

Hepaticae from Palau, Caroline Islands, I.¹

Phytogeography

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The Palau Islands are strategically located between New Guinea and the Marianas and due east of Mindanao, about long. 134°E. lat. 7°N. Because of their location, they could have served as a steppingstone in the migration of a diverse flora into Micronesia and the Pacific islands. The following study was undertaken to determine probable origins and affinities of the liverworts. The study was possible because of extensive collections available from the Miami University *Collegiate Rebel* Expedition in 1960 and the Miami University NSF Expedition to Micronesia in 1965.

Spread over ca. 600 square km, the Palaus have the largest island and greatest area of volcanic rock in the Carolines. Other volcanic islands in the archipelago are Kusaie, Ponape, Truk, and Yap. Only Yap and Palau are west of the sial line, theoretical eastern limit of an ancient Australasian continent. Palauan volcanic formations are mostly andesite, bauxite, andesite agglomerate with tuffaceous rock, some manganese, zinc, and gold. The volcanic rocks are a result of the late mesozoic-early cenozoic vulcanism, probably Eocene. The Palaus are topographically the most diverse of the Carolines with both volcanic and limestone islands. The volcanic islands are Babelthuap, Koror, Ngerkabesang, and Malakal. The southern and southeastern tip of Babelthuap, eastern Koror, all of Ngurukdabel and the southern islands are raised limestone. A barrier reef with several islets surrounds much of Palau. It is quite distinct on the western side, becoming a fringing reef along northeastern Babelthuap. The limestone islands date to Pliocene or Pleistocene. The atolls, low islands and reefs are Recent being formed about 3000 years ago.

Palau is tropical with an average temperature of 27–28°C and extremes of 22–33°C. The atmospheric pressure is a nearly constant 755–764 mm. The relative humidity averages 77–84%. Small cumulus clouds are dominant in 75–80% average cloud cover, and the average annual rainfall is 348.4 cm. Seasonal distribu-

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tion of rainfall is related to the wind patterns with the doldrums belt passing northward May to July bringing heavy storms and rain (35.5 cm/mo.). August to November is characterized by short storms alternating with clear weather as the doldrums sweep southward. Humidity is reduced from December to May (rainfall 19.4 cm/mo.) as the northeast trade winds dominate. Occasionally typhoons occur.

The varied substrates available support the richest and most diverse vascular flora in Micronesia with the vegetation being profoundly influenced by edaphic factors. Mangrove swamps occur in brackish water on outwash plains along the low shores of volcanic islands. *Sonneratia* is often on the outer edge with *Rhizophora* just inland. *Bruguiera* and *Xylocarpus*, which occur on well consolidated soil, are frequently invaded by *Clerodendrum*, *Derris*, *Acrostichum*, *Davallia*, *Nephrolepis* and some epiphytic ferns. The bryoflora of mangrove swamps is little known, but the Cheatham collection includes *Acromastigum obliquatum* and *Ptychocolea cumingianus* found on the bark of trees.

Behind the mangrove is a raised fringing reef forming a narrow coastal plain which originally supported a primary rain forest. The persisting fragments of this forest are dominated by large trees of *Camposperma*, *Ficus*, *Randia*, and *Fagraea*. Palms, including *Exorrhiza* and *Ponapea*, and *Pandanus* are present. Lianas, ferns, orchids, and other epiphytes are abundant. Bryophytes are well represented in the coastal plain forest with species of *Fissidens* and *Jungermannia ariadne* found on soil and *Pallavicinia lyellii* on wet rocks. Epiphylls include *Colura acutifolia* and *Leptolejeunea subacuta*. Species of *Cheilolejeunea*, *Lejeunea*, *Microlejeunea* and *Macromitrium* are corticolous. Rotting logs serve as substrate for *Neolepidozia wallichiana*, *Acromastigum obliquatum*, *Riccardia* spp., *Trichosteleum*, and other Sematophyllaceae. Such volcanic sites are the only locations reported in the Carolines for *Neolepidozia wallichiana*, *Acromastigum obliquatum*, *Colura acutifolia* and *Pallavicinia lyellii*. The "mossy" cloud forest as found on Ponape and Kusaie is not represented in Palau because of its low maximum elevation.

Grassland in Palau is found only on volcanic islands, but it is not a natural savanna as it can be maintained only by yearly burning. *Miscanthus*, *Casuarina*, *Lycopodium*, and *Pandanus* are characteristic grassland invaders. Bryophytes are rare in this disturbed area except in old battle trenches or small wooded patches.

