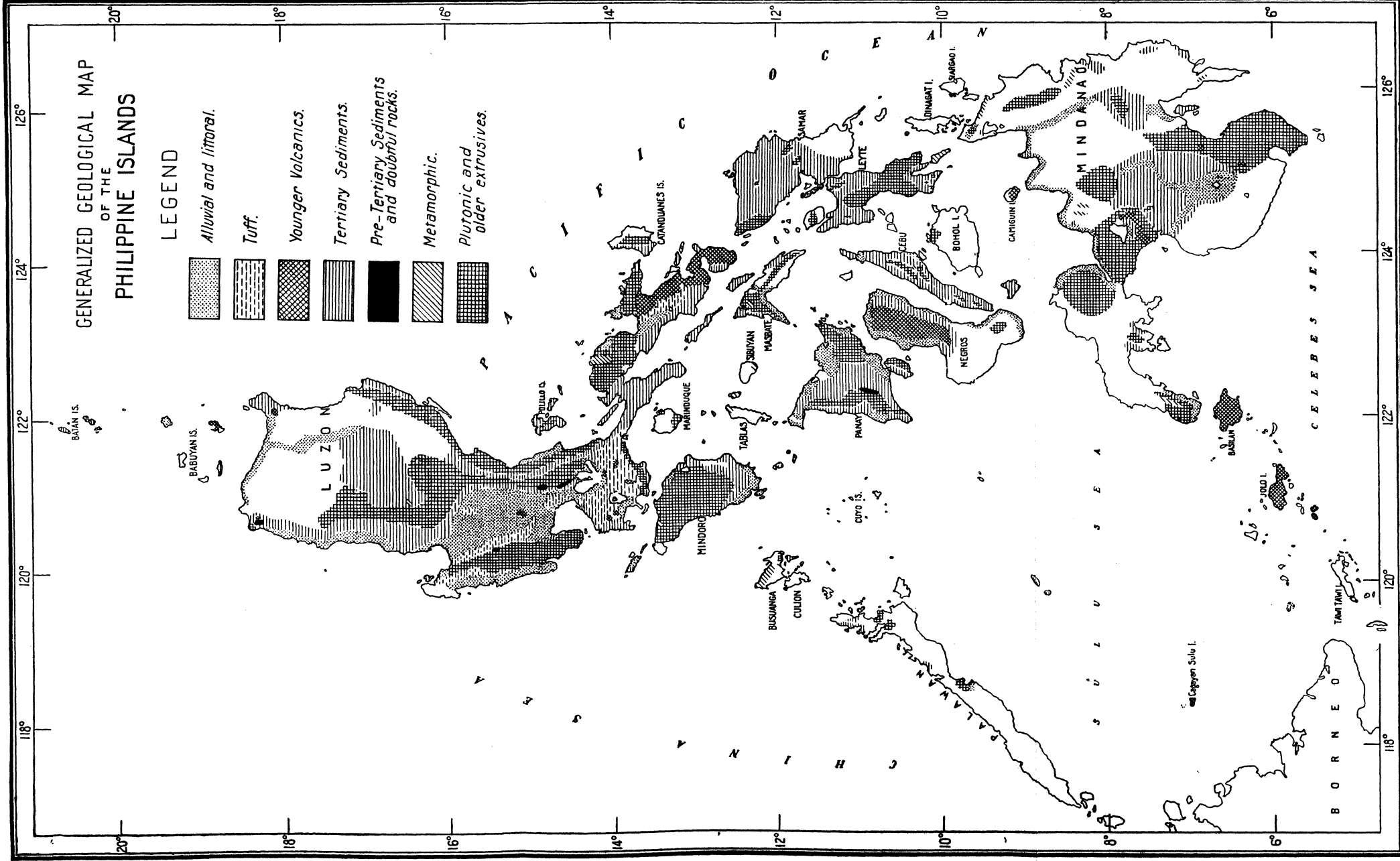


PLATE 39. THE PHILIPPINE ISLANDS, SHOWING THE GEOLOGIC FORMATIONS.

