

The Origin of the Native Flora of Polynesia¹

EDWIN BINGHAM COPELAND²

MY INVITATION to this symposium states that "It is desirable that a man should report on his own research, but no speaker should feel confined to this range. What we want is an evaluation of recent research in each field as it has come from or applies to the Pacific Basin, and then the speaker's own estimate of whither this may be leading."

My own research has been restricted to the ferns. If the Philippines be within the field of interest, this research has covered a period of 44 years. Twenty years ago, on the invitation of the Bishop Museum, I prepared and published in their bulletin series a fern flora of Fiji. A few years later, I did the same for the Society Islands. Comparing these two groups of islands, it was evident that their ferns had migrated eastward. Their common ferns are mostly common farther west, even as far away as Malaya, and their endemics are derived from these common, wide-ranging species.

The conclusion that the ferns of Polynesia were immigrants from the Malay region was at that time almost inevitable. It is old and reasonable dogma that evolution, in a large way, takes place on continents, and that islands draw thence their population. So, Asia, which used to include the Sunda Islands, seemed the natural source of the flora of the neighboring islands to the East—Celebes, and then New Guinea, and thence the Solomons, and Polynesia, and New Caledonia, and New Zealand.

This interpretation of nature was supported by a mental aberration: The flora of Java was

the first in this part of the world to be well known, and when we found in the Philippines a plant already known in Java, we simply assumed Javan origin. We used to speculate on the route of immigration, and to be surprised that this route seemed to be by Celebes oftener than by Borneo.

There were items which ought to have disturbed our confidence. For instance, a considerable number of species in the highland of Northern Luzon are common to China and even to the Himalayas. On the map, this looks like the beginning of a route from the continent to Polynesia; and men have migrated eastward from the Philippines. But not one of the plants in question reaches even to Southern Luzon.

My eyes were opened when, beginning some sixteen years ago, I made a monographic study of the family Hymenophyllaceae, the filmy ferns. Contrary to anticipation, or even suspicion, this study led me unescapably to the conclusion that this family is entirely of Antarctic origin. I abstain from presenting the detailed evidence for this conclusion, because it has already been digested and published (Copeland, 1938). It is as positive as it will be when illustrated by fossil evidence—of which the first item, from the island Chiloe, reached me in May of this year.

The Antarctic origin of Hymenophyllaceae being positively established, it struck me that it would be very strange if some or many other ferns did not have a similar history. This was already recognized for a few genera and species, which were regarded as remarkable in this respect. A comprehensive study of distribution showed me at once that these were not in reality exceptional cases, but were the con-

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² Research associate in botany, University of California, Berkeley, California. Manuscript received April 22, 1948.

spicuous examples of a general rule—that not less than half of all ferns were of Antarctic ancestry. Before I was ready to publish, this figure grew to three-quarters; and I have more recently raised it to 90 per cent. These figures apply to the ferns of the world. Except for a possible half-dozen Hawaiian species of freakishly scattered apparent geographic affinity, there is not one of the ferns of the Pacific islands which I do not now regard as of reasonably direct Antarctic origin.

Let me presume to hammer this home, because, as to the ferns, I speak with some authority. Contrary to our old ideas, the rich fern flora of Malaya was not the source of Polynesian ferns—not of one Polynesian fern. For it to have been so, the sun would have had to rise in the west. New Guinea is richer in ferns, the richest land in the world, and is the immediate source of the most of the ferns of the Philippines, Malaya, and southeastern Asia. For a brief period, clinging to a fragment of earlier prejudice, I pictured Polynesia as likewise populated from New Guinea; but this is not so likely.

Fiji is a plausible center of radiation of Polynesian ferns. I do not believe that it received its ferns directly from New Guinea, but it may have done so from somewhere along the path of northward migration—from the general region of the New Hebrides, as a suggestion. Eastward migration in these latitudes is against the prevailing wind and against the direction of storms, which explains the rapid drop in population from Fiji to Tahiti, and eastward in general.

Only Rapa among oceanic islands shows some indication of having any ferns not of ultimate New Zealand origin. If Juan Fernandez and the Galapagos are included in the subject of discussion, their ferns are of either direct Antarctic (as to some of the ferns of Juan Fernandez), or American origin—ultimately Antarctic, but by way of Graham Land and Tierra del Fuego. Almost all Hawaiian ferns are derived ultimately from New Zealand.

So much for the ferns, about which I speak from personal knowledge. It is unthinkable that what occurred with ferns should not have happened with other plants, to the extent that there was a source of supply in Antarctica, and at least as far as they depend upon the wind for dissemination.

Doctor Hooker's original postulate of an Antarctic origin of austral floras was based on his observation of the distribution of flowering plants (Hooker, 1860). Skottsberg, 30 years ago (1915: 142), published a list of plants common to New Zealand and sub-Antarctic America, and without a plausible northern source. This list includes representatives of 49 families, including Leguminosae, Compositae, Rubiaceae, sedges and grasses. As to the species on Skottsberg's list, Antarctic origin is little less than certain. Polynesian plants, even if common to New Zealand, were excluded from that list. For today's purposes, they should of course be included. If they and their immediate relatives, presumably of more recent evolution, be included, a list thus compiled will include more than half of the flowering plants of Polynesia. At this point, my conclusion is that all Polynesian ferns and more than half of Polynesian flowering plants are of ultimate Antarctic ancestry.

