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Phil. Trans. R. Soc. Lond. B 1969 **255**, 549-566
doi: 10.1098/rstb.1969.0025

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Phil. Trans. Roy. Soc. B **255**, 549–566 (1969)
Printed in Great Britain

LAND FLORA

Geography of the flowering plants

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The phanerogam flora of the Solomon Islands resembles that of Malesia, but has fewer families, genera and species. A number of lines of evidence indicate that it is not a recent, immigrant flora, and has not arrived by long-distance dispersal. The implication to be drawn from phanerogam distributions in Melanesia is that there have been stronger land connexions within the region and with Malesia in the past. The poverty of the Solomons flora is partly explicable by incomplete immigration from Malesia. There is also evidence for chance extinctions within the Group such as could follow from the continually changing land–sea boundaries. In its present form with a uniform flora with few local endemics, yet disjunctions to neighbouring island groups, the archipelago may well represent a 'land-bridge'. Surprisingly there is no evidence of extensive species radiation in the Solomons despite gross geological viscissitudes; this is contrary to expectations based on temperate floras and suggests that flowering plant evolution in the tropics may be very slow. Further knowledge of the dates of land–sea changes in Melanesia should allow a time-scale to be set on the evolution of individual species.

Observations

The Solomons archipelago is part of the great Melanesian foreland where the East Indies and Australasia abut on the Pacific Ocean. It ranges as a double festoon of islands about 2500 km north-east of Australia, 1120 km long from north-west to south-east, separated by 176 km of open sea from New Ireland in the Bismarck archipelago to the north-west and by 352 km of open sea from the Santa Cruz Islands, geographically part of the New Hebrides, to the east-south-east. Within the Solomons inter-island distances are only 16 to 64 km. Beyond the Solomons Melanesia reaches out still further south-eastwards to the New Hebrides, and then to Fiji with Samoa and Tonga.

Biogeography based on present-day distributions can only be suggestive and never, in the nature of the evidence, finally conclusive. Nevertheless, there is strong evidence from the Melanesian phanerogam flora for more substantial land connexions within Melanesia and with Malesia to the west in the past. Here the evidence for this view is put forward mainly based on the Solomons' flora, which is also shown possibly to owe its present composition partly to unstable geological conditions. Finally certain general inferences on flowering plant evolution are made based on the Solomons' flora.

The botanical evidence for a former more substantial Melanesian land mass is contained in five different features of the flora, which in summary are as follows:

(1) The Melanesian flora is predominantly like that of Malesia, nearly all its links are to the west and there is no sharp boundary between Malesia and Melanesia.

(2) There is a small but distinctive group of non Malesian genera. This comprises first genera with a wide distribution through the Pacific including Melanesia, sometimes with a few outlying species in Malesia. Secondly there are also local endemic genera restricted to all or part of Melanesia, some of which have signs of great antiquity.

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(3) Some species distributions within Melanesia spread from archipelago to archipelago.

These first three features reveal a web of relationships which is strongest to the north-west.

(4) Several species within the Solomons have complicated patterns of infraspecific variation between populations which are the same as between their New Guinea populations.

(5) There is no predominance in the flora of Melanesia of any one dispersal mechanism, apart from the mainly water-dispersed Indo-Pacific strand element.

These features will now be considered in turn.

The boundary between Malesia and Melanesia

The Malesian floristic province has no sharp boundary with Melanesia, in distinction to its three other contact zones. In north Malaya 375 Malesian genera reach their northern limit, and 200 continental Asian genera reach their southern limit, a 'demarcation knot' (Van Steenis 1950) of 575 genera. At the Philippines/Formosa boundary, *ca.* 200 km of sea, the demarcation knot is 686 genera, and the New Guinea/Queensland boundary at Torres Straits, also *ca.* 200 km, has the strongest knot, 984 genera (see Van Steenis 1950 for further details). By contrast the knot at the Solomons–Bismarcks boundary (176 km of sea) is only 287 genera.*

Floristic elements

General

The Solomon Islands' flora is predominantly like that of Malesia but impoverished, with fewer families, fewer genera, and fewer species.† Thus, for example, neither Dipterocarpaceae, nor Fagaceae‡ reach the Solomons; Combretaceae is represented by only two of the five genera it has in Malesia (*Lumnitzera* and *Terminalia*); the scaly-fruited palms (subfamily Lepidocaryoideae) have only one out of nine of the genera of climbers and one out of four tree genera; the Ericaceae occurs solely as four *Rhododendrons* and one *Vaccinium*. At the species level the one climbing palm genus, *Calamus*, has four species against dozens in New Guinea (and one in Fiji); *Elaeocarpus* has only nine species against *ca.* 100 in New Guinea and *Macaranga* (Euphorbi) only 11 against *ca.* 60.

The poor flora is reflected in the dominance of the forests by only a few big tree species, and the speed with which a plant collector exhausts a single locality. On 3·6 ha of lowland forests at Shoulder Hill on north-east Kolombangara Island 104 species of tree $\geqslant$ 30 cm girth were counted. On 4 ha in lowland Malaya 383 species were found (Wong & Whitmore 1970).

The different elements in the Solomons' flora are best considered by first analysing the genera present and then the species.

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[*] Van Balgooy (pers. comm. April 1968). The knot was previously calculated (Van Balgooy 1960) as 266, demonstrating that this important phytogeographical parameter has not been much changed by all the recent botanical discoveries.

[†] Up to January 1968 there were known from the Solomons about 710 genera and 1750 species of phanerogams and 290 species of pteridophytes. More thoroughly explored Fiji, by comparison, has about 450 genera and 1840 species of phanerogams and 290 species of pteridophytes (Parham 1964; Smith 1955).

[‡] *Quercus guppyi* F. Muell. from Bougainville = *Litsea guppyi* (F. Muell.) F. Muell. ex Forman, *Kew Bull.* **19**, 461–462 (1965).

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Genus groups in the Solomons

Roughly 35 % of Solomons' genera are worldwide (e.g. *Carex*, *Commelina*, *Cyperus* and *Ipomoea*); roughly 28 % are Palaeotropical with or without ranges extending into Africa; roughly another 28 % are Malesian, some of which are east Malesian; about 2 %, 15 genera, are Pacific. No other group exceeds 1 % of the total. The small elements include four Australian genera (*Acianthus*, Orchid.; *Casuarina*; *Commersonia*, Tili.; *Hardenbergia*, Legum.) and three endemic genera (figures from Van Balgooy (1960), and personal communications, modified in the light of recent discoveries). These groups, of course, are not quite sharply separated and sometimes the placing of a genus is somewhat arbitrary. Also we must expect further exploration to yield new discoveries. The analysis nevertheless shows the main outline of the flora, and differences in placing a few genera and the further discoveries to be expected are unlikely to alter the picture materially.

Examples of the group of genera centred in the Pacific are *Cassidispermum* and *Chelonespermum* (Sapot.) Solomons and Fiji; and *Crossostylis* (Rhizophor.) Solomons eastwards to Marquesas. Some genera of this group have a few species to the west in Malesia. For example *Metroxylon*, the sago palm, has five locally endemic species through Melanesia from Bougainville to Niue, one aberrant species with lateral inflorescences in Micronesia, and two species in Malesia westwards to the Moluccas.