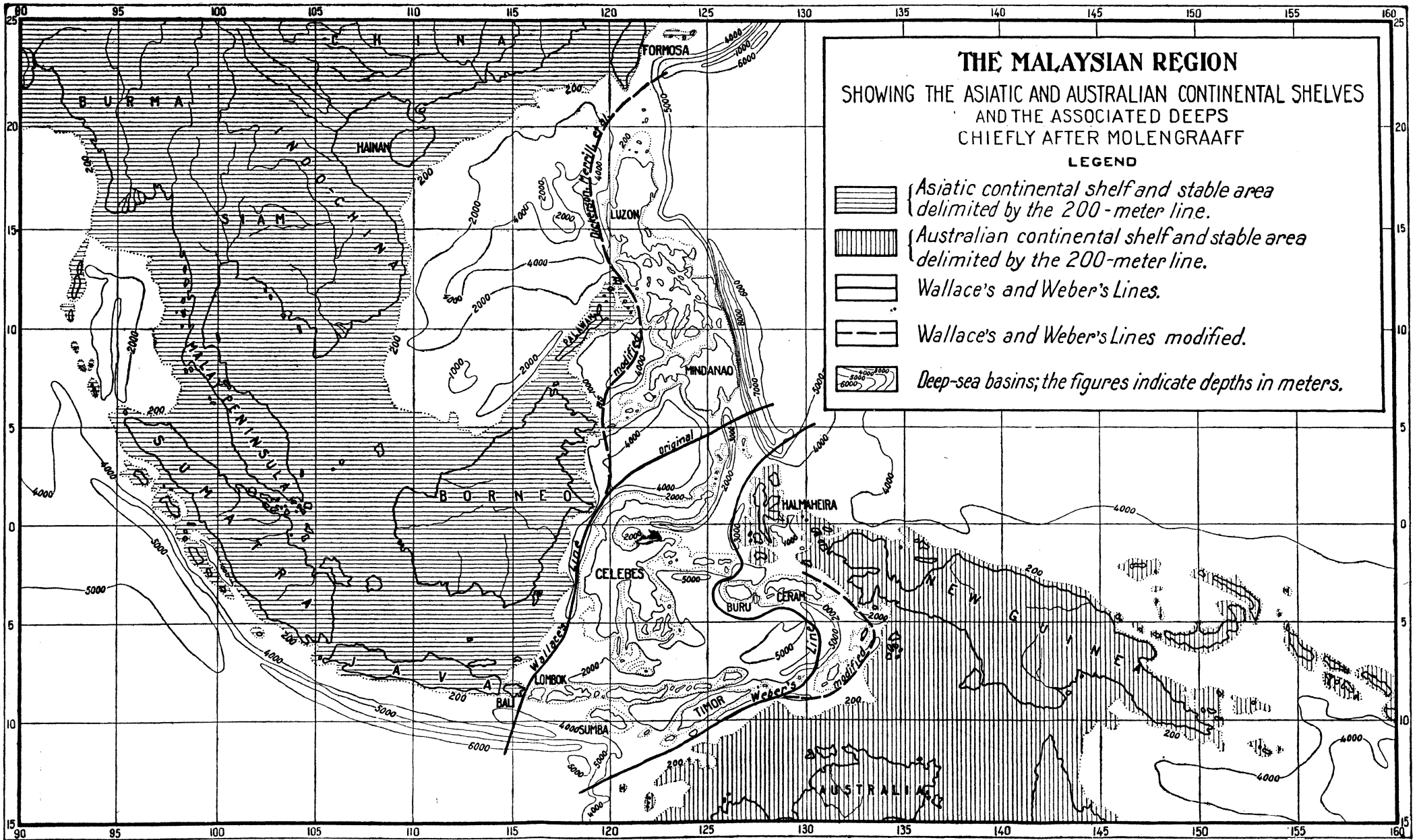


PLATE 40. THE MALAYSIAN REGION, SHOWING THE CONTINENTAL SHELVES AND ASSOCIATED DEEPS.

