Some Phytogeographical Relationships of the Angiosperm Flora of the British Solomon Islands Protectorate: Introduction

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DISCUSSION

Introduction

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The importance of the zoological collection made during the Royal Society Expedition to the Solomon Islands will only become evident when more detailed studies of the specimens have been published. The papers presented during this discussion meeting have provided an indication of the information that will then be available on a wide variety of taxa. The large collections must be considered in conjunction with the results obtained by other expeditions, particularly those organized to many Pacific Islands by the Entomological and Malacological departments of the Bernice P. Bishop Museum, Hawaii, and by the Copenhagen Museum to Rennell and other islands in Melanesia. It is to be hoped that all these investigations will benefit from the cross fertilization of information.

In the studies reported in this section of the meeting various distribution patterns have been demonstrated or suggested. These must reflect:

(1) The density and extent of collecting.

(2) The varying degrees of sophistication of taxonomic studies on the particular groups discussed.

(3) Biological attributes of the taxa and the history of the area considered. In spite of the limitations imposed by the first two factors attempts must be made to analyse the available information and weight given to those areas of general agreement, although discrepancies will arise in the consideration of individual examples.

All the papers have been concerned with the origin of distribution patterns, that have arisen in the Solomon Islands during the Tertiary and Quaternary. Speculation on the age of the taxa involved presents a further problem. Unfortunately a considerable body of the geological and biological data pertaining to these investigations, is open to various interpretations and therefore cannot be considered conclusive. In this context I would like to quote a pertinent extract from the concluding remarks of Mayr (1952) to another discussion meeting.

'First of all, it is now universally realized that zoogeographical conclusions must be based on biological (including paleontological) evidence, and geological conclusions on geological evidence in order to avoid circular reasoning (Rensch 1936). Subsequently, the independent conclusions of both fields must be compared to see whether or not they are in agreement. If several solutions are equally probable according to the evidence of one field, the one should be favored that is most probable according to the evidence of the other field.

'Furthermore, the shortcomings of each field must be clearly realized.'

It is important that hypotheses generated in any discussion relating to biogeography should agree with all available information and if possible be formulated in a manner

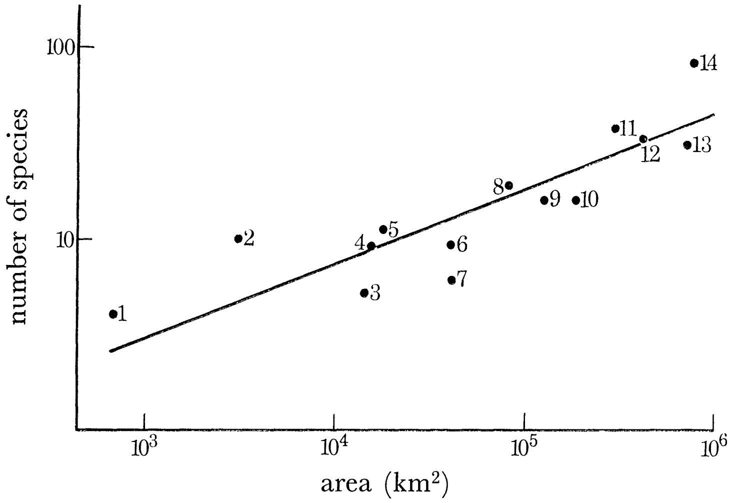

FIGURE 197. The relationship between island area and the numbers of species of *Cyathea*:

1 Tonga
2 Samoa
3 New Hebrides
4 New Caledonia
5 Fiji
6 Solomons
7 Bismarcks
8 Moluccas
9 Java
10 Celebes
11 Philippines
12 Sumatra
13 Borneo
14 New Guinea