Most villages are on open beach with access to the reef and sea. The strand bryoflora in the vicinity of villages parallels that of the wetter atolls of the Carolines with *Calymperes*, *Leucophanes*, *Archilejeunea mariana*, and *Lopholejeunea subfusca* common on coconut trunks. Coconut rootlets support *Cololejeunea kapingaensis* and *Lejeunea* spp., while rotting coconut husks serve as substrate for *Cololejeunea wightii*, scattered *Leucophanes* and *Riccardia* spp. Sandy soil along paths is the site of *Bryum* and *Brachymenium* with moister soil supporting *Ectropothecium*. Rocks wet with fresh water as those surrounding wells are frequently covered with *Hyophila*. *Symbiezidium* grows on the bases of trees at the edge of the beach where it may be occasionally sprayed with sea water. Flow regions on the stems of trees support Lejeuneaceae.

Raised, undercut coral islands with nearly vertical walls support a much richer flora than the beach. Conspicuous on the steep slopes are *Gulubiopsis* palms, *Dracaena* and *Pithecellobium* with vines as *Mucuna* and *Nepenthes* hanging off the edge of the island. Undergrowth on these islands is sparse being composed of scattered shrubs and small tree ferns. Rough coral rocks on the limestone islands are often covered by mats of *Thuidium* and *Pelekium*. Epiphytic bryophytes and those which grow on decaying vegetation are similar to those of the strand near villages. Masses of *Frullania nodulosa*, *F. gracilis* and *Radula javanica* were collected from branches overhanging a small, nearly enclosed lagoon on Ngurukdabel.

Prior to this study, thirty-eight species of hepatics in twenty-two genera were reported from Palau. Some revisions of the names applied have been made in Part II. Of the thirty genera dealt with in this study, ten are new to Palau including two new to Micronesia. These genera are represented by approximately sixty species of which twenty-two are new to Palau and eight new to Micronesia.

SYNOPSIS OF PHYTOGEOGRAPHIC ELEMENTS

The hepatic flora of Palau contains species with different geographic ranges. Isoflors embracing the total range of individual species indicate that several phytogeographic elements based on floristic affinities occur in Palau. An isoflor for a single species may not include the total area of a phytogeographic element, but its limits are within the element. As phytogeographic elements can indicate possible migration paths, the recognizable elements and the species associated with them are summarized.

Pantropical Element: Species which are known from all major tropical regions where suitable conditions exist belong in this group. On Palau, only *Frullania nodulosa* and *Calypogeia arguta* are pantropical.

Indo-Pacific Element: Species extending into the Pacific and Indian oceans from tropical Asia and Indonesia comprise this element. Thirty of the sixty Palauan hepatics fall within this distributional pattern. For thirteen, the range does not extend eastward beyond Micronesia: eight of these species extend northward to temperate Japan, the Ryukyus and Taiwan; and five species neither extend east of Micronesia nor northward out of the tropics.

Temperate species: *Pallavicinia lyellii*, *Cheilolejeunea imbricata*, *Jungermannia ariadne*, *Neolepidozia wallichiana*, *Lopholejeunea applanta*, *Chiloscyphus argutus*, *Frullania gracilis*, *Lejeunea wightii*.

Tropical species: *Radula anceps*, *Acromastigum echinatum*, *Mastigophora diclados*, *Colura acutifolia*, *Drepanolejeunea vesiculosa*.

Of the seventeen species which are known from islands east of Micronesia, four species, *Archilejeunea mariana*, *Radula javanica*, *Chiloscyphus communis*, and *Lopholejeunea subfusca*, extend northward to temperate Japan and southward to Australia and New Caledonia. An example of this pattern can be seen from the distribution of *Archilejeunea mariana* (Fig. 1). A fifth species, *Plagiochila frondes-*