For the most of the remainder of the flowering plants, no other ancestry or origin can be postulated with greater plausibility. The situation as to them is simply that the evidence has not yet been discovered, or is not yet digested and understood. There are no important families of flowering plants except Myrtaceae (regarding Proteaceae as relatively unimportant) for which a nearly completely austral origin can be affirmed with the same confidence as for the ferns. I suspect all Polynesian Rubiaceae of Antarctic origin; also, excepting a few ubiquists, all Cyperaceae and Gramineae.

As is true of ferns, the "flowering floras" of Polynesia and Malaya have much in common, and the time has been when men could conclude therefore that the poorer flora of Polynesia was

derived from the comparatively rich flora of Malaya. Today, it is more generally recognized that the better explanation is that the two floras have a common origin of their common elements, and New Guinea is looked to for the common source. But again, taking a lesson from the ferns, and bearing in mind the difficulty of direct eastward migration, it seems more reasonable to look for a common outside source than to suppose that one area was colonized from the other. To the extent that this common flora is of ultimate austral origin, it would have had to back-track to the Solomons and New Hebrides before entering Polynesia, and to do this against the winds and the oceanic currents; I cannot believe that on any major scale this ever happened. So, of present land areas, I regard New Caledonia and the New Hebrides as the roughly approximate region from which Fiji and thence Polynesia received the bulk of their vegetation.

Some such history as I propose has been rejected by some very respectable authorities. Thus Diels, in the *Setchell Festschrift* (1936: 191), treating of groups of plants of distinctively austral occurrence, wrote that "it is impossible to infer that they originated in the south." This is evidently not true, because I do so infer, and so have Hooker, and Christ (1910: 248), and Skottsberg, and still others.

More disquieting to me, and not so summarily to be dismissed, is Merrill's recent (1945) statement: "It has also been suggested that scattered throughout this vast region are certain types that were apparently derived from ancient Antarctica. But this idea is purely theoretical and is one that can scarcely be proved." As I am expounding this theoretical and scarcely provable idea, I must of course concede that direct proof is impossible. But other proof can carry conviction. A frog in the milk pail is not direct proof that the milk has been diluted. None of us has seen any plant emigrate from Antarctica, and no plants are now so emigrating. In the absence of direct evidence, the indirect evidence by present dis-

tribution, coupled with the fact, unknown to Hooker and to Christ, that Antarctica was at a definite and not too remote past time a fit place for plants, is the nearest possible approach to direct proof that they did migrate thence, into and across temperate lands.

Although migration from Antarctica has long ceased (the last warm era there was Miocene, say twenty million years ago), I suppose that it goes on now along the old paths where the climate now permits. Because Merrill has provided dependable figures on the distribution of species, I will use them to show how this migration seems to have occurred more recently in two families, *Elaeocarpaceae* and *Orchidaceae*.

The pertinent figures on the occurrence of species of *Elaeocarpus* are:

New Guinea	114
Philippines	49
Borneo	40
Java	18
New Caledonia	30
Fiji	12
Samoa	6
Rarotonga	1
Hawaii	1

Merrill concludes, in harmony with general practice, that New Guinea is the focus of distribution. As to all lands farther west, I read his evidence in the same way. As to the rapid decrease in number of species from group to group in Polynesia, his figures agree with the evidence of the ferns in showing the great difficulty of eastward migration in this region. But his figure of 30 species in New Caledonia is very significant to me. New Caledonia has one-fortieth of the area of New Guinea, but has more than one-fourth as many species of *Elaeocarpus*. The winds and the currents are always from New Caledonia to New Guinea, and I find it hard to doubt that this is the direction of migration. The genus is of minor importance in Polynesia, but what species there are seem most probably to have come from the west or southwest, not from the northwest, not from New Guinea.

As to the orchids, now regarded as the largest family of plants, Merrill presents these figures on the number of species:

New Guinea	2,000
Philippines	900
Fiji	125
Tahiti	30
Marquesas	4
Hawaii	3

New Zealand has 66 species, and an old figure (Hooker's) for Tasmania is 74—large enough to point strongly to Antarctic origin.

The overwhelming mass of tropical orchids are epiphytes. I have compiled no figures, but am advised that in the Philippines, and in all that part of the world, the ratio of epiphytes to terrestrial species is more nearly ten to one than five to one. In New Zealand, there are 7 epiphytes and 59 terrestrial species; in Tasmania, 1 epiphyte and 73 terrestrial species. The paucity of epiphytes in the far south may be explained by the climate. But Polynesia is tropical. Its ratio of epiphytic to terrestrial orchids is about three to one—not more than half of what should be expected if colonization had been from New Guinea. The obvious conclusion seems to be that it was colonized from farther south, and that adaptation to tropical conditions remains incomplete.

Conclusion: The ferns, and a considerable part of the flowering plants, of Polynesia are of austral origin. As to the bulk of the flowering plants, I cannot claim, against Merrill's recently published judgment, that the present tendency of thought is in support of my views, but have shown that some of his detailed figures do support them.

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