The three small genera endemic to the Solomons, are *Kajewskiella* (Rubi.) 1 sp., *Allonoodsonia* (Apocyn.) 1 sp. and *Homalocladium* (Polygon.) 1 sp.

Other islands and island groups in Melanesia also have small numbers of localized endemic genera. Arecoid palms in particular are common. Thus New Hebrides has *Carpoxylon* and *Kajewskia*, 1 sp. each, and Fiji has *Goniocladus* (1), *Neoveitchia* (1), *Taveunia* (1) and *Vitiphoenix* (8) out of totals of 3 and 12 endemic genera respectively.

Species groups in the Solomons

Species have on the whole much narrower ranges than genera and the worldwide and palaeotropical species groups are very tiny in comparison. At the species level the following main groups may be recognized in Melanesia:

(1) Species of the mangrove, seashore and beach forest which range widely through the lands of the Indian and Pacific Oceans. This is the Indo-Pacific strand flora, which in the sparsely populated Solomons is still seen in its primeval glory. Typical examples are *Barringtonia asiatica* (Lecythid.), *Calophyllum inophyllum* (Guttif.), *Ipomoea pes-caprae* (Convolvul.), *Rhizophora mucronata*.

(2) Species found throughout Malesia reaching into Melanesia to the Solomons and sometimes beyond to the New Hebrides or Fiji (see figure 188). Examples in the Solomons are *Calophyllum soulattri*, *Elaeocarpus sphaericus*, *Gonystylus macrophyllus* (Thymele.), *Parinari glaberrima* (Ros.), *Terminalia calamansanai* (Combret.).

(3) Species found in Celebes, Moluccas and/or New Guinea, sometimes in Queensland, and into Melanesia, that is species of the Sahul shelf area in Malesia east of Wallace's line (see figure 189). Examples in the Solomons are *Endospermum medullosum* (Euphorbi.), *Gmelina moluccana* (Verben.), *Prunus schlecteri* (Ros.), *Schizomeria serrata* (Cunoni.).

(4) Pacific Island species with their ranges from Melanesia eastwards into Polynesia

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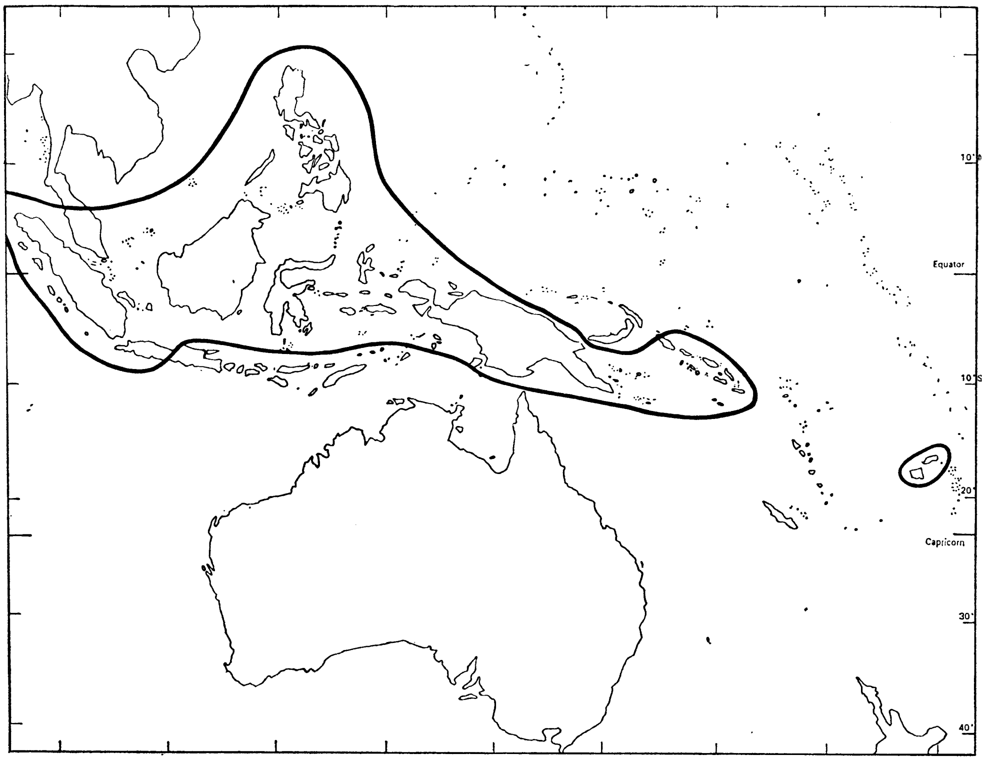

FIGURE 188. *Gonystylus macrophyllus*: Malesia and Melanesia.

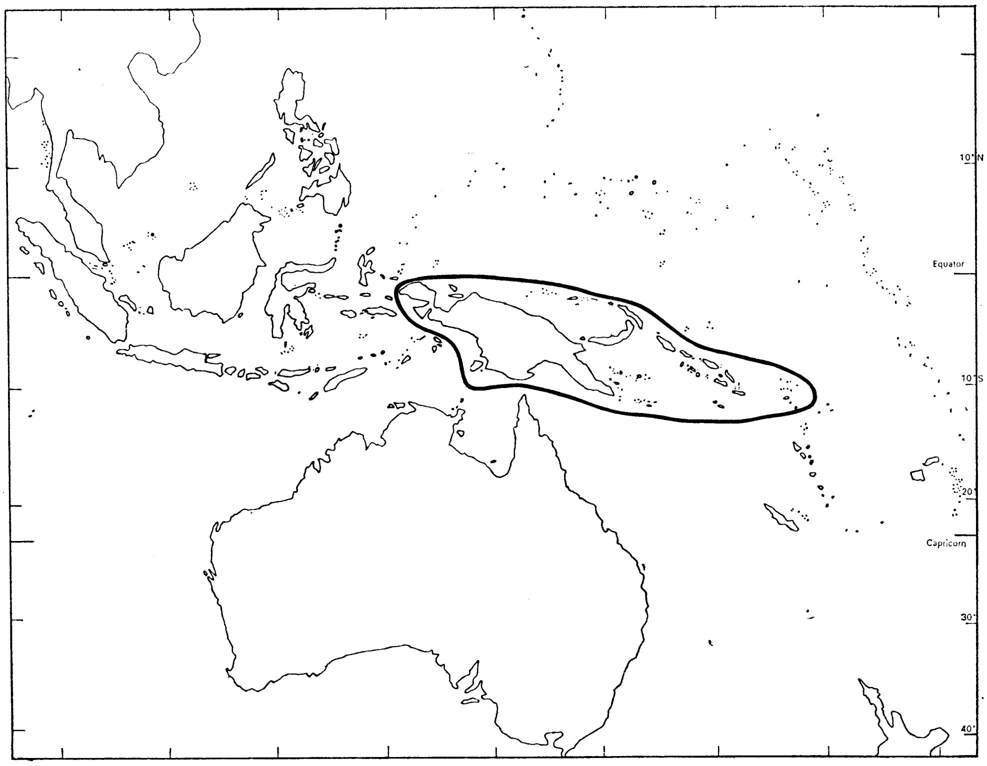

FIGURE 189. *Endospermum medullosum*: Eastern Malesia and Melanesia.