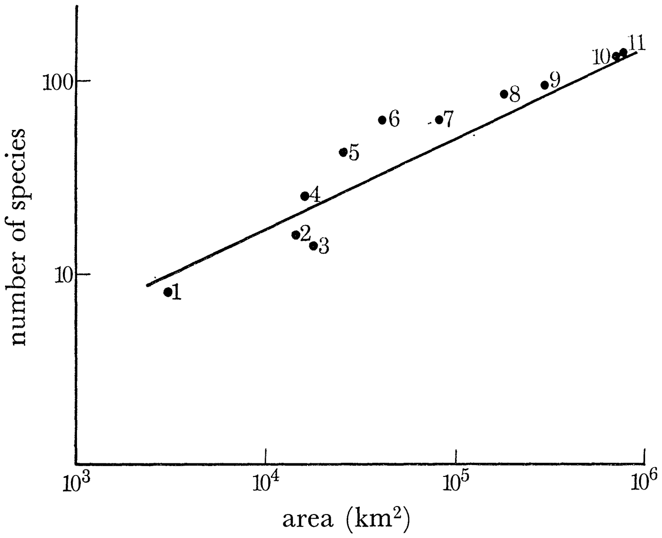

FIGURE 198. The relationship between island area and the numbers of species of *Ficus*:

1 Samoa
2 New Ireland
3 New Caledonia
4 Fiji
5 New Britain
6 Solomons
7 Moluccas
8 Celebes
9 Philippines
10 Borneo
11 New Guinea

suggesting further methods of investigation and analysis. Such an approach has been generated by the work of MacArthur & Wilson (1963, 1967), commencing with the species area relationship and progressing to the Equilibrium models and theory. It is these ideas that have been the basis for various analyses of the fauna produced in this meeting. These concepts are not confined, however, to analyses of faunal relationships, but have wider implications. Figures 197 and 198 demonstrate species–area relationships for two genera of plants and emphasize the difficulties involved in comparing islands of different sizes; data for these graphs being obtained from Corner (1967) and Holtum (1963, 1964). On the basis of these correlations the species representation of the two genera may be considered saturated on these islands plotted in the graphs.

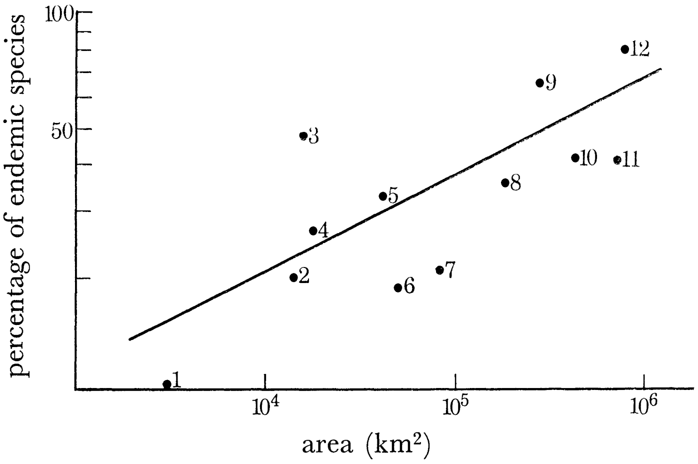

Figure 199. Percentage of endemic species of *Cyathea* plotted against island area on a double logarithmic scale:

1	Samoa	5	Solomons	9	Philippines
2	New Hebrides	6	Bismarcks	10	Sumatra
3	New Caledonia	7	Moluccas	11	Borneo
4	Fiji	8	Celebes	12	New Guinea

