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R. F. Thorne

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Floristic relationships between New Caledonia and the Solomon Islands

By R. F. Thorne
Rancho Santa Ana Botanic Garden, Claremont, California

(*Paper read at the Discussion by* E. J. H. Corner)

New Caledonia and the Solomon Islands are compared briefly as to location, size, climate, and other physical features. Possibly 585 seed-plant genera known from the Solomon–Santa Cruz groups are indigenous there, and 692 similarly may be indigenous in New Caledonia. Unknown from New Caledonia are 272 of the Solomons genera and unreported from the Solomons are 379 of the New Caledonian genera. Thus only 313 genera, or 32·5 %, of the 964 total genera are common to both archipelagoes. It is suggested that the relatively smaller generic flora of the Solomons reflects the more limited botanical exploration of the Solomons as well as the greater variability of climate, substrate, and vegetation types of New Caledonia. Also New Caledonia is believed to have a much older, more relict flora than the Solomons, as indicated by the numerous conifers and primitive angiosperms (four genera of which are primitively vesselless). The far greater generic endemism (perhaps 94 genera or 13·5 %) of New Caledonia as compared with the Solomons (5 genera or 0·86 %) is explained by the much greater isolation in space and time of New Caledonia from other land masses. New Caledonia has its closest botanical relationships with coastal Queensland and New Guinea, with which it shares 474 and 482 genera respectively. Its floristic affinities are less with New Zealand and the Outer Melanesian Arc. The Solomons, on the other hand, have their closest botanical ties with New Guinea through New Britain and New Ireland. At least 572, or almost 98 %, of the 585 genera recorded from the Solomons are represented also in New Guinea. As with the fauna, however, the Solomons flora is much attenuated, lacking many of the characteristic New Guinea genera, especially those of the montane and alpine regions. The break between the Solomon Islands and the Santa Cruz Islands is much greater than that between New Guinea and the Bismarcks and between the Bismarcks and the Solomons.

The principal island of New Caledonia, la Grande-Terre, is a mountainous, mineral-rich, geologically complex island about 250 miles long by an average 28 miles wide, totalling about 6360 square miles in area. Located at 20° 0′ to 22° 25′ S latitude and 163° 56′ to 167° 03′ E longitude, it lies about 225 miles south-west of Aneityum of the New Hebrides; 700 miles south of San Cristobal in the Solomons; 760 miles east of Sandy Cape, Fraser's Island, Queensland; 780 miles south-west of Viti Levu, Fiji; 1000 miles north-west of North Cape, New Zealand; and 1140 miles south-east of South Cape, New Guinea. Though now stable and without any volcanic activity since the Oligocene, New Caledonia has had a rather long and violently unstable geological past. Many of the rocks are metamorphics of possibly Cretaceous or Eocene age, and there are extensive areas of mineraliferous serpentines and peridotites that bear a rich, endemic flora of sparse, sclerophyllous scrubby vegetation (*maquis*). Despite the mountainous terrain of the island, the highest mountain, Mt Panié, of gneissic rocks, is only about 5400 ft. high. The climate is mildly tropical and relatively dry, with the rainfall varying from an average 40 in. a year on the leeward west coast to about 80 in. on the windward east coast and perhaps to about 120 in. on the higher, northern mountains. Aside from the drier season from August to November, the rainfall is rather evenly distributed through the rest of the year. Temperatures vary

from means of 68 °F in July to 80 °F in February. (For further data see Compton 1917; Jensen 1924; Faive, Poirier & Routheir 1953; Schmidt 1944; Thorne 1965).