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and sometimes northwards into Micronesia (see figures 190, 191). Examples are *Fagraea berteriana* s.l. (Logani.) widespread through Melanesia, Micronesia and Polynesia; *Lepinia solomonensis* (Apocyn.) a common small tree throughout the Solomons known also from Ponape and Tahiti, a range, as pointed out by Van Steenis (1962), comparable to

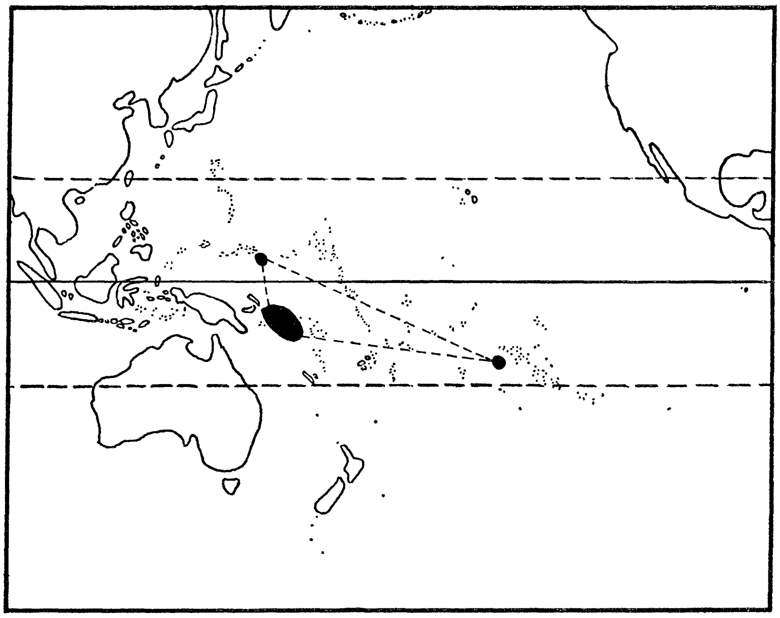

Figure 190. Monotypic *Lepinia solomonensis*, widely disjunct in the Pacific.

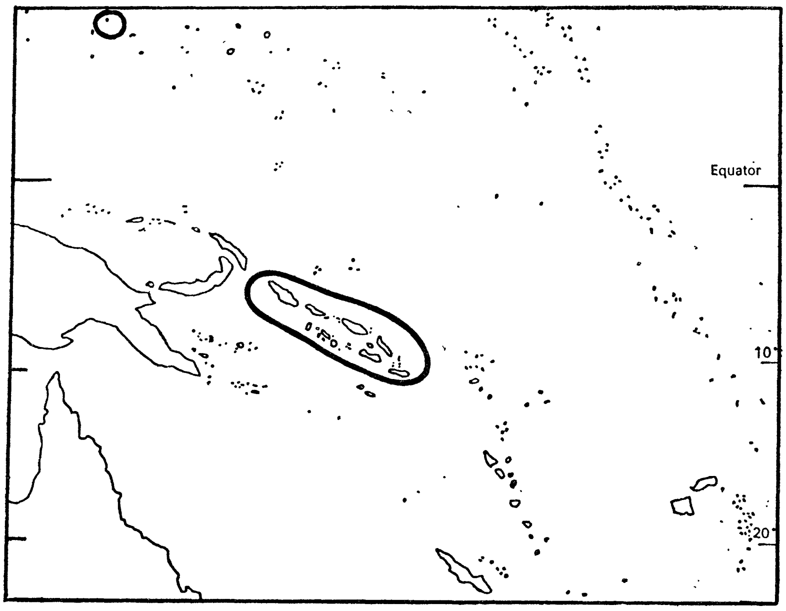

Figure 191. *Pandanus cominsii* growing in Melanesia and Micronesia.

Barcelona, Amsterdam and Kabul; *Meterosideros polymorpha* (Myrt.) Solomons, New Zealand and Hawaii; *Pandanus cominsii* Solomons and Ponape.

(5) Species centred in Melanesia. These presumably have evolved here from immigrant ancestors. Some are very local, others are more widely spread. It is important to observe

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that many are not restricted to one archipelago, or to one island, but occur variously through Melanesia.

Examples of species spreading across several archipelagos (see figure 192), are *Buchanania attenuata* (Anacardi.) and *Canarium vanikoroënse* (Burser.), Santa Cruz and Fiji; *Calophyllum vitiense* (Guttif.), and *Connarus pickeringii* Solomons, Santa Cruz and Fiji; *Canarium harveyi* (Burser.) Solomons, Fiji and Samoa; *Calophyllum cerasiferum* and *Pegiantha koroana* (Apocyn.) Solomons and Fiji; *Terminalia brassii* (Combret.) Solomons and Bismarcks.

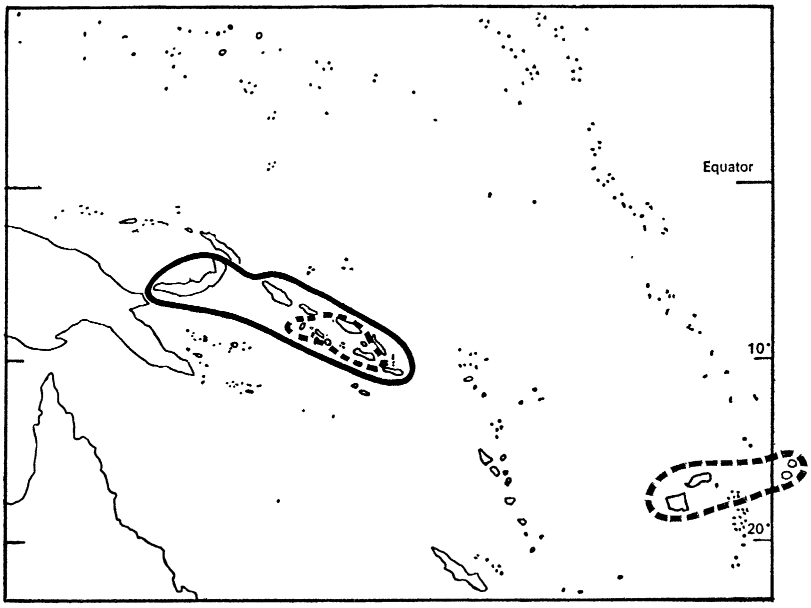

Figure 192. *Terminalia brassii* (solid line) and *Canarium harveyi* (dashed line), widely distributed Melanesian endemics, spanning two archipelagos.