A more speculative approach is indicated in a recent note by Mayr (1965) regarding the 'turnover' of the avifauna on islands. The basis for his suggestions is the rise in the percentage of endemic species of birds with increase in island area; this relationship probably being due to continual extinction of species on islands at a much higher rate than hitherto suggested. On the smaller islands the rate of extinction being faster than on the larger more diverse land masses. Unfortunately the information available for many groups of invertebrates is inadequate for this type of analysis, but the data for *Ficus* and *Cyathea* are satisfactory. When the data are plotted on a double logarithmic scale a correlation between island area and the percentage of endemic species of *Cyathea* exists, similar to that recorded for the avifauna (figure 199). The absence of endemicity in Java does, however, provide an anomaly. No comparable relationship can be demonstrated for *Ficus*, but examination of the data suggests that the highest degree of endemicity occurs on the more isolated islands, for example Fiji, Samoa and New Caledonia indicating that isolation might be a more important factor in this genus. The biological interpretations of these relationships is open to discussion, but undoubtedly the extinction rates and dispersal properties of the taxa are extremely important in effecting both the distribution and speciation patterns. *Cyathea* has small spores that are probably widely dispersed, and this contrasts sharply with the more limited powers of *Ficus* species. Similar variations in the potential for dispersal exist amongst invertebrate taxa, for example molluscs and ants, and at least certain differences in the patterns of speciation can be attributed to such differences. These type of analyses provide important avenues for future discussion and consideration.

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R. J. A. W. Lever (*Commonwealth Institute of Entomology*)

I would draw attention to the active speciation at the subspecific level in the New Georgia group occurring in the weevil *Exophthalmida caerulescens* Gunther. The typical form *C. caerulescens* Mshl., is present on Vella Lavella with *c. ganongae* Mshl. on Ganonga and Gizo with *c. kolombangarae* Mshl. on Kolombangara. (As a matter of interest a similar evolutionary position occurs among birds, the white eye *Zosterops rendovae*, also having different subspecies in the various islands.)

Two other species of *Exophthalmida* occur on the small islands of Savo and Santa Ana, viz. *E. savona* Mshl. and *E. santanae* Mshl. respectively. Somewhat unexpectedly, no specimens of this genus appear to have been taken on any of the main islands of the Solomons. The easternmost of the main islands, San Cristobal, provides a good example of a thinning out of mammals, birds and insects as described in 1936 (*Proc. Linn. Soc.* **148** (2), 82–83). Owing to its still more isolated position, the Santa Cruz group has not only a similarly impoverished fauna, but shows a closer affinity with the New Hebrides than with the Solomons. This is well seen in two widely separated orders of insect pests, the hispid *Promecotheca opacicollis* Gestro and the coreid *Mictis profana*, the latter extending as far east as Samoa but not present in the main Solomon archipelago.

Mention having been made by some speakers of the possibility of another expedition to these islands, it might be found worth while to carry out some ecological study in a specially selected habitat. This was attempted on the grass plains of Guadalcanal (*J. Anim. Ecol.* **6** (2), 291–297, 1937) with the lowest rainfall in the Solomon Islands, over 100 species of insects being collected in an area dominated by the grasses *Themeda australis* and *Imperata cylindrica*.

T. C. Whitmore

Greenslade and Peake's papers attempt to describe the size and composition of the Solomon Islands' fauna in terms of a mathematical theory of biogeography developed by zoogeographers (e.g. MacArthur & Wilson, *The Island Theory of Biogeography*, Princeton, 1967).

Peake confined his remarks to the snails, which are known mainly as a result of his own work during $5\frac{1}{2}$ months at scattered localities along the archipelago.

Greenslade spoke of insects and birds. He chose a few groups of insects selected because he considered collecting of them had been adequate, but was able to consider also the whole avifauna, as the birds of the Solomons are well known.

Cain's paper, however, attempted to show that bird zoogeography is open to several alternative explanations.

Most botanists would probably not wish to deny that in certain circumstances the theory and its explanation of size–area relationships and species replacements can occur. At present, however, the evidence for it in the Solomons remains very slender. Further it is unlikely that the same theory can be applied to plants as animals without modification because of the major differences in population structure and dynamics. Many plants (and cetainly woody ones) persist many years without the necessity to reproduce, so they can out-ride temporary unfavourable fluctuations in the environment, which may have drastic selective effects on short-lived organisms such as insects or birds. The old plants live alongside their progeny with the possibility of crossing, so genetic stability is enhanced. Some trees live several hundred years.

Any theory of plant geography has to explain the five features of the flora outlined in my paper, which were exemplified and expanded by the other botanists (Braithwaite, Corner, Good and Hunt), and are based on fairly complete knowledge of the floras of New Guinea and all the Melanesian archipelagos except New Hebrides.

