

NOTHOFAGUS, KEY GENUS OF PLANT GEOGRAPHY, IN TIME AND SPACE, LIVING AND FOSSIL, ECOLOGY AND PHYLOGENY

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SUMMARY

Data are given on the taxonomy and ecology of the genus.

Some New Caledonian species grow in or descend to the lowland. Details are provided on the distribution within New Guinea. For dominance of *Nothofagus*, and *Fagaceae* in general, it is suggested that possibly symbionts may contribute to this. Some notes are made on regeneration and germination in New Guinea.

A special chapter is devoted to a discussion of dispersal which appears to be extremely slow, with the implication that *Nothofagus* indubitably needs land for its spread, and has needed such for attaining its colossal range, encircling onwards of New Guinea the South Pacific (fossil pollen in Antarctica) to as far as southern South America. Map I.

An other chapter is devoted to response of *Nothofagus* to the present climate. The possibility is envisaged that it could have grown along the border of the Antarctic Continent during a milder climate in the Cretaceous and Tertiary.

The fossil record is ample, both by macrofossils and fossil pollen. Of the three pollen types, the *brassii* and *fusca* types are already found in the Upper Cretaceous in Australia, New Zealand, and Antarctica, and in the Eocene in Fuegia the *menziesii* type being found hitherto not earlier than the Lower Tertiary. Table I.

No reliable *Nothofagus* fossils have ever been found on the northern hemisphere. There it is represented by its counterpart, *Fagus*, with which it forms the subfamily *Fagoideae* of the family *Fagaceae*. Macrofossils of *Fagus* are known from the Tertiary and possibly also from the Upper Cretaceous (on the northern hemisphere to a fairly high latitude. Map I.

Nothofagus is called a key genus for plant-geography because it meets the three criteria for safe biogeographical reasoning, viz. it has a sound taxonomy, an ample fossil record, and diaspores for which long distance dispersal is excluded.

Fagoideae occupy a remarkable hour-glass-shaped bi-hemispheric range, with the contraction in the Malasian tropics. Map I. Whereas even at present the largest amount of morphological diversity of *Fagaceae*

in the world is found in Malesia (*Lithocarpus*: various sections, *Quercus*, *Castanopsis*, *Trigonobalanus*, and *Nothofagus*), with *Castanea* and *Fagus* in the Sino-Himalaya, it is likely that the cradle of *Fagoideae* was somewhere in the region stretching from Yunnan to Queensland. It is reasonable to assume that from this initial pre-Upper Cretaceous Fagaceous matrix *Fagus* emerged in the northern part and *Nothofagus* in the southern part, for which Queensland looks the most likely.

It is shown that the evolution and spread of *Nothofagus* can be explained in an unforced way under the steady state principle, which implicates that certain oceanic areas in the South Pacific have been land in the Cretaceous or Early Tertiary.

This north-south bi-hemisphere pattern of distribution is found in many groups, sometimes in the rank of family, sometimes in the lower rank of genus or even in rare cases of species. Ranges may be almost intact in the tropical-montane zone, as happens to be in *Euphrasia* which possesses a range almost replicating that of *Fagoideae*. Map 2. In others the tropical transition relicts are very rare or even absent. The rare ones are sometimes taxonomically highly interesting by being systematically isolated and showing unusual characters.

It is advocated that the tropical montane representatives of this pattern of distribution have gained their range synchronously or almost so, as the series of opportunities enabling such ranges to develop is supposed to have happened only 'once' in geological time. This implies that taxa belonging to 'morphologically advanced' groups are of greater antiquity than formerly often supposed.

The main conclusions have been framed in a number of theses (Chapter 13).

I. INTRODUCTION

A few words of introduction for those who have no ready access to my monograph (van Steenis, 1953) and subsequent notes (van Steenis, 1953a, 1954, 1955).

Southern beeches range (van Steenis & van Balgooy, 1966) in the southern half of the Pacific in South America from *c.* 33° S southwards to *c.* 55° S, and occur further in New Zealand, Tasmania, East Australia, New Caledonia, and New Guinea (incl. the d'Entrecasteaux Islands Goodenough and Normanby, and New Britain).

There is the leaf-shedding section *Nothofagus* (7 or 8 spp.) which is confined to South America except for the Tasmanian *N. gunnii* (Hk. f.) Oerst.

The evergreen section *Calusparassus* (*c.* 28 spp.) is, 3 South American species excepted, confined to the Old World. Within this section the 21 Papuan—New Caledonian species occupy a special taxonomic position in that they are characterized by 2-valved cupules¹⁾ and are therefore accommodated in a special subsection *Bipartitae*. This comprises a series *Triflorae*, with 4 species in New Guinea and 4 in New Caledonia, in which the cupule contains 3 nuts, the others belonging to series *Uniflorae* in which the cupule has 1 female flower, hence 1 nut.