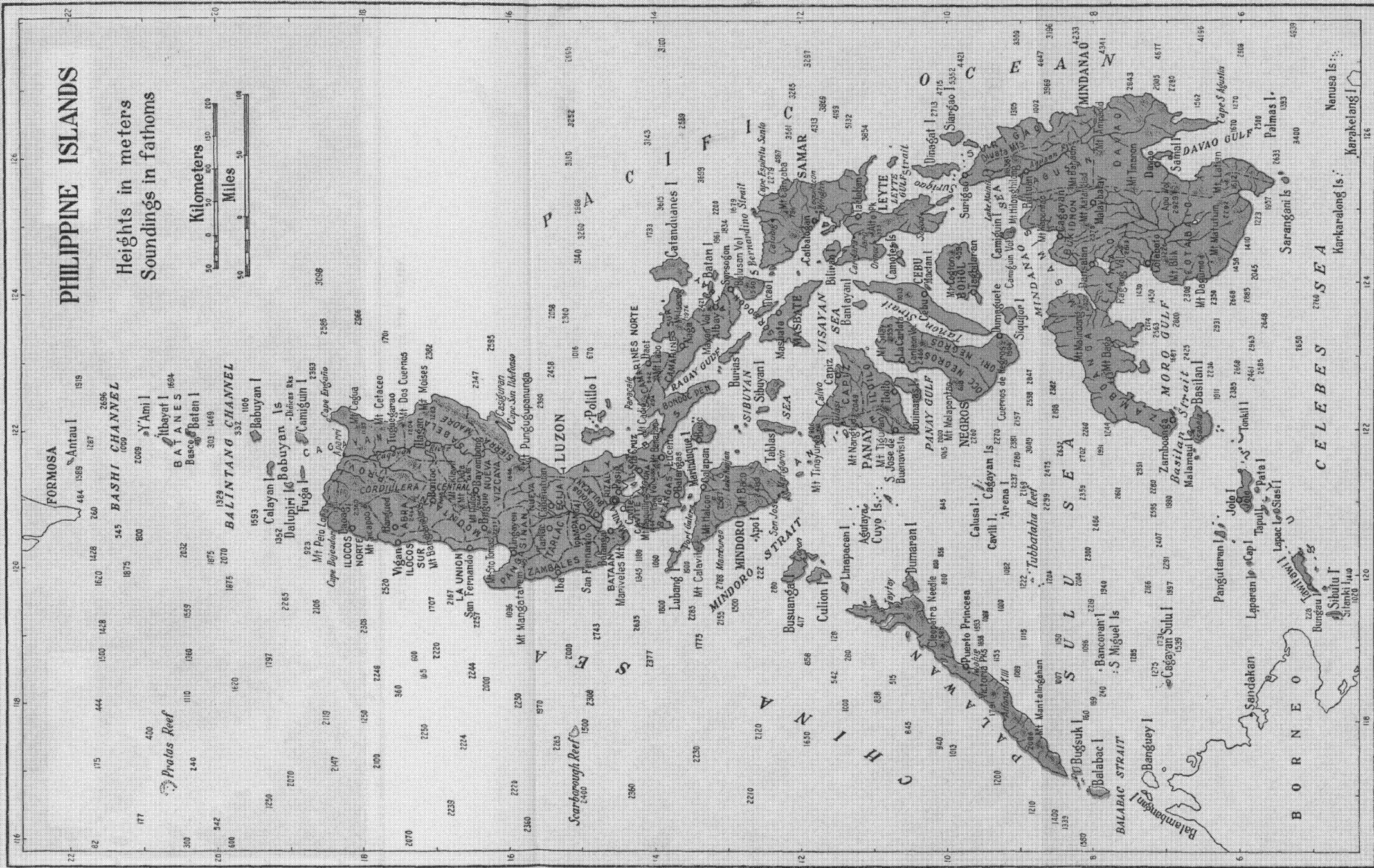


PLATE 41. THE PHILIPPINE ISLANDS.