The Island Theory of Biogeography has not yet been demonstrated adequately, and the most encountered hypothesis to account for the existing conditions in Melanesian plant geography remains that there were more land connexions in the past, although how these lay is a detail undecided. There is no need for stronger wording. Concerning the graphs of flora size against island area, the islands lie from west to east. The diminishing flora eastwards into the Pacific may depend on the distance from source, and any apparent correlation with area may be fortuitous. Actually we have to explain not just the distribution patterns of a few species but of whole floras. If chance dispersal operated, species distributions would be at random and one would not find whole groups of species with identical ranges. As a striking example, 2400 of the 2600 species growing in New Caledonia are endemic; although the island lies in a cyclone belt, none of these species has been found in the nearby Solomons, New Hebrides, or Fiji archipelagos. Then, in as striking contrast by their extended range, several kinds of plant, such as *Sararanga*, and some birds and butterflies are distributed from the Solomons through the Bismarcks, along the north coast of New Guinea or offshore islands to the Philippines.

One may recall that 15 years ago geophysicists refused to countenance continental drift despite strong biogeographical evidence. In the present case it is the botanists who have the evidence and need to stand firm. The distribution of flowering plants demands a historical explanation in the former existence of a greater Melanesia. Studies of regional geology are incomplete and of the sea bottom almost non-existent, though they have been started.

Before the issue can be advanced or decided we await on the one hand more geological data, and on the other hand a fuller knowledge of the Solomon Islands fauna.

P. S. Ashton (*Department of Botany, University of Aberdeen*)

I have two questions to raise concerning Dr Whitmore's papers. The relative floristic poverty of the Solomons forests suggests a less evolved forest ecosystem than that of Malaya. Would this not imply less stringent competition and hence the broader ecological ranges? Could the lower density of individuals in Solomons forests, compared with those in Malaya, also be explained in the same way? If the ecosystem were less evolved, many niches would remain unexploited and production per unit area, of which forest density is a manifestation, would be lower. On the other hand, forests in all climates tend to be denser but of smaller stature on poor soils, and less dense (though of taller stature) on fertile soils. The preponderance of basalts and other basic rocks in the Solomons may provide more fertile soils than in Malaya.

In contrast with Professor Cain's comments on the evidence in support of climatic changes during the Pleistocene in tropical Africa, I would point out that oil company palynologists have confirmed the great stability, at least in North Borneo, of the climate of south-east Asia since the mid-tertiary.

B. L. Burtt (*Royal Botanic Gardens, Edinburgh*)

Results of studying the Expedition's Gesneriaceae fall into line with much that has been said already about the uniformity of the flora. The genus *Cyrtandra* is particularly instructive as it is richly developed both in Malesia and in the Pacific (though absent from New Caledonia), and has a great reputation for local endemism. There are about 15 species in the Solomons: one, found in the more easterly islands, also occurs in Santa Cruz and the New Hebrides; the remainder are endemic to the group, some having their closest affinities to the west, others to the east. Within the Solomons the same species are found on a number of different islands. [For example, *Cyrtandra filibracteata* is already known from Bougainville, Choiseul, Bagga, Kolombangara, New Georgia, Santa Isabel and Guadalcanal.] This distribution through the islands is in striking contrast to the position in Fiji where 22 out of 35 species are restricted to a single island in this very compact archipelago.

The frequent glib comparisons that we have heard between the Solomon Islands and New Guinea, as though they were equivalent regions, are dangerous. [Lippincott's gazetteer gives the area of New Guinea as 304200 square miles, that of the Solomon Islands as 16000.] There are greater differences between the floras of north-eastern and south-western New Guinea than are found through the Solomons. As exemplified by Gesneriaceae the Solomon Islands behave as a small land-mass with few internal barriers: Fiji behaves as an oceanic archipelago with much insular endemism: New Guinea behaves as a continental land-mass with considerable internal barriers and much internal differentiation.