Baumann-Bodenheim (1953), who referred the New Caledonian species to a separate genus *Trisyngyne*, stated that all New Caledonian species have 3 female flowers per cupule, but this has turned out to be an erroneous generalisation: *N. aequilateralis* and *N. codonandra* indeed have 3, but at least *N. discoidea* has only 1 female flower per cupule.

The affinities of the species within sect. *Bipartitae* run, however, across the distinction of these two series showing that this systematic division is artificial and should be abandoned. Morphologically, the presence of three female flowers in a cupule is of course more primitive than of one, but this reduction has obviously taken place independently in several specific lineages.

¹⁾ Though not immediately related to the purpose of this essay, I want to mention in passing a remarkable morphological replica of the Fagaceous cupule in a totally unrelated plant, *Blepharocarya involucrigera* F. v. M., belonging to the *Anacardiaceae* or closely related to these. The flowers in this dioecious tree are borne in a bracteate woody involucre which according to Shaw (1966) is formed 'by the flattened, externally grooved and partly crescent ultimate branches of the inflorescence', that is, exactly as I have formerly (1953) interpreted the Fagaceous cupule. This remarkable plant is found (by coincidence?) in N. and E. Australia.

2. NEW CALEDONIAN SPECIES

In New Caledonia at least 5 well distinct species occur; all belong to the subsect. *Bipartitae* which otherwise only occurs in New Guinea. Two of these show a distinct resemblance to New Guinean species, viz. *N. discoidea* resembles *N. perryi* from New Guinea and *N. aequilateralis* resembles *N. starkenborghii* from New Guinea, emphasizing the ancient plant-geographical relation between New Caledonia and New Guinea. In passing it may be said that in spite of intentional intensive research by Professor Corner c.s. on Guadalcanal at suitable height, no *Nothofagus* has turned up in the Solomons. This absence from the Solomons is shared by *Araucaria* and *Agathis*. The absence of these three genera is not unexpected if the very poor dispersal capacities of these genera and the relatively young age of the present Solomon Is. are taken into consideration. See chapter 8.

The New Caledonian species exhibit a remarkable vegetative difference from the Papuan species, not realized before, namely that whereas the Papuan ones have a strictly distichous phyllotaxis, the New Caledonian ones share a spiral phyllotaxis. This dualism in phyllotaxy is, however, also found in some other Fagaceous genera and though remarkable, because clearly geographical in *Nothofagus*, need not alarm us about the generic consistency. In addition I may point to the fact that Vink noted that in young seedlings of *N. rubra* the first leaves are always spirally arranged, and that distichy starts to occur on the first lateral twigs (Vink 17473). The New Caledonian species have all thick large leaves with entire or crenate margin.

In New Caledonia *Nothofagus* shows also an ecological behaviour slightly different from that in New Guinea, viz. in altitude.

3. ALTITUDINAL RANGE OF NOTHOFAGUS IN NEW GUINEA C.A.
AND NEW CALEDONIA

Nothofagus was hitherto assumed to be bound to rain-forest under cold to cool climatic conditions. Accordingly it is found towards the tropics at steadily increasing altitude.

New Guinea proper. — In New Guinea, at 7° S, 98 % of the collections were made between 1000 and 3100 m.

All species ascend to various heights above 2000 m, two excepted, viz. *N. nuda* and *N. cornuta* which are both known only from their type specimens, collected at 1200 and 1750 m respectively. Six species are not found higher than 2400 m, five others occur as high as 2800—3000 m, the highest locality so far recorded is 3100 m for *N. pseudoresinosa*.

Besides *N. nuda*, there are four species descending below 1500 m, viz. *N. womersleyi*, *N. carrii*, *N. starkenborghii*, and *N. flaviramea*. The first two of these are too rarely collected to gain a good idea of their total range. The latter two, however, are common and are also found below 1000 m. The occurrence of *Nothofagus* below this critical altitude for mountain plants in Malesia was already reported by Brass (in Archbold, Rand & Brass, 1942) in an 'outlier body of *Nothofagus* dominated forest' at 850—900 m southwest of Bernhard Camp, West New Guinea, but I have not seen voucher specimens sustaining this record. However, recently a similar report was made of even dominance by *Nothofagus* in Fago-Lauraceous forest by Schodde & Hitchcock (1968) near Lake Kutubu at c. 143° 15' E and 6° 20' S, found on karst limestone topography at 800—900 m. The voucher specimens belong to *N. starkenborghii*.

N. flaviramea has also been collected repeatedly at 750, 850, and 900 m, but not especially stressed as dominant, though common on Mt. Genofa.

D'Entrecasteaux Islands. — Hitherto *Nothofagus* has been found in two islands of this group which is adjacent to the north of the eastern tip of New Guinea. All four collections are sterile, save one which carries male flowers. I have tentatively referred them to two species and if these identifications are correct the data are as follows:

In Goodenough I. (highest elevation *c.* 2500 m) *N. carrii* is found on a narrow crest at 1750 m. This species ranges in New Guinea from 2850 m downwards to 1400 m.