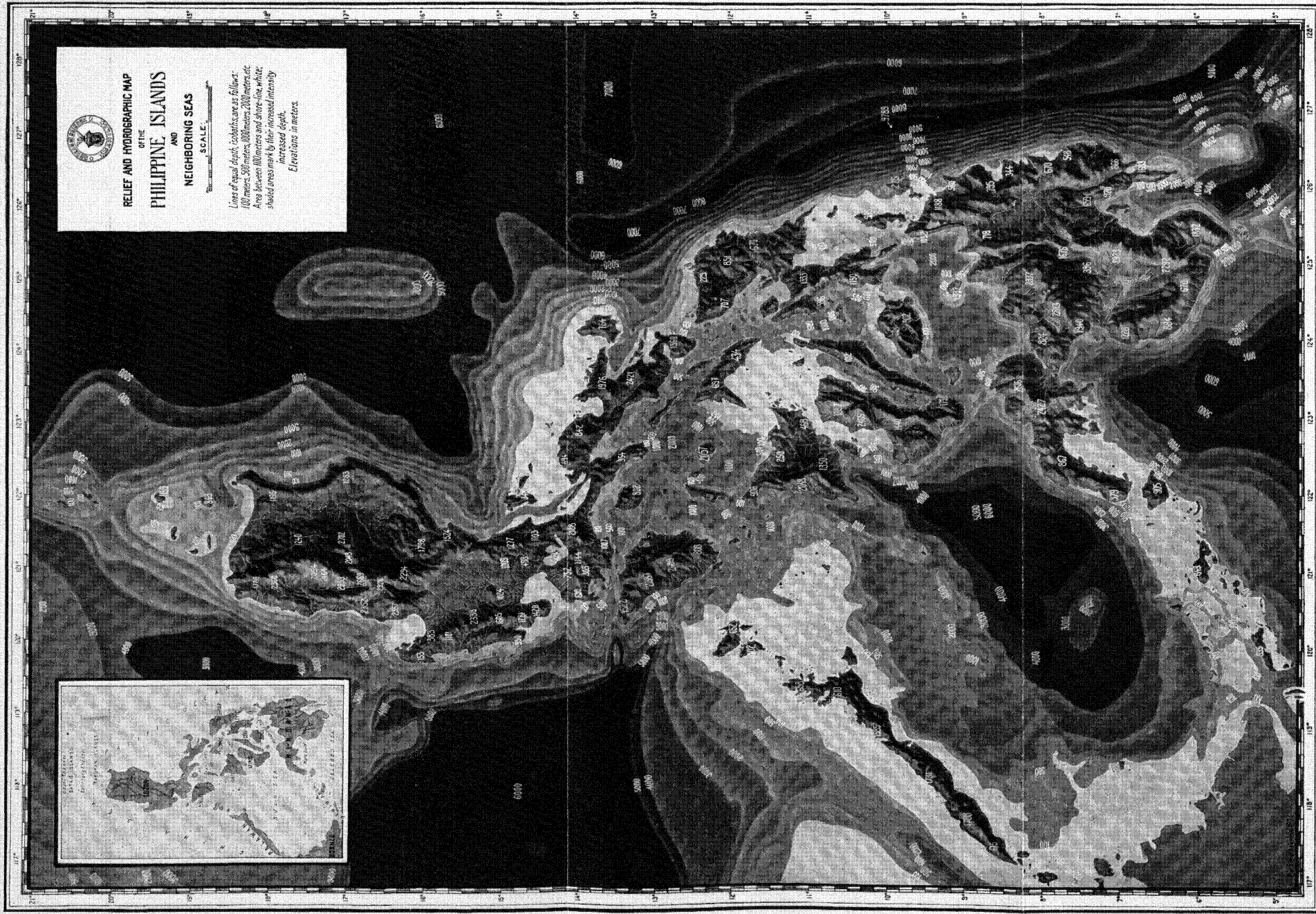


PLATE 42. THE PHILIPPINE ISLANDS, SHOWING THE RELIEF.

DISTRIBUTION OF LIFE IN THE PHILIPPINES

BY

ROY E. DICKERSON

IN COLLABORATION WITH

ELMER D. MERRILL, RICHARD C. MCGREGOR, W. SCHULTZE
EDWARD H. TAYLOR, AND ALBERT W. C. T. HERRE



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