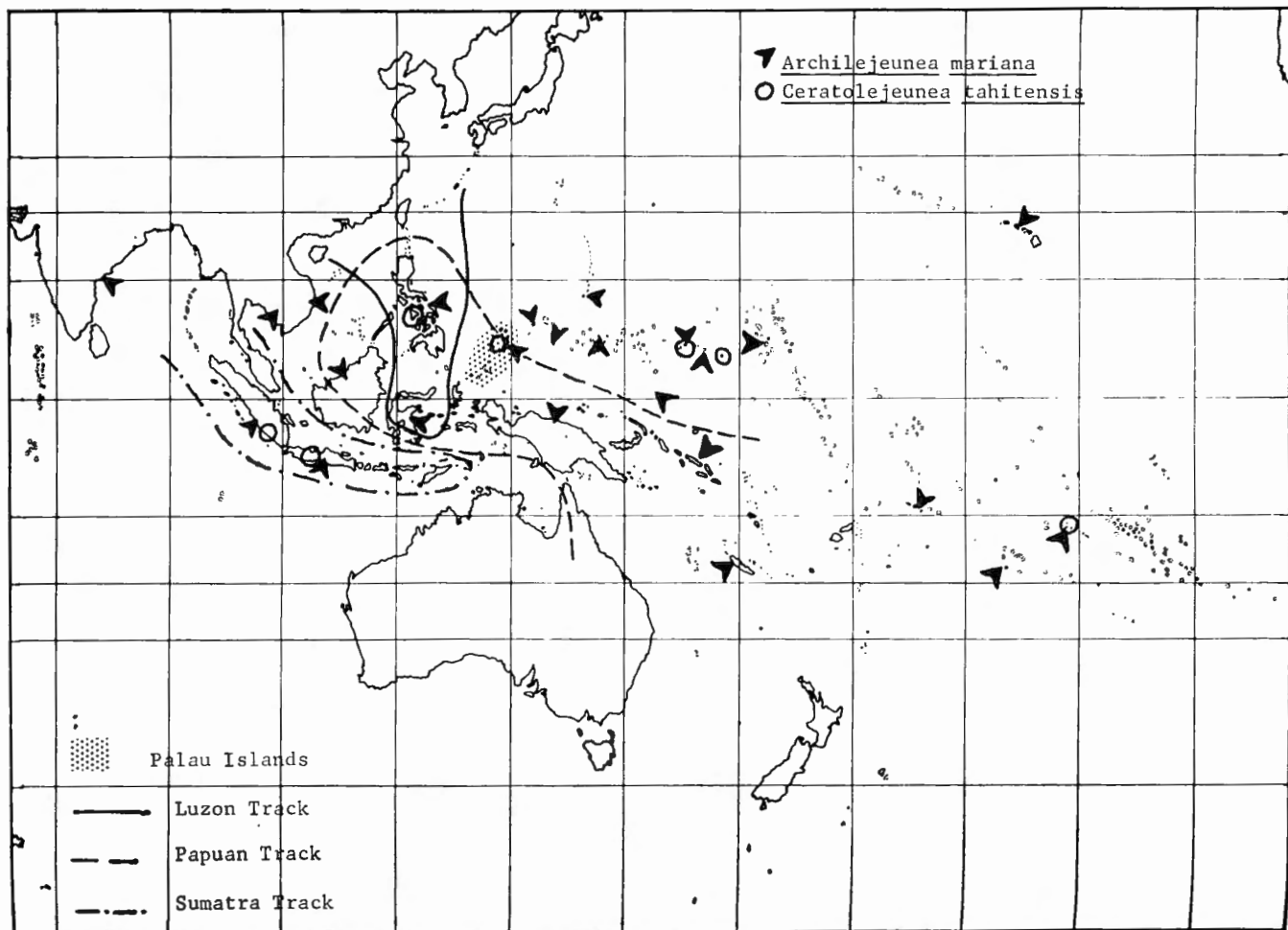


Fig. 1. Map of the Indo-Pacific region showing the distribution of *Archilejeunea mariana*, *Ceratolejeunea tahitensis*, and the van Steenis tracks. The Palau Islands are shaded.

cens, does not make the southward penetration. Four species, *Frullania gaudi-chaudii*, *Ptychocoleus cumingianus*, *Caudalejeunea reniloba*, and *Microlejeunea cucullata*, are tropical and austral in distribution. The eight remaining species are strictly tropical: *Mastigolejeunea ligulata*, *Frullania hypoleuca*, *F. apiculata*, *Hygrolejeunea devexiloba*, *Radula nymannii*, *Ptychocoleus pycnocladus*, *Thysananthus spathulistipus*, *Pycnolejeunea bidentula*.

The hepatics with an Indo-Pacific distribution are found throughout the Carolines with some species also reported from the Bonins and Marianas. The flora of the Marshalls contains no Palauan species which does not extend beyond Micronesia, but three broadly distributed species are common with Palau.

Sunda-Pacific Element: Species extending from the Malaysian archipelago into the Pacific via New Guinea are in this division. Ten Palauan hepatics have this range. Half do not extend beyond the Carolines. Of those with broader Pacific distribution, *Ceratolejeunea tahitensis* has a typical distribution (Fig. 1).

Caroline limited species: *Cololejeunea campanulata*, *Riccardia platyclada*, *Lopholejeunea javanica*, *Ceratolejeunea moniliata*, *Leptolejeunea subacuta*.

Broad Pacific species: *Caudalejeunea stephanii*, *Lejeunea pattersonii*, *Hygrolejeunea sordida*, *Radula paucidens*, *Ceratolejeunea tahitensis*.

Taiwan-Japan Element: Species extending from Japan, the Ryukyus and Taiwan into the tropical Pacific are in this element. The three species which belong here are *Lejeunea boninensis*, *Rectolejeunea barbata*, and *R. obliqua*.

Melanesian Element: Melanesia includes New Guinea and the associated archipelagos to the east. Six Palauan species are restricted to Melanesia and Micronesia. *Cheilolejeunea intertexta*, *Lejeunea gracilis*, *Radula novae guineae*, *Cololejeunea wightii*, *Hygrolejeunea latistipula*, *Acromastigum obliquatum*. Some species are reported from the atolls.