In Normanby I. (highest elevation *c.* 1000 m) Brass collected *N. carrii* once on the summit of Mt. Pabirama at 900 m as a major constituent in shrubby growths 2—5 m high. This occurrence is distinctly below its lowest altitude in the mainland of New Guinea.

In Normanby I. Brass collected *N. rubra* once at 850 m as a common canopy tree in tall mossy forest (male fl.) and once at 750 m in stunted open *Dacrydium* forest. This is also distinctly lower than in the mainland of New Guinea where *N. rubra* ranges from 1750—2850 m.

In both islands the lowest localities of the genus are the same as in the mainland of New Guinea, viz. *c.* 750 m.

New Britain. — In New Britain (highest elevation of the non-volcanic mountains *c.* 1900 m) *N. starkenborghii* has been collected twice (both specimens sterile), once at 1350 m and once at 600 m (area between 5° 30'—6° S, 151°—151° 30' E). In the New Guinea mainland *N. starkenborghii* ranges from 2400 m down to 750 m. In New Britain this species shows hence the lowest occurrence of the genus in Papuasia *sens. lat.*

I have formerly tentatively concluded that specimens below 1000 m remain sterile, and that the lowest records would concern occasional specimens. The new records show that this is not true, both male and female are collected at these lowest altitudes¹⁾. Though it remains to be proved that low occurrences are found throughout New Guinea, there are several localities where *Nothofagus* is abundant at 750—900 m. Furthermore, they are found fertile at these altitudes. Obviously lowest occurrences concern largely two species, *N. starkenborghii* and *N. flaviramea*. But it should be added that there are no signs that *Nothofagus* descends in Papuasia to the lowland or that species would solely occur in the lowland.

There is, however, a tendency that *Nothofagus* species descend to lower altitudes on smaller and lower, more oceanic lands as shown by *N. carrii*, *N. rubra*, and *N. starkenborghii*.

Among the New Guinea species some possess large leaves (*N. perryi*, *N. grandis*, *N. flaviramea*), some very thick-coriaceous leaves (*N. rubra*, *N. brassii*), and some always small leaves (*N. pullei*) and it might be supposed that leaf-size and leaf texture go parallel with altitude, the first category indicating lower and the two other categories high altitude species. However, there is hardly any correlation in this aspect. Two species with thin and fairly large leaves, *N. resinosa* and *N. pseudoresinosa*, belong to the highest ascending species, both admittedly sharing a conspicuous exudate of waxy resin on the leaves and flush.

New Caledonia. — This oceanic island is situated at *c.* 20—22° S, that is still within the tropics. Its highest elevation is considerably lower than that of New Guinea, the two

¹⁾ The statement by Melchior (1964) that *Nothofagus* is dioecious is an error; alle are monoecious.

highest peaks reaching only c. 1640 m altitude. Five species occur; in proportion to the New Guinea species they are all large-leaved and very coriaceous.

Well-documented data on altitudinal range of *Nothofagus* in New Caledonia are as yet scanty and are not mentioned by Virost. According to Baumann-Bodenheim (1953) all are confined to serpentine bedrock.

Combining the published data by Baillon (1873) with the collections at hand and unpublished data kindly provided by Dr. H. S. McKee, the following picture emerges of the altitudinal range of the New Caledonian species: *N. discoidea* c. 150—250 m, *N. aequilateralis* c. 200—600 m, *N. codonandra* c. 150—1350 m, *N. balansae* c. 300—1350 m, and *N. baumanniae* c. 1000—1200 m. These altitudinal data agree with the altitudes given by Baumann-Bodenheim (1956); he even admits descent of three species to the lowland at 100 m.

The situation is obviously very different from that in New Guinea in that New Caledonian *Nothofagus* clearly does not shun the tropical lowland.

Judging from the macroclimate, one would expect in New Caledonia an altitudinal behaviour similar to that in New Guinea (750—3100 m, 600 m in New Britain), as New Caledonia is situated from 20—22° S, that is within the Tropic of Capricorn, anyway not so much different as its altitudinal range in New Caledonia really is, namely from 150—1350 m. New Caledonia is admittedly further away from the equator than New Guinea, but I doubt whether this can be the reason. The experience with other mountain plants is, that we have for example never found a consistent difference in altitudinal behaviour of the same mountain plant species in Java at 7° S or Central Celebes at 0° as compared with northern Luzon which is at 20° N.

One would have expected that in New Caledonia *Nothofagus* would be crowded in the summit zone of the higher peaks and, giving allowance to the elevation effect (van Steenis, 1961; Backhuys, 1968), estimate a descent to possibly 500 m, but then of the same species, and no species confined to the lowland.

