

# THE ORIGIN OF THE HAWAIIAN FLORA

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The Hawaiian Islands afford perhaps the most important problem in plant distribution that exists anywhere. The most isolated land area of equal size on the globe, the origin of their extremely peculiar and interesting flora opens a wide field for research and speculation.

There is much difference of opinion as to whether or not the Islands have had at any time connection with any of the great continental areas. Hillebrand,\* whose flora of Hawaii is well known, and has been followed in the tables given in this paper, believed that the Islands had always been isolated, having been thrown up from great ocean depths through volcanic action. This view has been recently advocated by Muir† as the result of his studies on the insect fauna of the islands. On the other hand, Wallace,‡ on the basis of the occurrence of certain north temperate genera in the high mountains of Hawaii, believed that there had been a land connection with west North America. Recently, Pilsbry§ has brought forward evidence which he thinks proves conclusively some ancient connection of the Islands with the Malaysian region. The peculiar land-snails, so largely developed in the Islands, are, according to Pilsbry, ancient forms, whose survival outside of the Pacific Islands is known only in the Malaysian region.

The writer, up to the present time, has taken it for granted (largely on Hillebrand's evidence) that the Islands always had been completely isolated; but the evidence offered by Pilsbry for an ancient land connection seems very strong, and, moreover, is

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\* Hillebrand, W. *Flora of the Hawaiian Islands*. 1888.

† Muir, F. *Proc. Haw. Ent. Soc.* 3: 198-200. 1916.

‡ Wallace, A. R. *The geographical distribution of animals*, 1: 447. 1876.

§ Pilsbry, H. A. *Mid-Pacific land-snail faunas*. *Proc. Nat. Acad. Sci.* 2: 429-433. 1916.

quite in line with certain facts of plant distribution which appear to have been overlooked.

The occurrence in the Islands of many hygrophilous liverworts and the filmy ferns (Hymenophyllaceae) seems to make it practically certain that, as in the case of the snails cited by Pilsbry, the presence of these in the Islands can be explained only by considering them as remnants of the flora of a formerly much more extensive area connecting the Islands with some ancient continent. These plants are peculiarly unfitted for transportation over long distances and it is difficult to see how they could possibly have survived the exposure to heat and dryness to which they must have been subjected, assuming that they have come directly from either the American tropics or the remote tropical regions to the south. These plants inhabit, for the most part, the cool dark rain-forests and are quickly destroyed by exposure to the heat and sunshine of the lower levels.

During the past summer the writer made a brief visit to the Islands, with a special view to examining the hepatic flora; and although the collections made were not as comprehensive as it was hoped to make them, owing to the remoteness of the collecting grounds, the results tend to confirm Pilsbry's view of a connection with the Malaysian and Australasian region.

The most conspicuous of the liverworts in the lower forests are two species of *Dumortiera*, a genus peculiarly adapted to wet dark conditions. According to Stephani's\* list of the liverworts of Hawaii, these species are *D. trichocephala* (Hook.) N. ab E., a species widely distributed through the eastern tropics, and *D. hirsuta* (Sw.) R. Bl. & N., an even more widely spread species. It is probable, however, that a critical examination of the Hawaiian plants will show that they are not identical with those species. The so-called *D. trichocephala* is certainly quite different from material of the same species collected in the Malayan region, and the form attributed to *D. hirsuta* resembles very closely the Javanese *D. velutina* Schiffn. Stephani states also that the monotypic genus *Wiesnerella*, which is closely related to *Dumortiera*, occurs in Hawaii, and immature material collected by the writer perhaps belongs here. This species occurs also in Java, the Himalayas, and Japan.

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\* Stephani, F. Hepaticae Sandvicenses. Bull. Herb. Boiss. 5: 840-849. 1897.

The writer found repeatedly a species of *Megaceros* closely resembling the species first described by him from Java\* but afterwards found abundantly throughout the Malayan region. This genus, like *Dumortiera*, is characteristic of very wet, shady localities, and its thin-walled, green spores are certainly not fitted to being dried up and transported over long distances by the wind. The same may be said of the related genus, *Dendroceros*, which inhabits the dripping rain-forest of the higher altitudes. The latter was found by the writer only at an elevation of about 4000 feet, in regions of almost constant rain.

Other characteristic thallose liverworts of the upper rain-forests were species of *Pallavicinia*, *Symphyogyna*, and *Aneura* (*Riccardia*). One of the last-named genus appears to be very close to *A. maxima* Schiffn. of Java.

It may be safely asserted that there is a marked resemblance between the liverwort floras of Hawaii and the Malaysian region, but further material is necessary before the exact degree of relationship can be established.

The Islands at present consist almost solely of volcanic masses, and it is very evident that the volcanic activity has proceeded from the northwest to the southeast.