Pacific Element: Species restricted to Micronesia and Polynesia are *Radula oceanica*, *Symbiezidium samoanum* and *Microlejeunea lunulatiloba*.

Micronesian Element: This division includes four species restricted to Micronesia: *Lejeunea aloboidea*, *L. clavata*, *Cololejeunea kapingaensis*, and *C. micronesica*. All these species are known from atoll islands. A single endemic, *Bazzania watanabei*, is known from Palau.

REVIEW OF PREVIOUS PHYTOGEOGRAPHIC INTERPRETATIONS

Glassman (1957), who studied the flora of Ponape, suggests that there is no connection between Melanesia and Micronesia. Good (1964) indicates a close relationship among the floras of Melanesia, Micronesia, and Polynesia as almost entirely Malayan and Australian in affinity. Fosberg (*In Arenes*, 1957) proposes a line between Yap and Truk as a limit of islands with continental affinities and the beginning of disharmonious insular floras. Fosberg's line approximates the andesite line which is the terminal point in the Pacific distribution of many angiosperms (Thorne, 1963). This supports Thorne's idea that the open sea acts as a sieve pro-

ducing an eastward attenuation of biota. As summarized by Arenes (1957), van Steenis has outlined three major dispersal paths in the western tropical Pacific (Fig. 1). The Sumatra track is predominately eastward from Malay and Sumatra to Timor, and the Luzon track is a southward dispersal from coastal China and Taiwan to Mindanao where it fuses with the Papuan track. Van Steenis indicates a direct path from Mindanao to Palau. The Papuan track extends southeastward to the Solomons and New Caledonia. Gressitt (1954) suggests a diverse origin of the Palauan insect fauna with major affinities with New Guinea, the Philippines and Malaysia.

Ocean currents are of little significance in liverwort dispersal because of general intolerance of these plants to sea water. Prevailing winds could carry spores, gemmae and plant fragments as could storm winds in directions opposite to prevailing winds (Gressitt, 1954). The significance of jet streams is yet unknown, though they strengthen the argument for long-distance dispersal (Fosberg, 1963). Hepatic propagules could have been transported by migrating birds or by man.

The phytogeographic elements suggest a sweepstake migration from the western tropical Pacific following approximately van Steenis' tracks. The Sumatra track is seen in the Indo-Pacific and Sunda-Pacific elements where no north or south extension is present. The Luzon tract includes those species in the Taiwan-Japan element and those of broader distribution including this northern area. Gressitt further reports bird migration routes from Japan to Palau via the Marianas, Bonins, and Volcanos, and directly from the Philippines to Palau. These and the winds from Taiwan to New Guinea across the western Carolines suggest possible dispersal in the Luzon track. The Papuan track is supported by the broad western range of many Indo-Pacific species with an eastern extension into New Guinea, the Solomons and New Caledonia. Palau is on the northern edge of the Papuan track.

The Melanesian element in the flora supports Good rather than Glassman in associating Melanesia and Micronesia. This floristic affinity suggests a diverse origin rather than the single path from Mindanao proposed by van Steenis.

In Micronesia 60% of the flora of Yap is common with Palau; 87% of the Trukese flora is common; but the richer rainforest floras of Ponape and Kusaie are 34% and 35% common with Palau, respectively. If we view the Caroline high island floras from the point of view of the percentage of the Palauan flora which reached them (Table 1), the situation is somewhat different. From either point of view, however, Fosberg's line does not seem to apply to the distribution of Palauan hepatics.

The thirty genera of hepatics on Palau represent only a sample of about two hundred genera known from the western tropical Pacific. Many are large with over one hundred species and all are genera which produce abundant spores or other disseminules. They are common and abundant in the Asia-Pacific tropics. The abundance of diaspores produced by these species throughout their range increases the possibility for their dispersal to Palau and their subsequent establishment. Thus, the Palauan hepatic flora is comprised mostly of large successful genera and

Table 1.

Island	Number of Species Known	Number of Species Common With Palau	% Flora Common With Palau	% Palauan Flora Represented
Kusaie	75	26	34	43
Ponape	101	35	35	58
Truk	39	34	87	57
Yap	27	16	60	27
Palau	60	—	—	—

Table 1. Synopsis of hepatic species known from high islands in the Carolines with comparisons of numbers of species common with Palau.

aggressive species.

This disharmonious hepatic flora is the result of random dispersal and establishment rather than a terrestrial migration of a single flora. Additional collecting throughout the western tropical Pacific may extend the known range of individual species. However, my study supports the migrational paths suggested by van Steenis, Good and Gressitt and significant changes in the basic patterns seem most unlikely.