As to response of altitude with climate we have, in Malesia, the impression that sometimes lower altitudes are reached in a seasonally dry climate, namely in the Lesser Sunda Islands. But several New Caledonian species do not behave in this way, though it should be admitted that New Caledonia is averagely less wet in total annual rainfall as compared with New Guinea. Lower rainfall may hence contribute to some degree to lower occurrence of the genus in New Caledonia.

But it should be kept in view that it is not so much the descent of species, but that two species are confined to the lowland and low hills. And I have shown formerly (van Steenis, 1933) that in attempting to correlate altitude with climate one must be very careful in comparing data of the same species, not of different species. All New Caledonian species are certainly specifically different from those of New Guinea.

In conclusion, it appears not well possible to correlate the altitudinal behaviour of *Nothofagus* in New Caledonia with environmental factors. For the present I believe we have just to accept that the New Caledonian species behave as they do and show a different ecological response from the New Guinea species. Obviously the total ecological tolerance of the genus is somewhat wider than hitherto assumed, running from tropical to cold-temperate.

There are other examples that on isolated oceanic islands in the West Pacific genera occur at lower altitude than on larger land masses, but a true comparison can only be made if this relates to exactly the same species. I refer in this respect to the general remarks on altitudinal behaviour of *Nothofagus* made above under New Britain, in which island it reaches its lowest altitude in Papuaia at 600 m.

It would be worthwhile to make some experiments with *Nothofagus*, viz. to transplant New Guinea species to New Caledonia and vice versa, in order to see how they behave.

4. NOTES ON DISTRIBUTION OF NOTHOFAGUS SPECIES IN NEW GUINEA

At the time of my monograph of the genus (1953) the total number of collections of the 16 species distinguished was only 47, including the sterile ones. Largely through the great activity of the Division of Botany, Lae, and the Land Research section of C.S.I.R.O., Canberra, the material amounts at present to some 380 collections.

There is gradually coming more insight in common and rare species: of *N. grandis*, *N. perryi*, and *N. pullei* I have now over 40 collections, and of *N. flaviramea* some 30.

In 1953 many collections were only known either from the eastern or the western part, but this restricted occurrence has a tendency to fade away, 6 of the commoner species being now known from both East and West New Guinea. But it appears that 2 very common species remain to be restricted to East New Guinea, viz. *N. perryi* and *N. grandis*.

Though collections are now abundant the complete inventory cannot yet be made, I am afraid, because still new, clearly good species turn up, *N. womersleyi* in 1960 and *N. muda* in 1966, each consisting of a single collection.

I have been compelled to reduce a few species and among the species with reduced cupules there is still some uncertainty about specific status for a few. This is not so much due to an assumed indistinctness of specific delimitation or doubt about the importance of the cupule characters of Papuan species of *Nothofagus*, but to the inadequacy of most collections. Complete fruiting material gives never difficulty in identification, but sterile collections, often taken from too young trees, and those with only male flowers or with very young female flowers are sometimes difficult to place, because in contrast to the New Caledonian species, which can all easily be recognized in sterile state, there are half a dozen Papuan species which are very much alike in vegetative characters.

Though they are often closely resembling in vegetative characters my strong belief is that there are at least over a dozen good species. I derive this from the fact that of a goodly number of species I have now 10—40 exactly matching specimens of which the cupule characters are completely constant. In addition, since writing the first attempt towards a revision in 1953 I have found that, though the detail characters of the male flowers provide no clue, their number per catkin, one or three, has proved to be constant for the species, most having three, one being found only in *N. pullei*, *N. crenata*, *N. resinosa*, and *N. pseudoresinosa*.

Hybridisation is known from *Nothofagus*, both in South America and New Zealand, and could occur in New Guinea as well. Though this would infer that such hybrids would bear fruit which should not occur with good species, we do not know whether these fruits are viable.

In dissecting nuts in the herbarium of indubitably good species, one finds many nuts barren, as also often happens in *Fagus*, often depending on the year's climatic conditions favourable or not for pollination. As male anthesis is short in New Guinean *Nothofagus*, heavy rains in that particular period may be unfavourable for fruit-setting.

In passing I may observe that in comparison with specimens of New Zealand and South American beeches the New Guinean (and New Caledonian) species carry very few cupules per collection. It is not only that in a number of species the cupules are small and inconspicuous or even absent, but also the real number of nuts per sheet is extremely small, 0—1(—3). One has often to scan the specimen carefully to find them. Of course the trees are extremely large in good situations, 30—45 metres and over with a columnar bole of

c. 1—1½ metre through (the record in thickness of the bole being 2½ m dbh, by a height of 45 m, noted in *N. grandis*, *Cruttwell 899*) and the number of nuts produced by one tree must hence be considerable. But a large proportion of the nuts appears to be not viable, and possibly only those which become earth-covered will germinate successfully.