Years ago, when working on the early Waterhouse collections from Bougainville, I noted (*Kew Bull.* 1935, pp. 298–306; 1936, pp. 459–466) some plants seeming to have affinity directly with those of the Philippines rather than through the species of the mainland of New Guinea. These species need re-examination in the light of the recent additions to our knowledge of these floras, but if the assessment holds it is of interest and perhaps relevant to the absence from the Solomons of a marked Australian element. The westward floristic relations may be along the northern fringe of New Guinea. In any case we need to know whether the Solomon Islands' species in New Guinea are found in the areas where the Australian element is well developed.

C. Jeffrey (*Royal Botanic Gardens, Kew*)

A comparison of the Solomons flora with that of the Seychelles may be of interest. The latter shows all the features of the Solomons flora—the comparatively small size, the comparatively few species in each genus, a moderate endemism, the compression of altitudinal belts and the widening of the ecological tolerance of species—but to a much more marked degree. For example, the Seychelles flora has about 300 indigenous higher plant species, compared with some 1750 for the Solomons, both being tropical rain-forest areas. This is no doubt due largely to the much smaller total land-area of the Seychelles archipelago. This indicates that the similarity in these floristic features of the two areas is largely a result of the fact that they are both island groups, probably with similar geological histories. The peculiarities of the Seychelles flora and its geographical affinities are consistent with the hypothesis that the Seychelles bank represents a continental area comparative to the ancient blocks of India, Africa, Madagascar and Australia, and that the floras of all had a common source, from which they have diverged subsequent to the splitting-up of the Gondwana continent. In Permian times, it is probable that the Seychelles were part of a land-locked area lying between Madagascar, Ceylon, Borneo and Eastern Antarctica. The Seychelles flora (apart from its strand-flora elements), seems to be one that has evolved *in situ* and is no doubt a remnant of an originally much richer vegetation which has throughout its history formed closed communities on a land-area constantly being reduced by denudation and marine erosion. The inland endemics of the islands (of which *Lodoicea* is the most striking) are not, and could never have been, capable of dispersal across large oceanic distances, and only the strand flora seems to have reached the islands in this way.

The Solomons (unlike the Seychelles) have been subjected to considerable volcanic and tectonic activity, by which old land surfaces have disappeared and new ones formed. Nevertheless, new land areas have probably always been formed near enough to those already present for the Solomons to be regarded as also having had throughout their history a vegetation forming closed communities in which competition, marine erosion and tectonic subsidence have all contributed to keeping the flora numerically small. This too can be regarded as an ancient flora that has largely evolved *in situ*. Its geographical affinities are consistent with the hypothesis that in pre-Cretaceous times the proto-Solomons formed a land-area or archipelago inclusive also of the fore-runners of the present Celebes, northern New Guinea, New Britain, the New Hebrides and Fiji, which was probably situated at about where the Line Islands are now found.

P. S. Green (*Royal Botanic Gardens, Kew*)

Dr Lee's descriptions of the two main types of vegetation on the ultrabasic rocks of the Solomon Islands have been of particular interest to me because of their contrast with my own observations on the vegetation growing on similar but more extensive rocks in New Caledonia. Having worked on the floras of both New Caledonia and the Solomon Islands, I had come to realize from personal experience, as well as from the remarks of others, how little floristic affinity there is between the two sets of islands; yet, with the plants of the ultrabasic rocks which make the outstandingly unique element in the New Caledonia flora, I have wondered how it is that none of these characteristic New Caledonia plants are to be found on the Solomon Islands. Dr Lee has described how the undisturbed vegetation overlying the rocks in the Solomon Islands is a closed community and this contrasts with the situation in New Caledonia where over most of the area the vegetation is an open 'maquis'. This I think must be due in part to the lower rainfall in New Caledonia where, on the ultrabasic rocks, one has to go to the upper slopes of the higher mountains to meet with dense closed forest. Furthermore, we have heard that in the Solomon Islands one gets large nodular lateritic concretions only where vegetation has been burned and an open community of plants established. In New Caledonia one finds extensive, even more abundant, lateritic concretions and an open community, but in this case, by contrast, it is a naturally occurring one with many endemics, e.g. the remarkable monotypic fern genus *Stromatopteris*, adapted to this normally inhospitable 'soil'. On the ultrabasic rocks of both the Solomon Islands and New Caledonia it is interesting to find, wherever the plant cover has been burnt, the development of extensive areas of almost impenetrable *Gleichenia*.