Examples of species locally endemic to a single archipelago (figure 193) are: *Agathis macrophylla* (Araucari., New Hebrides and Santa Cruz), *Allowoodsonia whitmorei* (Apocyn., Solomons), and *Dillenia crenata*, *D. ingens*, *D. insignis*, and *D. salomonensis* with overlapping ranges in different parts of the Solomons (see fig. 10 in Whitmore 1966). Other examples, of endemics local to the Solomons, will be given in a later section.

The species of individual plant families fall into these five categories, but the proportions differ from family to family. For example, to consider the larger monocotyledons, nearly all the species of aroids occur in New Guinea as well as the Solomons, a very small number are endemic, one species only (*Epipremnum pinnatum*) has been recorded in Fiji. The gingers have their strongest connexions with New Guinea, a few species grow throughout Malesia, a few are endemic, one *Guillainia purpurata* is also in east Malesia, New Caledonia and the Carolines. The Pandanaceae have perhaps one-third to one-half their species endemic, the others are Malesian or Pacific in distribution.

The palms (H. E. Moore, personal communication) have perhaps the strongest endemic element. Eighty per cent of the 45 native species are endemic. The others have their strongest links with New Guinea. At the generic level the strongest connexion is with New Guinea and Malesia generally (14 or 15 genera) and four Malesian genera end their ranges at the

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Solomons.* In addition, there are three essentially Melanesian genera (*Clinostigma*, *Metroxylon* and *Physokentia*).

Finally *Heliconia* must be mentioned separately. Green (in press) considers there is only one Old World species. In the Solomons this is common and widespread. *Heliconia*'s chief interest is as an example of the pan-Pacific element in the Solomons flora. Both *Heliconia*, and indeed the majority of the genera of Solomons' Araceae, also grow in lowland tropical Latin America. All together 25 Solomons' genera or their close relatives do (see appendix A).

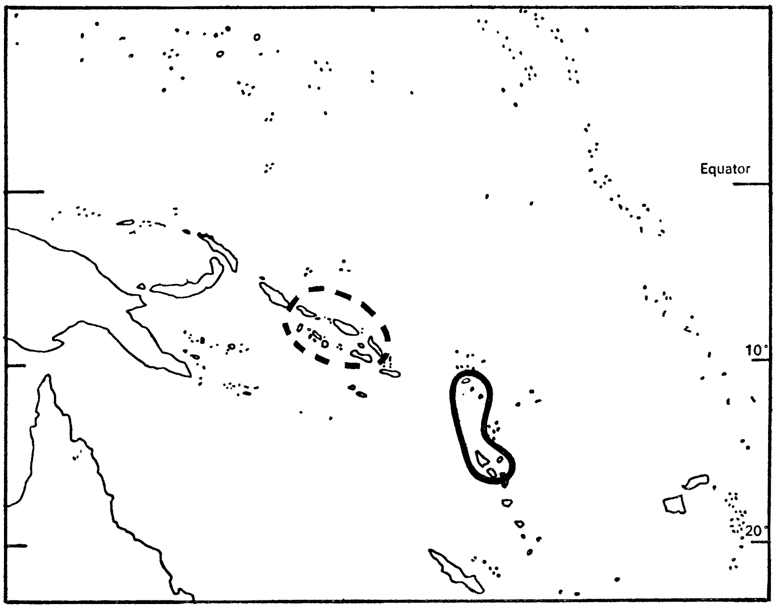

FIGURE 193 *Agathis macrophylla* (solid line) and *Allowoodsonia whitmorei* (dashed line); local endemics within Melanesia.

Ancient elements in the Melanesian flora

The family Winteraceae, related to Magnoliaceae in the Ranales, is of particular interest to Melanesian phytogeography. The family spans the Pacific as it also has members in South America. The centre of diversity, that is the main centre of genera and species, is clearly in the Old World (Smith 1943).

The Old World Winteraceae are concentrated in New Guinea, the Solomons, New Hebrides (6 gen.) and New Caledonia with outlying *Drimys* spp. as far west as Borneo, and eight species (*Bubbia*, *Drimys*) in eastern Australia, which do not appear to have evolved from recent immigrants. In addition there is an endemic genus *Pseudowintera* (2 pp.) in New Zealand and the monotypic *Degeneria*, often given a family of its own, in Fiji.

Many botanists consider that on floral and vegetative anatomy Winteraceae are the most primitive living flowering plants, for a full review see Bailey & Nast (1945). The genera show complex reticulate taxonomic relationships and no one is clearly more primitive than the rest (Smith 1943). Careful study has led Smith (1945) to consider that

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* *Areca*, *Caryota*, *Livistona* and *Nypa*. In addition, the Malesian *Licuala* reaches to New Hebrides and *Calamus* to Fiji.

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the probable origin of the Winteraceae was in the New Guinea–Queensland region at a time when there were land connexions into Melanesia. Paleo-endemic genera of the family are now scattered through Melanesia.

The Solomons' flora has a number of other ancient elements, *Allowoodsonia* (Apocyn.) already mentioned as an endemic genus was discovered by the B.S.I.P. Forestry Department and is the far eastern counterpart of a West African–South American genus, *Malouetia* (Markgraf 1967). *Sararanga* is a remarkable genus of Pandanaceae with the inflorescences like huge bunches of grapes 130 cm (4 ft.) long, not compact heads, and takes its name from a Solomons' vernacular for *S. sinuosa*, common through the Group and otherwise only known from north-west New Guinea, and the Philippines (*S. philippinensis*) (Stone 1961). *Archidendron* (Mimos.) is the only Old World legume with several pods per flower, it ranges from the Moluccas eastwards, with two endemic species in the Solomons where the range ends. The coryphoid palm genera, *Licuala* and *Livistona*, reach their eastern limits in the Solomons, so does the palm *Nypa*.

Infra-specific variation patterns

I have made a careful study of the Solomon Islands' populations of a number of big tree species to sort out their taxonomy prior to their commercial exploitation (Whitmore 1967). I have discovered that the infra-specific variation within the Solomons is closely similar to that in New Guinea. Thus *Schizomeria serrata*, a big cunoniaceous tree, shows a complex reticulate pattern of morphological variation untreatable taxonomically, and all facets of this pattern are present in the Solomons, just as throughout the rest of its range in eastern Malesia. *Buchanania arborescens* (Anacardi.), *Calophyllum soulattri* (Guttif.) and *Endospermum medullosum* (Euphorbi.) are other examples.

This pattern of infra-specific variation is, I suggest, most easily explained by postulating previous breeding contact with the Malesian populations. Invasion of a virgin habitat by long-distance dispersal of a few seeds on several separate occasions would most likely have led to a different variation pattern, consisting of divergent relatively uniform populations. Variation would be much less intricate within the populations due to the limited gene pool available, and one would expect to find regional differences between different parts of the Solomons, not an archipelago-wide intricate pattern.

Macaranga tanarius (Euphorbi.) has, in the Solomons, just as in New Guinea, an occasional form with promimently glanded leaves, sometimes segregated as the species *M. quadriglandulosa*, which is in fact an incipient species still evolving.