5. DOMINANCE OF NOTHOFAGUS

In the New Guinea highlands *Nothofagus* is one of the most important components of the frame of the forest, whether or not mossy, at altitudes between 1500 and 3000 m, rarely lower. Frequency on labels reads often 'abundant', 'common', 'very common'.

This tropical-montane mesophytic forest, generally known as the Fago-Lauraceous forest type, consists for a large part of *Fagaceae* (*Castanopsis* and *Lithocarpus*); other genera often frequent are *Araucaria*, *Libocedrus*, *Weinmannia*, *Engelhardia*, *Dacrydium*, *Podocarpus*, *Eugenia*, and *Cryptocarya*. Frequency of *Nothofagus* is often very high and is especially easily observed when the trees are in reddish flush.

Dominance is reported on field labels of almost all species, in particular of *N. pullei* (8 times), *N. grandis* (5 ×), *N. perryi* (5 ×), *N. starkenborghii*, *N. rubra*, and *N. flaviramea* (each 3 ×).

Dominance is easily observed from the air and maps (e.g. of Mt. Giluwe area) can be composed in which the stands of dominant *Nothofagus* are indicated in detail. Of course through human interference there are also degraded areas where *Nothofagus* occurs scattered, in restricted groves or stands, etc. And there is plenty of forest where *Nothofagus* is not dominant.

Kalkman and Vink confirmed older data of Brass and of Robbins that the co-dominance with other *Fagaceae*, notably *Castanopsis* and *Lithocarpus*, is in their experience not so manifest as collectors suggest. They have observed on Arfak, Doma, and Kubor that the proper *Nothofagus* zone is always situated higher than the *Lithocarpus* or *Castanopsis* dominated lower forest. They have also studied in more detail (Kalkman & Vink, 1970) the regeneration on Doma Peaks and found *Nothofagus* in restricted, sharply demarcated stands with plenty regeneration inside, but not beyond the stands, and also no *Nothofagus* trees in surrounding forest. Obviously, and this is no news, dispersal of beech nuts must go very slow indeed.

This brings me to an other general aspect of interest, viz. why certain groups of plants play such a dominant role in numbers in the vegetation over immense surfaces and get dominance or co-dominance by their social behaviour, and maintain this, as proved in *Nothofagus*, for geological epochs, at least onwards of the Cretaceous. A similar thing can be said of Conifers, of the Dipterocarps in western Malesia, and of *Eucalyptus* and *Acacia* in Australia, though in the latter two cases the mass development is certainly less ancient. Is it too bold to put forward the hypothesis that their virility as exhibited by abundance is due to their capacity to produce toxic substances, either by exudation or exhalation, or substances in their litter which in some way or other are toxic to or inhibit germination or growth in the soil of other plants? This concept, called *allelopathy* by Molisch, is extremely difficult to prove, because in experiments one can not exactly imitate the processes going on in nature, especially the decomposition of litter by micro-organisms, and besides calculate or eliminate root-competition, the reaction of mycorrhiza, the whole process being an extremely complicated complex of interacting factors. Though in some simple cases it seems rather clear that allelopathy exists, I feel that the concept has not yet been sufficiently examined which is probably the reason that it is hardly

introduced into ecology. Mostly the dominance of the said groups is claimed to be due to the excessive shade they cast, prohibiting growth of shade-intolerant other plants. But to this can be opposed that mixed rain-forest without dominance or co-dominants provides also abundant shade, but nevertheless remains mixed. The same can be opposed to declare it a matter of root-competition. For Conifers still an other explanation has been advanced, viz. the fact that many plants cannot germinate on a layer of litter or too humous topsoil, and that for successful germination their seeds have to be in contact with the mineral soil. This may be true in temperate countries and in mountain rain-forest where such humus accumulation is often found. And it is also true that in mixed lowland tropical rain-forest abundant litter is mostly hardly existent because of its rapid decomposition. But such reasoning could also be explained by the allelopathy hypothesis (Grümmer, 1959; Rovira, 1969), whereby accumulation of humus produces a high percentage of toxic substance whereas rapid decomposition combined with constantly high rainfall dissolves the toxic substances to such low percentages to be no more effective. In dry climates, as for *Eucalyptus*, litter is so slowly decomposed not to have sufficient effect.

I am myself not certain about the significance of allelopathy in ecology, in particular in the wet tropics, but the idea that it may be important should not be suppressed. Whatever the merits given to it, I have come to believe that the solution for the dominance of *Fagaceae* and others lies probably rather in their living as symbionts with ectotrophic mycorrhiza. I am much impressed by the data provided by mycologists.