If I may I should like to make one observation on Dr Thorne's valuable paper. It concerns the so-called *Melaleuca* savanna. One would like to know more about the origin of this community, for in the field it has every appearance of being anthropogenic and, except perhaps on the strongest ultrabasic soils, is, I believe, gradually encroaching on the surrounding natural vegetation in all parts of the island. Unintelligent burning is a great danger to the unique plant cover in New Caledonia, almost as great perhaps as the danger from the encroachment of mining, even in the remoter areas in the northern parts of the island. I suspect that either this savanna-like community, dominated by *Melaleuca quinquenervia* (Cav.) S. T. Blake, is not a naturally occurring and indigenous one or else, before the arrival of man, it was restricted to relatively small areas of somewhat limited topographic or edaphic conditions.

Dr Whitmore has mentioned *Heliconia*. This is a remarkable plant and one would like to know more about the variation in size and position of the inflorescence in different stages of growth, both of the inflorescence itself and the plant. The studies I have been able to make on the valuable dried and pickled material brought back by the Expedition, together with all the specimens from the Old World in the herbaria of Kew and the British Museum, has led me to conclude that one single native species is involved, for which the oldest name is *H. indica* Lam. In the past it has been suggested that *Heliconia* had been introduced from the New World but I am sure that this one species is native with a distribution from the Moluccas in the west, across the Pacific Islands as far as Samoa, occurring also in New

Guinea, New Britain, Solomon Islands, New Hebrides, New Caledonia and Fiji, and providing an excellent example of the Melanesian element in the Solomon Islands flora.

Frances M. Jarrett (*Royal Botanic Gardens, Kew*)

Floristic work being carried out at Kew led me to make a comparison between the fern floras of the Solomon Islands (including Bougainville and excluding the Santa Cruz Islands) and East Tropical Africa. This shows that they are remarkably similar both in the number of species, which is rather over and rather under 300 respectively, and in the species to genus ratio, which is about three and equals that shown by Professor Good for the flowering plants of the Solomon Islands. The areas involved are widely disparate, as East Africa has about fifty times the land area of the Solomon Islands, and yet both floras can also be conisdered as depauperate. The impoverishment of the pteridophytic flora of Africa extends to the entire continent—in the whole of tropical Africa there are probably about 500 species (the number found in Malaya)—and this may be attributed largely to climatic factors, including wide fluctuations in the past and restricted availability of habitats in the present. The Solomon Islands, on the other hand, are adjacent to the very rich fern flora of New Guinea, and Dr Whitmore has emphasized the luxuriant growth of Pteridophyta on the islands. The uniformity and lack of endemism in the fern flora which we have found in determining the material collected on this expedition and previously, as brought out by Dr Braithwaite, are therefore unexpected. They may again be attributed mainly to an extreme of climate, in this case of wetness.

Finally, it may be noted that, although differentiation of the fern floras of neighbouring areas is often difficult, with two such widely separated regions distinctions do appear. In the Polypodiaceae (*sensu stricto*), for example, there are three genera found in Africa, but not in the Solomons, while eight genera in the Solomons (mainly rain-forest epiphytes) do not reach Africa. Six genera are common to both. Local speciation also occurs in different taxonomic groups. In Africa as a whole it is more frequent, as might be expected in the much larger area with a longer history of isolation, but if rain-forest types alone are considered, local evolution is shown by different genera. In Africa examples are *Blotiella* Tryon (*Lonchitis* auct.), *Ctenitis* C. Chr. and *Lomariopsis* Fée, whereas in the Solomon Islands *Tectaria* Cav. can be said to be the only genus to show a significant degree of local speciation.