The Solomon Islands, excluding Rennell, Bellona and the Santa Cruz Islands, are an archipelago consisting of a double chain of seven larger volcanic islands or tight island groups, each more than 1000 square miles in area, and many smaller volcanic or coral islands. The total land area is somewhat in excess of 15000 square miles. The two largest islands are Bougainville, about 3880 square miles, and Guadalcanal, about 2500 square miles. Stretching south-eastward almost 700 statute miles from little Buka to the south-east end of San Cristobal Island, the archipelago reaches from about 5° S, 154° 40′ E to about 11° S, 162° 30′ E. Shortest distances are approximately 110 miles from Buka to New Ireland; 150 from Buka to New Britain; 250 from San Cristobal to Ndeni, Santa Cruz Islands; 400 from Bougainville to New Guinea; 415 from San Cristobal to Espiritu Santo, New Hebrides; 700 from San Cristobal to New Caledonia; 900 from Bougainville to Cooktown, Queensland; and 1130 from San Cristobal to Nandi, Viti Levu, Fiji. The main Solomon Islands are mountainous and of volcanic origin, with their rocks largely igneous and possibly dating from Cretaceous time (Gressitt 1958). Limestone terraces near the coasts indicate recent elevation. The highest mountains are Mt Balbi, 9000 ft., of the Emperor Range on Bougainville, and Mt Popomanaseu, 8005 ft., on Guadalcanal (*National Geographic Magazine* 1962). The climate of the Solomons is equatorial, hot (ranging from 72 to 95 °F), humid, with no dry season, and with rainfall on most islands more than 100 in. a year and on some to 120 in. The resultant vegetation on the fertile soils is rain forest except for grassland, perhaps fire-maintained, on the north coast of Guadalcanal in the rain shadow of the Mt Popomanaseu range (Whitmore 1966). As on New Caledonia, the aboriginal population, perhaps 175000, is Melanesian.

With these facts of the physical environment in mind, we can turn to the floristic relationships between the Solomons and New Caledonia. The *Guide to the forests of the British Solomon Islands* recently published by Whitmore (1966) is the most important source of information on the flora of the Solomon Islands. I have estimated roughly that possibly 585 of the phanerogam genera listed as recorded from the Solomon and Santa Cruz Islands are indigenous on these two island groups. Because of the difficulty in determining which plants are indigenous and which naturalized, it is likely that some of the genera counted have been introduced intentionally or accidentally by man. Using the same, probably too generous, approach upon my much annotated copy of Guillaumin's *Flore analytique et synoptique de la Nouvelle-Calédonie*: *Phanerogames* (1948), I believe that 692 of the phanerogam genera listed therein might be indigneous on New Caledonia. Apparently 272 of the 585 Solomons–Santa Cruz total are unknown from New Caledonia and 379 of the 692 New Caledonia total are unreported from the Solomons and Santa Cruz Islands. Thus of a total of 964 genera found on the two archipelagoes, only 313 genera, or 32·5 %, are known from both groups.

These figures, though based upon quite incomplete information, are none the less rather instructive. They suggest two questions that demand some explanation: (1) Why does an equatorial archipelago close to the New Guinea–Bismarck source area and totalling more than 15000 square miles of densely forested terrain have a smaller flora of phanerogamic genera than a much more isolated island less than 6400 square miles in area and

rather dry and but mildly tropical in climate? (2) Why do two island groups now separated by only 700 miles of open water and more or less closely linked by the New Hebrides–Santa Cruz chain of islands have such relatively distinct floras? I shall devote the rest of this paper to an attempt to answer these two questions.

The smaller total of phanerogamic genera listed as indigenous for the Solomons than that listed for New Caledonia reflects to a large extent the much greater botanical attention received by New Caledonia during the past century. The Solomons, like the Bismarcks and the New Hebrides, are still poorly known botanically. Dozens of wide-ranging marine, strand, freshwater aquatic, marsh, ruderal, and other angiosperm genera are still unreported but surely present in the Solomons. Many of them probably were collected by the Royal Society Solomon Islands Expedition in 1965. Ultimately one can expect the total of genera indigenous to the Solomons to equal or even to exceed the New Caledonian total.