Dispersal

Concerning dispersal mechanisms, there is no preponderance in the Solomons of species with light, easily transported, windborne diaspores, and there is no increase in this element south-eastwards to Fiji; nor is there a preponderance of species with water-borne diaspores (see species lists in Parham (1964), Whitmore (1966)). The Solomons have a number of inland species with big heavy fruits, e.g. *Gonystylus macrophyllus* (Nicobars and Malesia, to Fiji, figure 188), *Parinari glaberrima* (Ros., Malesia to Carolines and Fiji) and *Xanthophyllum papuanum* (Polygal., east Malesia, Solomons) which are unlikely to have attained their present distribution across present sea barriers.

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The Solomons' flora has a proportion of dioecious species which also grow elsewhere. Successful establishment of these by long-distance dispersal would be most precarious. Examples are *Canarium* (Burser.), for instance *C. asperum*, Malesia to Solomons, *C. harveyi*, Solomons, Fiji and Samoa (figure 192); most Euphorbiaceae, for example *Macaranga* and *Mallotus*; some *Evodia* spp. (Rut.).

The Burseraceae reach the eastern limit of their Old World distribution in Melanesia, as do Proteaceae (*Finschia chloroxantha* is in Palau, west Micronesia). Neither family is thought to have diaspores suitable for long-distance dispersal (Leenhouts 1955; Sleumer 1955).

INFERENCES

An ancient Melanesia

Thus it is seen that the Melanesian flowering plant flora has a number of distinctive elements which imply a long history. It has a number of features which could not arise under present-day conditions. The evidence seems to suggest the former existence of stronger connexions within Melanesia and with Malesia which means the former existence of more land above the sea. The evidence contradicts any suggestion that the region has a recent immigrant flora, or that it arrived by long-distance dispersal from a source area to the west. Croizat (1958) discusses the animals, mainly the birds, and considers this evidence also points to the same conclusions; and in his earlier book (1952) he has reached from plant geographical evidence the same conclusion as myself, in fact going even further by labelling the south-west Pacific region as one of the three 'gates of angiospermy'.

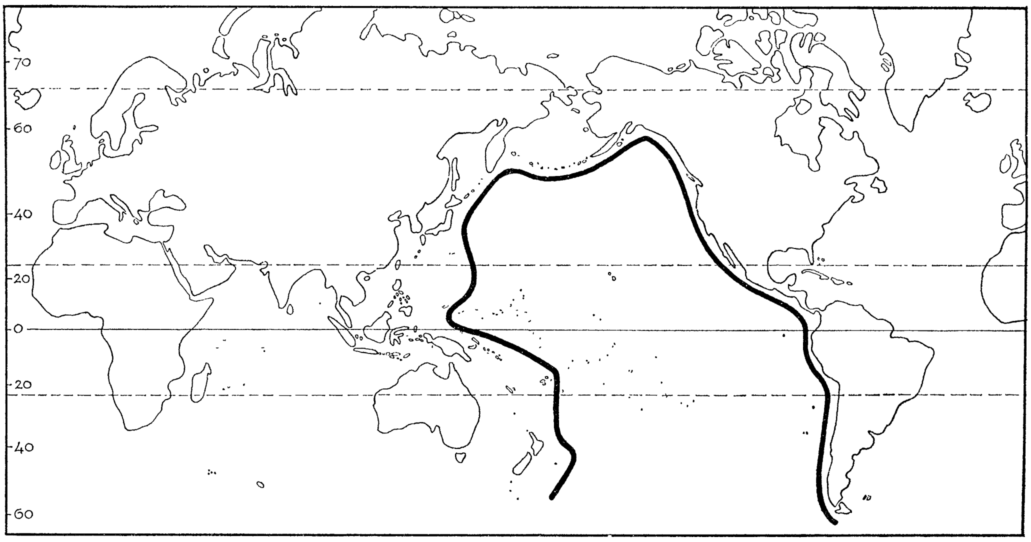

FIGURE 194. The circum-Pacific 'andesite line'.

There is geological evidence to support the suggestion that the Solomons are a continental archipelago lying on a continental shelf, not oceanic islands. The 'andesite line' figure 194, marking the edge of the Pacific basin proper, lies east of the Solomons, whose lavas are of continental rather than oceanic type. In fact the whole of Melanesia lies on the Australian side of the andesite line except Samoa east of Fiji (see, for example, Chubb

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1934). The actual position of the andesite line is somewhere very near the Santa Cruz Islands which lie 352 km east-south-east of the Solomons and whose lavas have recently been analysed and found intermediate to oceanic types (McCall 1965).

The Solomons are a very unstable part of the Earth's crust, witness the frequent earthquakes throughout the islands and the islands' highly volcanic nature. This unstable belt spreads all round the Pacific margin, through Japan and down the seaboard of America. The Coral Sea and New Guinea, west of the Solomons are well away from the margin.

A number of geologists have postulated a Melanesian continent which folded, fractured, and submerged in the Mesozoic or Tertiary, e.g. Chubb (1934) and David (1950). Sea troughs to 9000 m south of the Solomons and the Bismarcks are certainly witness to enormous crustal movements in the geological past of the region.

Coleman (1966) thinks it is premature to discuss the grand tectonics of the Solomons region. He considers the Solomons to be 'an auctochtonous geological system which had its origin in the Mesozoic, probably in Cretaceous time'. He finds that the Solomon block is not sharply demarcated from New Ireland in the Bismarcks to the north west nor from the Ontong Java Platform to the north.

The inference to be made from flowering plant distribution is that there is strong evidence for the existence of more land in Melanesia in the past (cf. Smith's conclusions (1951), etc., resulting from studies on the Fiji flora) but, as amplified below, this might as well have been a close archipelago as a single land mass.

Course of disappearance of the ancient land mass

The composition of the Solomons' flora allows us to make a further deduction about the way this land mass or archipelago might have foundered.

The Subantarctic–Pacific floristic element (Van Balgooy 1960) which is the group with its main distribution over the temperate part of the South Pacific, i.e. southern Australia, New Zealand, the subantarctic islands and temperate South America, is represented in the Solomons by only four genera,* *Belliolum* (Winter.) already discussed, *Dacrydium* (Podocarp.) *Dianella* and *Geitonoplesium* (Liliaceae s.l.). The group is also weakly represented in Fiji. Van Steenis (1962) has altogether 62 genera in this element (which he names South Temperate). *Nothofagus* is the most conspicuous absentee from the Solomons.

The intensive botanical exploration of the last few years since 1962 has failed to reveal any extension of the peculiar endemic New Caledonian flora northwards into the Solomons,* either on the ultrabasics (a major rock formation in New Caledonia) or in the high Kavo mountain range of Guadalcanal, which has a similar cool climate but an overwhelmingly Malesian mountain flora.

These two lines of evidence suggest that the Solomons were very early cut off from invasion from the south; the Antarctic finger, pointing north from New Zealand to the New Guinea mountains, skirts west of the Coral Sea. It is interesting to observe in this connexion that the submarine contours show the Bismarcks and Solomons on a 1800 m tongue

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* Gillett (1967) has recently described *Coronanthera grandis* (Gesneri.) from the Solomons. The genus was previously endemic to New Caledonia. B. L. Burtt tells me that the Solomons' species looks very different from the New Caledonian ones and he considers its place in *Coronanthera* open to question.