6. SYMBIONTS OF NOTHOFAGUS

A striking fungus occurring on the branches of *Nothofagus* is the Discomycete genus *Cyttaria*; it is peculiar to *Nothofagus*, causing big galls covered by gelatinous stromata. This has not been found on any of the species of the New Guinean-New Caledonian subsect. *Bipartitae*. It is a parasite, not a true symbiont: *Nothofagus* has no profit of it. Heim (1951) reviewed the fungus flora of the New Zealand beech forests and remarked that there are many genera, especially among *Agaricales*, which are profusely represented both in the Eurasian *Fagaceous* forests and in the *Nothofagus* forest.

The mycorrhiza of *Fagaceae* offer a most interesting feature. Singer & Morello (1960) generalized the occurrence of ectotrophic mycorrhiza which occur abundantly on the northern hemisphere with *Pinaceae*, *Salicaceae*, *Betulaceae*, *Alnus*, and *Fagaceae* (also *Fraxinus*, *Allophylus*, and some *Caesalpinioideae*). They are so closely bound to these that the symbiosis is by them considered to be of a similar nature as in lichens. In the Americas the ectotrophs extend southwards on *Quercus* to Columbia and are connected southwards in a narrow montane line along the Andes, consisting of *Alnus*, with the southern *Nothofagus* belt. The fungus components largely belong to the *Agaricales* of which genera as *Russula*, *Cortinarius*, *Lactarius*, *Inocybe*, *Boletus*, etc. are extremely well represented, and some *Gastromycetes* and *Aphyllorphorales*. Quoting these authors: 'These southern ectotrophs find their natural geographical continuation in the *Nothofagus* areas of New Zealand, E. Australia, New Caledonia, and New Guinea. The ectotroph as a biological unit generally possesses higher plasticity than any comparable forest element without mycorrhiza. In an association, the ectotroph is usually the element with the highest fidelity and regularity of distribution, and is commonly the first to establish itself among its consociates. The distribution of mycorrhizal dominants and subdominants of this type shows an even distribution throughout the stand which causes the ectotroph mycelium to occupy the soil almost homogeneously. Fidelity and regularity may be explained by trophic reasons favoring the ectotroph over the non-mycorrhizal elements and making

it more aggressive and often more resistant to unfavorable climatic conditions and to diseases. The development of ectotrophs is limited by two factors, (i) dryness, and (ii) humidity if accompanied by generally high temperatures throughout the year; in very humid climates with relatively low temperatures ectotrophs are common, frequency and abundance increasing with a humid heterothermic climate.'

Singer & Moser (1965) explored forests south of Valdivia at 39° 30' S, in which they corroborated that in *Nothofagus*-free stands the percentage of ectotroph-forming fungi is zero. In the *Nothofagus* forest they found a clavarioid ectotroph fungus *Ramaria zippelii*, of tropical Asiatic distribution. They found it reasonable to assume 'that its origin must be in a region where the areas of *Quercus* and *Nothofagus* 'touch', viz. New Guinea'.

Moser (1967) stressed again that ectotrophs have wider capacities than endotrophs or trees without mycorrhiza, for example as pioneers on disturbed soils, after fire, and near the tree limit. In his list of ectotrophs are also included, besides almost all *Pinaceae*, *Fagaceae*, *Betulaceae*, *Salicaceae*; a few *Rosaceae*, some tropical African *Caesalpinaceae*, *Tilia*, and *Eucalyptus*.

Summarizing, it seems that the ectotrophic mycorrhiza play an essential role in *Nothofagus* forests, and must have had that role also in past geological ages. It could well be that through them they are capable to maintain their abundance, virility, and dominance.

7. REGENERATION AND GERMINATION OF NOTHOFAGUS IN NEW GUINEA

About fire I can be short: *Nothofagus* is not encouraged by fire. In New Guinea forest officers have never observed actual basal suckering after a lightning strike or wind damage. Fallen trees in mossy forest, e.g. of *N. pullei*, do produce side shoots which grow vertically and also produce roots. This leads to thickets of saplings, but Mr. John Womersley, to whom I owe these field observations, has no idea how many, if any, eventually reach mature tree size.

No regeneration has been observed in New Guinea which suggests a reservoir of seed in the soil. The impression is that the seed has a very short viability.

New seedlings may rise from dispersal of trees in adjacent forests. But as it seems that dispersal goes slowly and is only of short-distance reach, large devastated areas offer, even in upspringing secondary growth only an opportunity to regenerate *Nothofagus* along the margins bordering old forest with *Nothofagus*.

Germination is said to be epigeal, but in the old meaning of the word this means that the seed is elevated by the hypocotyl above the ground. In the modern improved meaning of this concept it means that the stem is produced centrally between the spreading cotyledons, irrelevant whether these enlarge or not and whether the seed is on the soil or elevated on the hypocotyl. Also in this meaning epigeal germination must surely be the case in *Nothofagus*, as it is in *Fagus*, though I have never seen a young seedling in the herbarium.