There would still remain, however, the relatively richer flora on New Caledonia when its much smaller land area and greater present isolation are taken into account. New Caledonia has a much greater variability in climate, ranging from wet to dry and hot to cool, and distinctive substrates varying from serpentine and gneiss to eroded limestone rock and fine coral sand and mud. The resultant vegetation types are likewise most diverse, including mossy-forests and mossy-thickets on the peaks and patches of tropical rain forest on the slopes of the higher mountains; sclerophyllous scrub on the serpentine and peridotite soils; open marshes on the Plaine des Lacs; fire-controlled niaouli (*Melaleuca*) savanna and grassland in coastal areas; strand vegetation on the sandy beaches; and extensive mangrove swamp and marine meadow in the quiet, shallow, muddy bays and estuaries (Virot 1956; Guillaumin, Thorne & Virot 1965).

The vegetation types of the Solomons are reportedly much less diverse. The larger islands are heavily forested from the coasts to the mountain peaks. Whitmore (1966) reports grassland only from the north coast of Guadalcanal. There certainly must be much local variation in the tropical rain forests, and Whitmore mentions as the most striking variant the lower, more depauperate forest found on ultrabasic igneous rocks.

The greater age and isolation of the neocaledonian flora helps to explain both the greater richness and the greater distinctiveness of its generic flora. I have discussed the relict nature of the New Caledonia flora in some detail elsewhere (Thorne 1965), but will summarize the salient points briefly here. Nearly 40 species of conifers are endemic on New Caledonia in addition to the widespread cycad, *Cycas rumphii* Miq. Araucariads and podocarps predominate but the Taxaceae are represented by the endemic *Austrotaxus* and the Cupressaceae by *Callitris*, also on Australia and Tasmania, *Libocedrus* (as narrowly defined by Florin 1963), also on New Zealand, and the endemic *Neocallitropsis*. Of the nine primitively vesselless angiosperms recognized in the world flora, New Caledonia possesses four: the endemic and monotypic *Amborella* and three genera of Winteraceae (the endemic *Zygogynum* and the more wide-ranging *Belliolum* and *Bubbia*, in which I include the earlier recognized *Exospermum*). *Belliolum* is found also in the Solomons and New Guinea; *Bubbia* also on Lord Howe Island, Queensland, New Guinea, and Madagascar. Many other taxa generally regarded as possessing primitive characteristics and probably of Cretaceous origin include the numerous Annonaceae, Monimiaceae, Lauraceae, Rutaceae,

Escallonioideae, Cunoniaceae, Proteaceae, *Nothofagus*, Sapotaceae and Araliaceae. 'Modern' taxa are poorly represented in the largely endemic and woody flora. Predominantly herbaceous families are mainly represented by ruderals or other wide-ranging species, if at all.

Endemism in the neocaledonian flora is astounding. Of the excessively liberal 692 indigenous genera mentioned above, 94 are believed to be endemic, or 13·5 %, on New Caledonia, the Isle of Pines, and the Loyalty Islands. Baumann-Bodenheim (1956) estimated the indigenous seed-plant flora of New Caledonia at 2660 species, with about 2450, or more than 90 %, endemic on the island group. Careful research will probably reduce these totals, but perhaps not significantly. Some of the peculiar, relict genera are so isolated from presumed relatives that they are generally treated as distinct families (Amborellaceae, Strasburgeriaceae) or may some day receive general recognition as distinct families (*Canacomyrica*, *Memecylanthus*, *Oncotheca*, *Paracryphia*). Whatever their ultimate treatment, they deserve thorough study as evolutionary and geographic relicts.