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reaching eastwards and southwards from New Guinea with waters exceeding 3600 m deep lying to their south (David 1950, figure 197).

I have already mentioned (p. 261) the absence of the Australian genera *Banksia* (Prote.) and *Eucalyptus* (Myrt.) from the dry savannah forests of north Guadalcanal despite the climatic similarity to parts of New Guinea and Queensland where both grow, also the absence of any rain-forest eucalypt. The implication is that the Solomons were isolated from the north-west before the invasion of these distinctive genera occurred.

Solomons' floristic poverty analysed

A question which arises is why the palaeotropical and Malesian elements, which contribute about 56 % of the genera of the Solomons' flowering plant flora, are weaker in families, genera and species than the source areas to the west?

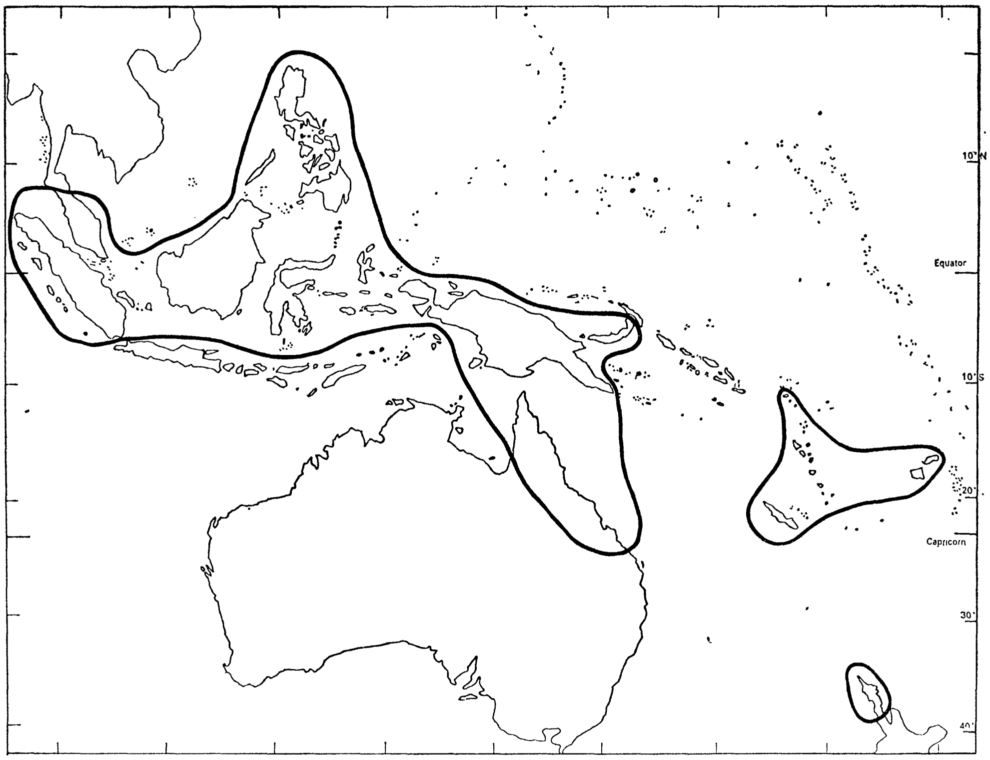

FIGURE 195. *Agathis*. Note absence from Solomons.

Part of the explanation must be historical, plants have migrated eastwards from the source area in Malesia and some have never reached Melanesia, e.g. Dipterocarpaceae. We cannot discount however the possibility of chance extinctions of some groups resulting from the long unstable geological history, continuing to the present day, with continual changes in land/sea boundaries. For example, the conifer genus *Agathis*, demonstrated experimentally by Guppy (1906) and Mirams (1957) to have poor powers of dispersal, grows in New Zealand, Fiji, New Caledonia, New Hebrides and Santa Cruz, Bismarcks, Queensland, New Guinea and westwards to Malaya but not in the Solomons, see figure 195. *Agathis* is an easily recognized big forest tree. The Santa Cruz *Agathis macrophylla* is well known to the Solomon Islanders, many of whom worked for the timber industry

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formerly based on it, and it is now planted by them as a village ornamental. None of them have ever seen *Agathis* wild in the Solomons and no botanist has found it either. Its absence from the Solomons is, I suggest, to be explained as a chance extinction, a failure to hop in time as an island submerged.

In appendix B is given a full list of the 87 genera known from Fiji and/or the New Hebrides and from New Guinea but which have not yet been found in the Solomons. Some of these will probably turn up, the herbs for instance remain relatively under collected. Others are probably genuine absentees, for example *Berrya*, *Grewia* and *Microcos*, small tiliaceous trees of forest fringes which collectors are unlikely to have overlooked. *Santalum*, the sandalwood, is a noteworthy absentee and because of it the Solomons escaped the worst depradations of the nineteenth-century gun-boat traders, though suitable seasonally dry climates exist for it, e.g. on north Guadalcanal.

The Solomons have in all probability been more densely populated in the past. I have already described how the long history of population and cultivation has strongly affected the lowland vegetation (p. 264). Long continuing destruction of the forest may also have led to the extinction of some species, particularly on some of the smaller islands.

Mountain flora and vegetation

I have already described (p. 268) the strong compression of the vegetation belts with increasing elevation and the very marked poverty of the mountain flora, which is weaker even than the lowland flora in Malesian elements.

The present high mountains of the Solomons all date from the late Tertiary or Quaternary; the Kavo range itself is Pliocene or Pleistocene. I suggest that many characteristic New Guinea mountain plants are absent because these mountains arose after contact with the north-west was cut off, and that there were no earlier immigrants on earlier, now eroded, high mountains within range to colonize the new habitats. In short, the Solomons either had no high mountains when in contact with New Guinea or else went through a phase without high mountains after contact was broken, and the present high mountain flora consists of species which had survived at much lower elevations and which moved back to fill the new habitats when they arose in the late Tertiary or Quaternary. Myrtaceae is prominent in the high mountain flora, and there is a mixture of other New Guinea mountain species, e.g. on Popomanaseu *Eurya hellwigii*, *Gahnia javanica*, *Haloragis secunda*, *Hedyotis schlechteri*, *Macaranga lanceolata*, *Polyosma integrifolia*. Very few mountain endemics are known, e.g. the four *Rhododendron* species in the Solomons.

Balbi is part of the Emperor Range, a big mountain block on Bougainville above 1800 m elevation, hence similar in habitat to the Kavo Range; almost nothing is yet known of its flora; perhaps there will be found traces of the missing montane element.

Vertebrate fauna

The poor vertebrate fauna compared with New Guinea implies early isolation, for instance the only marsupial in the Solomons is one species of the most widespread genus, the Australian opossum or cuscus, *Phalanger orientalis*; and of kangaroos, marsupial mice, bandicoots and cats there are none, though several reach as far east as New Britain or New Ireland (Darlington 1947).