However, I would like to know in addition another ecological aspect of germination, viz. whether successful germination takes place if the seed is exposed on the soil, or whether the seed must be buried in the soil. The experience is namely that in *Castanea* and *Quercus* all nuts lying on the soil are attacked by fungi and doomed to decay; only those which happen to come into the top soil (worm holes, washing over and covered by some soil, moved by ground animals, etc.) produce seedlings. Kalkman and Vink found in Lei (Doma Peaks) the largest number of seedlings often on fallen, dead tree trunks which were thinly covered with moss.

In East New Guinea Papuans plant *Nothofagus* in their homesteads, along tracks and

around their garden lands, it is said for ornamental purpose. This is reported of *N. grandis*, *N. perryi*, and *N. pullei*. But they do not raise them from seed, but invariably transplant seedlings from the forest.

More information on germination and regeneration by seedlings is desired.

8. DISPERSAL IN NOTHOFAGUS AND ITS IMPLICATIONS FOR THE GENESIS OF ITS DISTRIBUTION

Distribution always brings along the question of dispersal. It has been observed that this goes in *Nothofagus* very slowly, both in New Guinea and in New Zealand, and over very small distances, that is, effective dispersal including regeneration.

In addition there are experiments recorded by Holloway (1954) who found that neither the Conifers nor *Nothofagus* can stand transport by seawater; besides nuts sink.

Streams and rivers can effect dispersal over larger distances, but of course only downstream.

Transport of the wingless nuts by wind is also only a matter of hundreds of metres; Preest (1963) put the absolute maximum at 2—3 kilometers, and concluded that long-distance transoceanic dispersal by wind cannot be considered.

He reviewed also the situation in dispersal by birds, but the nut-eating birds are all endemic and sedentary. Besides nuts would not survive passage through the gut. Epizoid dispersal of the nuts can readily be discarded.

Transport by icebergs would not carry any living seed, as nuts cannot survive freezing.

The first point to make is, clearly, for these reasons, that to any plant-geographer who respects himself and wants to develop plant-geography as a critical branch of science, the dispersal of *Nothofagus* is bound to the presence of land.

This leads to the question how under formerly different distribution of land and sea, the present broken range of *Nothofagus* has developed in time. Because *Nothofagus* has an enormous history behind it and its South Pacific fossils range at least from the Upper Cretaceous, we will have to accept land where there is none today. The cornerstone of the explanation of the relict distribution of *Nothofagus* is the 'filling' of the three oceanic gaps in the continuous range round the South Pacific, that between Fuegia and Seymour Island, between Antarctica (McMurdo Sound) and New Zealand, and between Antarctica and Tasmania/Australia. Accepting more land in these gaps does not mean that this should all have been continuous land, and moreover need not to have been strictly synchronous. And if the land-connections were 'insular landbridges', these must have had the geography of 'very nearby-continuous' — even less spaced than in the Malesian landbridge — to permit short-distance dispersal.

This is the view held by a number of former plant-geographers (e.g. Diels) and advocated by myself (van Steenis, 1962) and by the late palaeobotanist Dr. Florin (1963). Also Corner (1969) for his classical research in the genus *Ficus* shares this view as may be illustrated by a few citations from his latest summary on Melanesian *Ficus*: 'The evolution of *Ficus* in Melanesia reflects its geological history. *Ficus* is not distributable except over land or through archipelagoes. There is no reason to invoke the risky means of long-distance dispersal by chance, except to explain the most casual, least effective, and freak occurrences. There is no evidence of random drift in the distribution of *Ficus*.' In short: distribution means land (in litt.).

To me the strongest evidence for the land theory is the distribution of *Nothofagus*, living and fossil, while Florin's data are independently derived from his classic study of Conifers and Taxads.

I was, and am still, aware that geomorphologists are not yet so generous to grant us this ancient land (cq. land-connections), even though it appears irrelevant from which source it might have come and by what processes it might have gone: foundered fore-continents, subsided continents, expanding or shrinking earth, continental drift, or plate tectonics.

To contemporary geomorphologists continental drift seems at present to be the more attractive theory. The land theory under the steady state postulate seems to some just heresy.

But I want to remind that to anyone who tries to follow the development of geomorphological knowledge it is clear that geomorphologists are continuously struggling with alternative solutions or models on the basic principles about the evolution of the crust of the Earth, one theory or reconstruction following an other in rapid succession. Geophysical thinking is at present in such a flux that it is impossible, at least for a biologist, to select interpretations, datings, and reconstructions which appear to be of lasting value. It appears therefore premature to venture on a highly hypothetical correlation.

Reversely, botany has some unshakable factual material for phylogenetical and plant-geographical synthesis, viz. (i) the taxonomic relations within the living plant world, (ii) the fossil record restricted to trustworthy evidence, (iii) the plant-geographical record of both living and fossil plants.