New Caledonia, during its long and geologically very active past, probably had much closer, though never continuous, terrestrial connexions with Australia, New Guinea, and New Zealand. Its lack of indigenous primary-division freshwater fishes, freshwater turtles, amphibians, terrestrial vertebrates other than vagile skinks and geckos, and freshwater mussels rules out land connexion with any continental mass. The neocaledonian land mass, whatever its position and extent in pre-Tertiary or early Tertiary time, was able to tap the Papuan flora indirectly via Queensland or perhaps directly also from southern New Guinea. The present flora shares 474 genera with Queensland and 482 with New Guinea. Fifteen genera are restricted to New Caledonia and Australia (14 of these mostly in Queensland but often with range extending into other parts of Australia). Only one genus, *Dubouzetia*, plus the section *Antholoma* of *Sloanea* of the same family Elaeocarpaceae, is currently known to be restricted to New Caledonia and New Guinea.

The botanical relationships of New Caledonia are less strong in other directions. It shares only 118 genera with New Zealand, with *Xeronema*, *Knightia*, and *Libocedrus* restricted to the two island groups. However, the montane biota of New Caledonia and the fossil record of New Zealand indicate much closer botanical relationships in the past.

Though New Caledonia and the Loyalty Islands are separated from the New Hebrides by a deep trough, the sea gap is not so wide (about 150 miles from Aneityum to Maré) as to prevent all botanical intercourse between the New Caledonian group and the New Hebrides, and presumably through the latter group with other island chains of the Outer Melanesian Arc. The 15 genera believed to be restricted to New Caledonia and the Melanesian islands from New Guinea to Fiji and Samoa offer rather strong support for this thesis. Restricted to New Caledonia and the New Hebrides are four genera (*Chambeyronia*, *Dizygotheca*, *Strobilopanax*, *Cyclophyllum*) and to New Caledonia and Fiji also four (*Acmopyle*, *Storckiella*, *Buraeavia*, *Piliocalyx*). No genus is restricted just to New Caledonia and the Solomons and only one to New Caledonia and New Guinea (*Dubouzetia*). *Alphandia* and *Guillainia* are shared with the New Hebrides and New Guinea; *Belliolum* with the Solomons and New Guinea; *Agatea* with the Solomons, Fiji, and New Guinea; *Trimenia* with Fiji and New Guinea; and *Kermadecia* with the New Hebrides, Fiji, and Samoa. A species of *Coronanthera*, with 10 species on New Caledonia and one reported from

Queensland, has recently been described from the Solomons (Gillett 1967). Further botanical exploration will change these restricted distributions considerably, but even in their incompleteness they show the pattern of relationship between New Caledonia and the Outer Melanesian Arc. It is of some interest to compare the 32·5 % of total genera given above as shared between New Caledonia and the Solomons with the percentages I listed earlier (Thorne 1965) of total genera shared by New Caledonia with the New Hebrides (37·8 %), Fiji (37·6 %), New Guinea (31·5 %), Queensland (32.8 %), New Zealand (13·4 %), and Tasmania (13·5 %). The function of proximity (or distance), also of similarity (or dissimilarity) of climate, in controlling floristic relationships can be readily observed from these data.

The later history of New Caledonia, certainly since the early Tertiary, has been one of continuous isolation from other land masses. Combined with the subharmonic, continental origin of the conifers and more primitive woody plants of New Caledonia is the disharmonic representation of the more recent angiosperm families, particularly the herbaceous ones. As with the disharmonic, oceanic fauna, this more recent, herbaceous, specialized segment of the flora consists of waifs that have reached the island over wide sea gaps. The ancient, relictual plants have been protected on the island through all or most of the Cenozoic from the more efficient, more aggressive competitors that have eliminated them or badly restricted them on the continental land masses and the more accessible islands, as perhaps the Solomons.