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The nature of a land bridge

Extensive plant collecting throughout the Solomon Islands since 1962 has led to the discovery that few species are localized to different regions, instead the islands have a monotonously uniform flora.

Quite a number of genera of flowering plants reach their limits either at the Bismarcks, 176 km from the Solomons; or at the Solomons, 480 km from the New Hebrides. Van Balgooy (1960) worked out that, of the 601 genera growing in the Bismarcks and Solomons, 266, 44 % of the total, only grow in one of the archipelagos not both. He also found that of 572 genera growing in the Solomons or New Hebrides plus Santa Cruz Islands, 342, or 60 %, grow in only one group or the other. Further discoveries have changed these figures in detail but not the presence of clear demarcation knots.

The presence of strong demarcation knots at both ends of the archipelago and the uniform flora within it suggests that the sea distances around the Solomons are effective barriers to dispersal but that the small inter-island distances of 16 to 64 km within the Group are not. This view is strengthened by the further observation that the New Georgia Islands are thought to be entirely of Plio-Pleistocene date (Coleman 1965) and must have been colonized from surrounding islands, yet they show no distinctive floristic features.

I conclude that the Solomon Islands archipelago might well represent an efficient land bridge of the kind postulated by many botanists (e.g. Van Steenis 1962) to explain the indubitable facts of plant distributions into and across the Pacific particularly of the genera in the lowland humid tropics of South America and Malesia–Melanesia already mentioned.

Species evolution in the humid tropics

The Solomons flora may be used as the base for some general inferences on species evolution in the humid tropics. There are several lines of evidence.

(1) There are numerous species in the Solomons whose ranges extend beyond the boundaries of the archipelago, examples have already been given. Investigation of some of these species has, as already stated, shown the same infra-specific variation patterns within the Solomons as in New Guinea.

(2) A few examples are known of pairs or small groups of closely related species with one member in the Solomons and the other in an adjacent region. The tree *Calophyllum cerasiferum* (Solomons and Fiji) has as counterparts on New Guinea mountains the very similar *C. congestiflorum* and *C. pauciflorum* (see figure 196). Small-leafed species of the tree *Weinmannia* (Cunoni.) shows signs of incipient speciation on isolated mountains (Bernardi 1964) but far more collections are needed to be sure. *Palaquium masuui* (Sapot.) of the Solomons lies morphologically and geographically between *P. supfianum* of New Guinea and *P. hornei* of Fiji.

(3) Many genera have had a few Solomons endemic species described. Of course in the absence of a recent monograph the number of species in the Solomons must be accepted with caution and even more so the number considered endemic. A few examples are known, however, where we can state reasonably confidently that there has been considerable evolution in a genus or family within the Solomons. Thus about half of the 230 or so orchid species recorded are endemic. The climbing pandan genus *Freycinetia* has 20 species, 15 of

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them endemic (Stone 1963 and pers. comm.), and *Boerlagiodendron*, the pachycaul araliaceous treelet, has seven species, apparently five of them endemic (Stone 1962); but the considerable number of endemic species described in *Astronidium* and *Medinilla* (Melastom.), *Dolicholobium* and *Hydnophytum* (Rubi.) and *Syzygium* (Myrt.) listed in Whitmore (1966), cannot be accepted without further study.

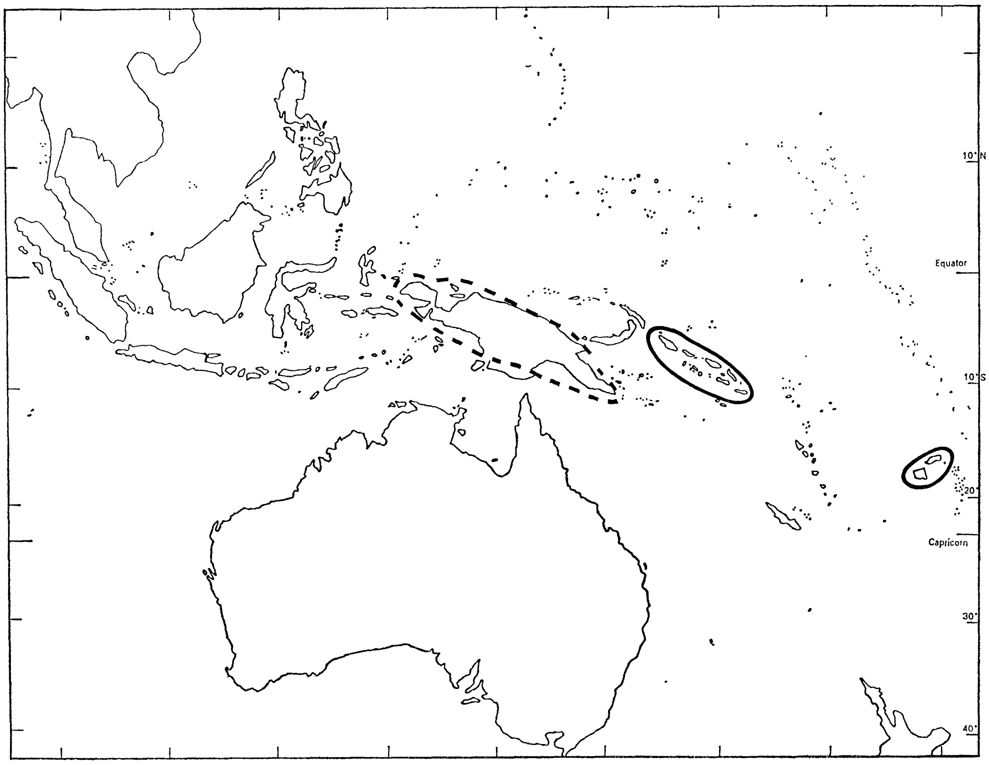

FIGURE 196. *Calophyllum cerasiferum* (solid line) Fiji and Solomons, replaced in New Guinea by *C. congestiflorum and C. pauciflorum* (dashed line).

As far as I know the groups in which considerable species evolution has been demonstrated in the Solomons are all fairly small plants with relatively short-life cycles; none are big, long-lived, forest trees, although the taxonomy of the latter has been closely scrutinized. In each instance the endemic Solomons' species do not all belong to a single taxonomic section of their genus or family, but instead are found a few in each of many sections. No examples are known of long species series evolved from a single ancestral species or group of closely related ancestral species and restricted to the Solomons.

It appears then, from the geographical ranges of different species, that evolution has proceeded at different rates in different groups and, from the evidence at present available, has gone furthest in some of the groups with short life cycles.

(4) It has already been noted that extensive plant collecting throughout the Solomon Islands in the last few years has led to the discovery that few species are localized to different parts of the archipelago, instead the islands have a monotonously uniform flora.* Some of the Solomons' endemic species are localized, for instance the remarkable lateral

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* This situation contrasts strongly with that of many island birds which have, for instance, different races from peak to peak in the New Georgia Islands (Mayr 1945).