R. Melville (*Royal Botanic Gardens, Kew*)

I have recently been examining Guppy's (1906) account of plant dispersal in the Pacific region. His observations were made mainly in Hawaii and Fiji, but extended also to the Solomons. Guppy found that about 10 % of the total floras of these island groups could be accounted for by dispersal by ocean currents. In this category come many well-known littoral plants such as *Ipomoea pes-caprae*, *Calophyllum inophyllum*, *Canavalia sericea* and *Sophora tomentosa*, all of which possess seeds capable of floating for months in sea water without losing their capacity to germinate. About 10 % more, Guppy claims, are dispersed by birds. In this group are many plants having fleshy fruits with woody endocarps or testas and a few like *Pisonia grandis* which have viscous secretions by which they adhere tenaciously to the bodies of birds. The total of 20 % thus accounted for is probably over estimated and it provides no explanation for the existence of the greater part of these island floras.

Island hopping along former island arcs and migration along land bridges have been invoked to account for modern plant distributions. The recent landbridge theory of van Steenis (1962) would require a series of isthmuses to span the Pacific from west to east. No geophysical mechanism is known that could temporarily raise the ocean floor over such vast distances to comply with this theory. It is much more probable that the true explanation is to be found in continental drift. In my own study of this problem I took into account several geophysical lines of evidence as well as the distribution of Permo-carboniferous floras. From this I was led to the conclusion, that from the late Paleozoic and through a large part of the Mesozoic, a continent existed in the Pacific centred over the present mid-ocean rise known as the Darwin Rise. The absence of any deposits older than Cretaceous in the North Pacific basin, except for a small area in the north near the Aleutians, suggests that the North Pacific continent was disrupted early in the Cretaceous, perhaps contemporaneously with the break up of the Atlantic continent. As in the Atlantic continent, the Carboniferous coal flora was cut in half one part remaining in Western Europe and the other in Eastern North America, so when the Pacific continent was severed the two portions of the Permo-carboniferous cathaysian (*Gigantopteris*) flora were drifted apart and are now found in China and Western North America on either side of the present Pacific ocean.

In the south Pacific there is evidence for a smaller continent contemporaneous with the North Pacific continent. This consisted of the submerged platform on which now stands New Zealand, New Caledonia, Fiji and Samoa, united with Peru, Chile and Western Antarctica. It was centred over the south-east Pacific rise and from the circumstance that in the south-east Pacific there are no deposits older than Tertiary, was probably disrupted at the end of the Cretaceous or in the Palaeocene.

If the convection theory of continental drift is accepted, many puzzling plant and animal distributions can be accounted for. The theory requires a rising convection current along the line of the Darwin Rise. This would have raised up a mountain range through the centre of the continent to a height which has been estimated at 3 to 4 km. The rise must have extended far enough to the south to bridge the strait between the northern and southern Pacific continents in the Triassic. Early angiosperms were then able to migrate northwards from their southern home-land. At this period, or later when drifting was taking place, connexions were made between New Zealand, New Caledonia, New Guinea and North Borneo. In my original reconstruction of the Mesozoic continents (Melville 1966) the whole of Borneo was placed to the south, but geological evidence more recently coming under my notice indicates a discontinuity across the island in line with the Sunda shelf. South of this line the rivers contain freshwater fish related to those of Javan and Sumatran rivers, whereas to the north the relationships are with Celebes.