The remainder of the answer to the second question regarding the disparity between the floras of New Caledonia and the Solomons must be sought in the present flora of the Solomons and its relationships. Because of their location on the Outer Melanesian Arc, probably as a continuation of the volcanic arc to the southeast of New Ireland, the Solomons should be readily accessible to the Papuan flora from New Guinea via New Britain and New Ireland and rather less readily to the Pacific flora from the east via the Fiji–New Hebrides–Santa Cruz island chains. Analysis of published data (van Balgooy 1960; Whitmore 1966; Corner 1967) shows clearly that such is the case. The seed-plant generic flora of the Solomons is overwhelmingly of Papuan origin or of wider-ranging elements that have reached the islands via the New Guinea–Bismarck Islands route. Van Balgooy's figures indicate that probably 91·4 % of the Solomons genera known to him reached the islands via New Guinea and the Bismarcks, 6·5 % from the Pacific Islands, including New Caledonia, and 1·4 % from Australia, with 0·7 % of the genera endemic.

A comparison of the genera in Whitmore's list (1966) with those genera listed from New Guinea by van Royen (1959) shows that at least 572, or almost 98 %, of the 585 possibly indigenous seed-plant genera recorded from the Solomon and Santa Cruz Islands are also represented in New Guinea. At present five genera are believed to be restricted to the Solomons: *Allowoodsonia*, *Cassidispermum*, *Kajewskiella*, *Rehderophoenix*, and *Strongylocaryum*. Of the eight additional genera unreported from New Guinea, *Coronanthera* and *Geissois* are quite likely of New Caledonian origin, but the latter genus has not yet been found beyond the Santa Cruz Islands. *Carruthersia*, *Crossostylis*, *Physokentia*, *Calycosia*, and *Chelonespermum* have probably reached the Solomons from the east. All are found in Fiji, and the first three, like *Geissois*, are also found in the New Hebrides. *Carruthersia*, however, is additionally reported from the Philippines. *Sebastiania* is represented in the Solomons by the

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coastal species *S. chamaelea* (L.) Muell.-Arg. which ranges from tropical Africa and India north to China and east to Queensland yet is still unreported from New Guinea, the Bismarcks, and eastern Melanesia. Not one genus in the Solomons appears to be of undoubted Australian origin.

The overwhelming Papuan aspect of the flora is attested to by mention of a few genera so characteristic of New Guinea but missing from New Caledonia and in many cases from the islands to the east of the Solomons: as *Archidendron*, *Areca*, *Begonia*, *Boea*, *Brownlowia*, *Calamus*, *Campnosperma*, *Caryota*, *Costus*, *Daphniphyllum*, *Dillenia*, *Dischidia*, *Dracontomelum*, *Elatostema*, *Finschia*, *Gnetum*, *Gonystylus*, *Hanguana*, *Leea*, *Licuala*, *Lophopyxis*, *Mangifera*, *Medinilla*, *Metroxylon*, *Myristica*, *Myrmecodia*, *Nauclea*, *Nypa*, *Octomeles*, *Phaleria*, *Planchonia*, *Pullea*, *Pygeum*, *Rhododendron*, *Sararanga*, *Saurauia*, *Schizomeria*, *Schuurmansia*, *Scirpodendron*, *Styrax*, *Vavaea*, and *Xanthophyllum*.

On the other hand, some of the most representative New Guinea taxa apparently have not reached the Solomons, in some cases not even the Bismarcks: as *Araucaria*, *Coriaria*, Dipterocarpaceae, *Drimys*, *Engelhardtia*, *Eucalyptus*, *Eupomatia*, *Eurya*, *Flindersia*, *Galbulimima*, *Gunnera*, *Helicia*, *Ilex*, *Impatiens*, Magnoliaceae, *Nepenthes*, *Nothofagus* and other Fagaceae, *Papuacedrus*, *Phyllocladus*, and *Tecomanthe*. As should be expected where present, and probably past, water gaps require that plants use a chain of islands as stepping stones, a good many taxa are filtered out. The Solomons thus have a rather attenuated Papuan flora. They also have had very considerable endemism within the genera reaching the islands from the west. Taking the largest genus in the Solomons as an example, Corner (1967) found that 23 of the 63 indigenous species of *Ficus* are restricted to these islands. He also found that most of these endemics are common throughout the Solomons.