The oldest formations in the north island, Kauai, and part of Oahu, show much weathering and disintegration, while in the newest and largest island, Hawaii, volcanic activity is still in progress.

Hillebrand made a careful study of the distribution of the vascular plants of the Islands and found that there is a marked increase in the number of species, especially endemic species, in the older islands, this being specially marked in Kauai, where presumably the evolutionary forces have been at work for the longest time.

The preponderance of the Australasian-Malaysian elements in the Hawaiian flora, indicated by a study of the liverworts, is amply confirmed by a comparison with the vascular plants. This will be sufficiently evident from an examination of the tables appended, based upon Hillebrand's Flora of the Hawaiian Islands.

It is evident at a glance that the Australasian, Polynesian, and

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\* Campbell, D. H. Ann. Bot. 21: 469. 1907.

Malaysian genera are much more numerous than the American. There are forty-five genera of Phanerogams belonging to the former regions which are entirely absent from the New World; while only eight genera are exclusively Hawaiian-American. One genus, *Gynandropsis* (Capparidaceae) belongs to South America and South Africa, while three endemic Hawaiian genera of Compositæ—viz., *Argyroxiphium*, *Wilkesia*, and *Raillardia* are closely related to certain Californian types.

The Pteridophytes emphasize even more strongly the intimate relation between the floras of the Australasian and Malaysian regions and Hawaii. No less than thirty-eight species, absent from America, are common to the two areas, while only two species are confined to Hawaii and the American continent.

While it is not unlikely that certain species of Phanerogams common to Hawaii and the southern Polynesian region may have been introduced in recent times, in most cases the Hawaiian species are distinct and peculiar to the Islands. The cocoanut, taro (*Colocasia*), sugar-cane, bread-fruit, and some other cultivated plants were undoubtedly introduced by man, and it is not unlikely that such useful trees as the kukui (*Aleurites moluccana*) and the mountain apple (*Eugenia malaccensis*) were also introduced, although now they form almost the entire forest of the lower elevations.

The American-Hawaiian genera are mostly found in the Andean region and as there is considerable evidence of a former connection of South America with the Australasian region, it is possible that some of these forms may have reached Hawaii from the south and have survived in the two extremes of their range, disappearing in the intermediate regions.

While it is extremely probable that some species reached the Islands since their complete isolation, either by means of ocean currents, wind, or the agency of migratory birds, this, as conditions are at present, could have taken place only under very exceptional circumstances. It is difficult to see how any of these agencies would account for the introduction of many plants of the cool rain-forest, which could hardly survive any such means of transportation.

As to the line of connection between Hawaii and some former

continental or sub-continental area, we can only conjecture. An examination of the water areas existing at present (see map 2, Century Atlas) shows that between the Islands and North America there is an enormous and perfectly continuous area of very deep water which extends to the north and to the south of the Islands, but leaves an opening on the west which is continuous with a large area of less depth comprising pretty much the whole of Polynesia. To the southwest are two very large shallow areas including respectively the Marshall and Caroline Islands, presumably the remains of large sunken land masses. A chain of similar but smaller shallows extends to the Malay Archipelago, and it is possible, at least, that this indicates approximately the line of connection between Hawaii and some ancient great southern continent—in short, that Polynesia comprises merely the remnants of a larger continent, or group of continental islands like Australia.

As to the period at which Hawaii became completely isolated, this of course can only be guessed. It could hardly have been earlier than the later Cretaceous or early Tertiary since few of the modern Angiosperms existed prior to the upper Cretaceous, so far as we know.

Hillebrand, reasoning from the absence of Conifers, thinks that the Islands must have been formed "subsequent to the age in which these were universally distributed." It is quite conceivable that Conifers may have existed formerly and become extinct as the result of the extensive volcanic activities subsequent to the isolation of the Islands. As the soils of the Islands at present are practically exclusively volcanic and are said to be strongly acid, this might well account for the absence of many plants which may have been found at an earlier period, but which require different soil conditions from those now existing.

The subsidence of the assumed ancient Pacific continent perhaps coincided with the great uplift during the late Cretaceous when most of the existing mountain systems of western America came into existence.

AUSTRALASIAN-MALAYSIAN GENERA OCCURRING IN HAWAII, BUT NOT IN AMERICA

<i>Pittosporum</i> Banks.....	Pittosporaceae
<i>Eurya</i> Thunb.....	Ternstroemiaceae
<i>Elaeocarpus</i> L.....	Tiliaceae
<i>Byronia</i> Endl.....	Illicaceae