The connexions indicated account for plant distributions linking New Zealand and parts of South America with New Caledonia, New Guinea and Borneo. At the time when these regions were linked, the Solomons did not exist and so did not participate in the early migrations. Geological evidence, as mentioned earlier in this Symposium, indicates a relatively late origin for the Solomons, which probably came into existence as a result of crustal folding in the later stages of the drift process, with its accompanied volcanism. The complex folding which took place between Indonesia, New Guinea and the Philippines must have resulted in connexions (land-bridges) being made between Java and Sumatra to Borneo, Borneo to the Philippines and Celebes and Celebes and the Philippines to New Guinea and on to the Solomons. With the release of pressure and by isostatic readjustments the links were broken, but not before considerable plant and animal migration had taken place. It thus appears that the major portion of these island floras reached their present stations over land connexions and that island hopping, whether by wind, sea currents or birds, played a very minor part in the process.

(Professor Corner asked for some of the botanical evidence.)

Many examples might be given of plant distributions linking the island groups of the East Indies and New Guinea with New Caledonia, New Zealand and with Chile or Peru. Others link New Zealand and South America with North America and China and Japan. *Coriaria*, for example, has its main concentration in New Zealand with species in Fiji, Chile, Peru, China and Japan, the Himalaya and an outlier in the western Mediterranean. The section *Psychrophila* of *Caltha* (Ranunculaceae) is confined to the southern hermisphere with sister species in Australia and South America and in New Zealand and South America. The interrelationships within the group can only have developed within one land-mass and are not compatible with transoceanic dispersal. *Populago*, the other section of *Caltha*, is dispersed across the Northern Hemisphere. Its least advanced member bearing the greatest resemblance to section *Psychrophila* is in U.S.A., while the pan-boreal *Caltha palustris* complex is most advanced and genetically complex. Within the genus, as a whole, the interrelationships are consistent with an origin in the former South Pacific continent and migration along the North Pacific continent with dispersal overland and diversification in the Northern Hemisphere after drift had occurred. A similar picture is given by *Euphrasia* (Scrophulariaceae) (Du Rietz 1960).

The southern Beeches, *Nothofagus* (Fagaceae) occur in New Guinea, New Britain, New Caledonia, New Zealand and South America and are known as fossils from Western Antarctica. The nuts are heavy and sink in water. They are soon killed by sea water and are not adapted for dispersal by birds. Nevertheless, sister species and groups of species are found on either side of the Pacific, for example *N. gunnii* in Tasmania and *N. pumilio* in Chile. The least advanced members of the genus are in Chile, where *N. alessandri* has the most primitive cupule type and also most characters in common with *Fagus* of the Northern Hemisphere. It is probable that *Fagus* and *N. alessandri* diverged from a common ancestor, *Fagus*, subsequently migrating northwards along the mountains of the North Pacific continent. Diversification of *Nothofagus* took place in the Southern Hemisphere and morphoclines can be distinguished within the genus in leaf, stipule, cupule, nutlet, perianth and staminal characters. Geographically, the less advanced ends of these morphoclines are found in Chile and intermediate states in New Zealand and Australia. Phylogenetic relationships link New Caledonian species to *N. solandri* in New Zealand and specialization along the morphoclines progresses from New Zealand to New Caledonia to reach a climax in New Guinea, where the female inflorescence is reduced to a single naked nutlet. Within the *Fagaceae*, parallel evolution with a similar climax has been described by Forman (1966) in *Lithocarpus* and *Castanopsis*.

Similar distribution patterns occur in *Oreomyrrhis* (Umbelliferae), *Lagenophora* (Compositae) and there are many others with varying degrees of completeness. *Nertera* (Rubiaceae) extends also to Hawaii, but the genera of the Lardizabalaceae are confined to Japan, China and the Himalaya in Asia and to Chile in South America, without any intermediate stations. A cursory examination of some of the literature reveals many animal groups with trans-pacific distributions, but in the past zoologists have not considered the possibility of a former migration path through the central Pacific and the evidence needs re-examination. The detailed study of the phylogeny and distribution of the chironomid midges by Brundin (1966) has established a distribution pattern exactly comparable with those of *Nothofagus* and *Caltha*. The complexities of their relationships would require so many migrations to and fro across the South Pacific to explain them, that trans-oceanic dispersal is highly improbable. On the other hand, the break up of a single landmass followed by drift can account completely for the biological and distributional data.

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