The vertebrate fauna of the Solomons is also an attenuated Papuan fauna. Marsupial carnivores, monotremes, strictly freshwater fishes, non-marine turtles, leptodactylid and brevicipitid frogs are not known east of New Guinea. Of the rich New Guinea marsupial and rodent fauna, the Bismarcks apparently have only one bandicoot, one wallaby (*Thylogale*), two species of *Phalanger*, one *Petaurus*, and four genera of rats. One *Phalanger*, three genera of rats, several groups of snakes, *Hyla* and eight genera of ranid frogs are established on the Solomons (Darlington 1957). According to Mayr (also in Darlington 1957) 125 species of land birds are found on the Solomons as compared with 520 on New Guinea. Cassowaries reach the Bismarcks but not the Solomons. Except for a few vagile lizards on the Pacific islands and an endemic iguanid and two genera of ranid frogs on Fiji, the Solomons mark the eastern limit of terrestrial vertebrates. Only 29 species of birds have been reported from the Santa Cruz Islands, 51 from the New Hebrides, 54 from Fiji, and 64 from New Caledonia (Mayr in Darlington 1957). The Bismarcks are separated from the Sahul continental shelf and likewise narrowly from the Solomons. Darlington considers that the fauna on the Bismarcks and Solomons forms an immigrant pattern of differential spread across water gaps on a fringing archipelago. Approximately the same can be said for the seed-plant genera on the two island groups.

The flora of the Solomons lacks the appearance of ancientness possessed by New Caledonia. The only araucariad on the whole group is a species of *Agathis* on Vanikoro of the Santa Cruz group. The only conifers listed by Whitmore for the Solomons proper are two species of *Dacrydium* and four of *Podocarpus*. *Belliolum* is the only vesselless angiosperm

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reported from the islands. If a relict flora comparable to that on New Caledonia ever existed on the Solomons, it has largely been crowded out by the highly adapted Papuan lowland tropical rain-forest flora. One might expect with two mountains 8000 ft. or higher that more of the Papuan montane rain-forest elements would be listed from the islands. If collected, they have not been reported.

Van Balgooy (1960) found a strong demarcation between the Solomons and the New Hebrides, in which he included the Santa Cruz group. He found that 97 phanerogamic genera reached their eastern limit with the Solomons, and 36 Pacific or southern genera reached their western limit in the New Hebrides–Santa Cruz group. Corner (1967) found that most of the 36 *Ficus* species common with New Guinea terminate their eastward range on San Cristobal; only nine extend to the New Hebrides and beyond. In addition to the vertebrate animals mentioned above, freshwater mussels and most of the Paleo-Oriental snail fauna also reach their eastern limit in the Pacific at the Solomons (Solem 1958). McMichael & Hiscock (1958) found that the distribution of freshwater mussels indicates that the Solomons could not have had terrestrial connexion with New Guinea.

In general, the ocean gap between the Solomons and the Santa Cruz group forms a useful boundary between western and eastern Melanesia. Elsewhere (Thorne 1963) I have treated biogeographically the Solomons and the Bismarck–Admiralty groups respectively as the Solomonian and Bismarckian Districts of the Bismarckian Province of the Papuan Subregion of the Oriental Region. In so far as biogeographical classification has any useful function, I still favor this treatment. At the same time I treated New Caledonia and the Loyalty Islands in a Neocaledonian Province and Subregion of the Oriental Region, primarily because of their long isolation and highly endemic, distinctive biota.

In summary, the floristic relationships between the Solomon Islands and New Caledonia are what one might expect considering the relative proximity of the two island groups to the same Papuan Region source areas and to the intermediate Santa Cruz–New Hebrides Islands, the 700 miles of ocean between the Solomons and New Caledonia, and the climatic, elevational, geological, and consequent vegetational differences between the two island groups.

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