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

fruited *Pandanus lamprocephalus* is only known from north-east San Cristobal; but more often these endemics are found all the way from Bougainville to San Cristobal, for instance the pachycaul treelet *Tapeinosperma pachycaulum*.

(5) Not only are the geographical ranges within the Solomons wide for most species but, as described above (p. 268), many species in the archipelago have wide ecological ranges, and I gave the extreme example of *Calophyllum kajewskii* growing on massive coral in brackish water as well as in well-drained inland forest.

These lines of evidence from geographical ranges and ecology of species together point to the conclusion that, considering the whole flowering plant flora, there has not been much evolution in the Solomons since effective contact with Malesia was broken,* which Coleman (1965) considers was in the Pliocene at the latest. In the prevailing circumstances of a poor flora, and consequently not very intense inter-specific competition compared with most tropical rain forests, the response has in many cases been a widening of ecological range, not accompanied by morphological differentiation.

Throughout their geological history and continuing to the present day the Solomon Islands have been subjected to a whole gamut of geological viscissitudes: inundation by the sea, emergence of new land surfaces, and mountain building by crustal movement or volcanic activity. It is perhaps remarkable that these changes have not resulted in more extensive speciation amongst flowering plants. This is to be contrasted with the species evolution in temperate plants, mainly herbs, engendered by strong climatic changes and mass migrations caused by the Pleistocene Ice Ages. It is often suggested (for instance, recently by Takhtajan (1967) in Jeffrey (1968)) that important factors in species evolution have been the splitting up of species into discrete, small, semi-isolated populations and also the availability of new bare land surfaces for colonization. The evidence mainly comes from the study of temperate plants though the generalization is often extended to the tropics (e.g. Federov 1966). These same circumstances must have occurred in the Solomons again and again and, from the evidence at present available, they have not led to the same results. The reasons for the different extents of species evolution in these temperate and tropical situations remain to be discovered. Doubt is cast on the universal working of some of the mechanisms for species evolution which have been proposed, resulting as they do from studies on temperate species, mainly herbs. Much remains to be discovered about evolutionary mechanisms in trees, and herein may lie the clue to the explanation we seek. The Solomon Islands provide an excellent venue for such studies.

In final conclusion we may note that the observed extent of evolutionary change in the Solomon Islands during the late Tertiary and Quaternary makes it seem improbable that the flowering plants as a group can have undergone their major evolution since the Cretaceous when their first fossils appear, unless the evolutionary rate has slowed considerably. When more details are filled in on the geological past of Melanesia, when and where the land connexions likely lay, the region will provide a fine workshop for the study of evolutionary rates. So far we can say that the evidence from the Solomon Islands is that, in the humid tropics, flowering plant evolution has been very slow, even in a region undergoing vigorous, one might almost say dramatic, geological change.

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* Moreover, there are only three endemic genera (see above) and all are only weakly distinct.

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I am grateful to the directors and staff of Kew, Lae and Leiden herbaria, members of the Royal Society Expedition, the Forest Department B.S.I.P., and the several persons mentioned in the text for providing some of the information on which this and my preceeding paper are based; and to my wife for extensive typing assistance.

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Appendix A. Genera of the Solomons with themselves or close relatives found also in lowland tropical South America (from Van Steenis 1962)

	Solomons	both	South America
Araceae		Homalomena Schismatoglottis Spathiphyllum	
	Monstereae 3 gen.		Monstereae 5 gen.
Balanophoraceae		Subfam. Helosioideae	
Celastraceae		Perrottettia	
Cunoniaceae		Weinmannia	
Cyperaceae		Machaerina	
Elaeocarpaceae		Sloanea	
Euphorbiaceae	Aleurites		Hevea
Lauraceae		Cinnamomum Endiandra Litsea	
Leguminosae		Ormosia	
Moraceae	Antiaris		Olmedieae
		Ficus subgen. Pharmacosycea	
Musaceae		Heliconia	
Polygalaceae	Eriandra		Barnhartia Dialidanthera Moutabea
Saurauiaceae		Saurauia	
Simaroubaceae		Picrasma	
Symplocaceae		Symplocos	
Theaceae	Eurya		Frezeria Killipiodendron
Verbenaceae		Callicarpa	

Appendix B. Genera occurring to north-west and south-east of Solomons but so far absent therefrom

Amaryllidaceae: **Eurycles*
Annonaceae: **Oncodostigma*
Araliaceae: *Tieghemopanax*
Araucariaceae: *Agathis*
Asclepiadaceae: *Gymnema*, **Secamone*
Celastraceae: *Celastrus*, *Maytenus*
Compositae: *Centipeda*, *Dichrocephala*, **Glossogyne*, *Keyserria*

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Appendix B. (*cont.*)

Convolvulaceae: *Aniseia*, *Evolvulus*, **Jacquemontia*, *Operculina*
Coriariaceae: *Coriaria*
Cucurbitaceae: *Gymnostemma*
Cuscutaceae: *Cuscuta*
Cyperaceae: *Lepironia*, *Scirpus*
Dilleniaceae: *Hibbertia*
Elatinaceae: *Elatine*
Escalloniaceae: **Quintinia*
Euphorbiaceae: *Austrobuxus*
Gramineae: *Aristida*, *Botriochloa*, *Cymbopogon*, *Erianthus*, *Eriochloa*, *Garnotia*, *Heteropogon*, *Miscanthus*
Labiatae: *Teucrium*
Leguminosae: *Abrus*, *Christia*, *Glycine*, *Rhynchosia*, *Sesbania*
Lemnaceae: *Lemna*
Limnanthaceae; *Nymphoides*
Lobeliaceae: *Lobelia*
Loranthaceae: *Korthalsella*
Melastomataceae: *Allomorpha*
Menispermaceae: *Pachygone*
Moraceae: *Malaisia*
Myoporaceae: **Myoporum*
Myrsinaceae: *Embelia*
Myrtaceae: *Cleistocalyx*, *Tristania*
Ochnaceae: *Brackenridgea*
Orchidaceae: *Acanthephippium*, *Anoectochilus*, *Cheirostylis*, *Didymoplexis*, *Earina*, **Epipogon*, **Gastrodia*, *Microtatorchis*, **Moehrenhoutia*, **Spiranthes*, *Vanilla*
Potamogetonaceae: *Halodule*, *Ruppia*
Primulaceae: **Lysimachia*
Rhamnaceae: *Dallachya*, *Ventilago*
Rubiaceae: *Airosperma*, *Antirrhoea*, *Coprosma*, *Xanthophytum*
Rutaceae: *Acronychia*
Santalaceae: *Exocarpus*, *Santalum*
Sapindaceae: *Alectyron*, *Dodonaea*, *Elatostachys*, **Euphorianthus*
Sapotaceae: *Manikara*
Simaroubaceae: *Suriana*
Tiliaceae: *Berrya*, *Grewia*, *Microcos*
Triuridaceae: *Andruris*
Umbelliferae: **Trachymene*
Vacciniaceae: *Agapetes*
Violaceae: **Hybanthus*

* Genera found in New Guinea and New Hebrides. All the rest are New Guinea and Fiji, and sometimes New Hebrides too.