<i>Alphitonia</i> Reissek	.....	Rhamnaceae
<i>Strongylodon</i> Vogel	}	.....
<i>Mezoneuron</i> Desf.		
<i>Metrosideros</i> Banks	.....	Myrtaceae
<i>Tetraplasandra</i> A. Gray	}	.....
<i>Reynoldsia</i> A. Gray		
<i>Gardenia</i> L.	}	.....
<i>Plectronia</i> L.		
<i>Coprosma</i> Forst.		
<i>Scaevola</i> L.	.....	Goodeniaceae
<i>Cyathodes</i> R. Br.	.....	Epacridaceae
<i>Embelia</i> Burm.	.....	Myrsinaceae
<i>Ochrosia</i> Juss.	}	.....
<i>Alyxia</i> R. Br.		
<i>Cyrtandra</i> Forst.	.....	Gesneriaceae
<i>Myoporum</i> Banks & Sol.	.....	Myoporaceae
<i>Plectranthus</i> L' Hérit.	}	.....
<i>Phyllostegia</i> Bent,		
<i>Achyranthes</i> L.	.....	Amarantaceae
<i>Wikstroemia</i> Endl.	.....	Thymeliaceae
<i>Santalum</i> L.	}	.....
<i>Exocarpus</i> Labill.		
<i>Viscum</i> L.	.....	Loranthaceae
<i>Claoxylon</i> A. Juss.	}	.....
<i>Aleurites</i> Forst.		
<i>Antidesma</i> L.		
<i>Pseudomorus</i> Bureau	}	.....
<i>Pipturus</i> Wedd.		
<i>Cypholophus</i> Wedd.		
<i>Anoectochilus</i> Blume	.....	Orchidaceae
<i>Cordyline</i> Commers.	}	.....
<i>Dracaena</i> Vand.		
<i>Astelia</i> Banks & Sol.		
<i>Dianella</i> Lam.		
<i>Joinvillea</i> Gaud.	.....	Flagellariaceae
<i>Pritchardia</i> Seem. & Wendl.	.....	Palmaceae
<i>Pandanus</i> L.	}	.....
<i>Freycinetia</i> Gaud.		
<i>Baumea</i> Gaud.	}	.....
<i>Gahnia</i> Forst.		
<i>Garnotia</i> Brogn.	.....	Graminaceae

HAWAIIAN-AMERICAN GENERA, NOT FOUND IN THE AUSTRALASIAN REGION

Genus	Family	
<i>Perrottetia</i> H.B.K.	.....	Celastraceae
<i>Vallesia</i> Ruiz & Pav.	.....	Apocynaceae
<i>Nama</i> L.	.....	Hydrophyllaceae
<i>Jacquemontia</i> Chois.	.....	Convolvulaceae
<i>Sphacele</i> Benth.	.....	Labiatae
<i>Hesperocnide</i> Torr. & Gray	.....	Urticaceae
<i>Sisyrynchium</i> L.	.....	Iridaceae

PTERIDOPHYTES\* COMMON TO HAWAII AND THE AUSTRALASIAN-MALAYSIAN REGION,  
BUT ABSENT FROM AMERICA

<i>Ophioglossum pendulum</i> L.	<i>Asplenium Nidus</i> L.
<i>Marattia Douglasii</i> Baker	<i>Asplenium normale</i> Don
<i>Schizaea australis</i> Gaud.	<i>Asplenium varians</i> Hook. & Grev.
<i>Gleichenia longissima</i> Blume	<i>Asplenium contiguum</i> Kaulf.
<i>Acrostichum gorgoneum</i> Kaulf.	<i>A. caudatum</i> Forst.
<i>Gymnogramme javanica</i> Blume	<i>A. horridum</i> Kaulf.
<i>Vittaria elongata</i> Sw.	<i>A. spathulinum</i> Hook.
<i>Polypodium Hookeri</i> Brack.	<i>A. Adiantum-nigrum</i> L.
<i>P. samoense</i> Baker	<i>A. polyphyllum</i> Presl
<i>P. tamariscinum</i> Kaulf.	<i>Odontoloma repens</i> Desv.
<i>P. lineare</i> Thunb.	<i>Microlepia strigosa</i> Presl
<i>P. Spectrum</i> Kaulf.	<i>M. tenuifolia</i> Metten.
<i>Phegopteris punctata</i> Hillebr.	<i>Pteris excelsa</i> Gaud.
<i>Aspidium aristatum</i> Sw.	<i>Trichomanes parvulum</i> Poir.
<i>A. caryotideum</i> Wall.	<i>T. meifolium</i> Bory
<i>A. truncatum</i> Gaud.	<i>Lycopodium serratum</i> Thunb.
<i>A. terminans</i> Wall.	<i>L. Phlegmaria</i> L.
<i>A. squamigerum</i> Mann	<i>L. volubile</i> Forst.
<i>Doodya media</i> R. Br.	

PTERIDOPHYTES COMMON TO HAWAII AND AMERICA, BUT NOT FOUND  
ELSEWHERE

<i>Asplenium fragile</i> Presl	<i>Pellaea ternifolia</i> Fée
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\* Nomenclature according to Hillebrand, Flora of the Hawaiian Islands.