One can of course dispute whether taxonomy and fossil evidence is 'factual' material and it is agreed that in too many cases the evidence has not reached the level of factual material. For *Fagaceae*, however, I feel there is no doubt whatsoever, if we discard some doubtfully identified macrofossils which are besides irrelevant.

The plant-geographical record I regard of the same level as factual material, if it is carefully sorted into intelligent distribution patterns.

Form-making, speciation, is admittedly erratic. For the present flora it is incomprehensible: it is impossible to tell from the past or predict why the array of living beings is composed in the way we observe it, why groups went extinct, some gradually, some rather abruptly, why certain groups exploded into rich development and other groups on diverse levels did not develop into profuseness, why some groups were of short duration and others maintained themselves for colossal periods of time though not necessarily attaining large size.

Biogeography is, however, not erratic, because once a species (hence necessarily a genus) is successfully created, it will start to expand. And this expansion process is governed, restricted, or directed, or whatever term one may prefer, by its environment, geographical and ecological. It will take advantage of this environment within the capacity of its dispersal rate, and this may differ from one plant to another. But all plants associated with it will take (or at least have) the same advantages within their ecological capacity, that means develop homologous patterns of distribution. And the closer their ecological amplitude the more homologous the patterns that will develop. Plants spread together.

From these considerations it must be clear that the study of homologous ranges becomes trustworthy factual material. Long ago I have analyzed the Malesian mountain flora by this methodology (van Steenis, 1933—34) with remarkably successful results.

There are botanists who doubt this reasoning in accepting a hypothetical random long-distance dispersal which to them would have played an enormous role, because this supposed dispersal would have gone on, admittedly rarely, through geological time, which would compensate for rarity. If this would have been really a general rule, it becomes clear that the orderliness of the homologous ranges would have been destroyed or at least completely obscured. As experience teaches to increasing degree, however,

there exists an undeniable, clear, orderly array of distribution patterns fitting in with the taxonomical data, so that we can safely discard hypothetical random long-distance dispersal as a major factor in having contributed to the genesis of present distribution patterns.

It is clear that the vicissitudes of the physiography of the earth, distribution of land and sea, extension and height of mountain ranges, and climate, have been shared by the plant world. The botanical net results of this history, that is, present plant distributions, must consequently ultimately be reconciled with a unanimously agreed history of the physiography. Obviously the latter branch of science has not yet been sufficiently stabilized for such final correlation. Provisionally, the botanist has to work out his own data.

The distribution of *Nothofagus* and *Fagus* agrees completely with the three criteria required for a critical biogeographical correlation on a factual basis: (i) taxonomists agree unanimously on the taxonomic relations, (ii) there is an ample trustworthy fossil evidence, and (iii) random long-distance dispersal is for these genera completely out of question.

Working on this sound basis the purpose is to frame the history of the *Fagoideae* into a reasonable picture of what must have happened in the course of time to cause the present pattern with its disjunctions. This will also show what physiographic changes (in land and climate) are required as implications. The simplest way towards this goal is to relate this to the steady state at least onwards of the time that the Angiosperms evolved or were expanding; it can be added in passing that most of the assumed major drifting of continents is usually supposed to have taken place before the Upper Cretaceous.

As will be shown, all data, including the ecological behaviour of *Nothofagus*, can be correlated nicely and in an unforced way by normal geological processes.

David's Geology of the Commonwealth of Australia (1950) (Burbidge, 1960) shows the complicated geology of the Australasian region, with immense changes in the distribution of land and sea, and large subsidences. Fleming (1962) illustrated this for the New Zealand region showing that New Zealand and the remote, wide-flung, speck-like islands 'surrounding' it are the emergent remnants of an immense drowned (that is subsided) Tasmantis bank stretching almost as far as New Caledonia. A glance at modern atlases shows immense submerged banks between Australia and New Zealand and Antarctica. And this is for me sufficient evidence that the land theory is not at all without vital background. How and when precisely these land connections have been situated is not my task to unravel and entirely outside my capacity to reconstruct. But the rough picture seems to be clear and sufficient for my purpose.

9. THE SOUTH PACIFIC AND SUBANTARCTIC CLIMATE, PRESENT AND PAST

In conjunction with the conclusion in the preceding chapter on the fact that the broken range of *Nothofagus* today cannot be reconciled with the present physiography of the South Pacific but must be correlated with palaeographic conditions, we will have to consider the climatic conditions, present and past, in relation to *Nothofagus* ecology.

Except in New Caledonia where some species are growing under almost tropical lowland conditions, the majority of the species grow under cool to rather cool everwet (rain-forest) conditions, the southernmost localities of *N. antarctica* and *N. pumilio* being at c. 55° S in Fuegia, where they extend as far as the tree limit.

We have to realize that we still live in the tail of the Pleistocene Glacial Epoch, maybe even in an inter-glacial period. We are so used to contemporary climatic conditions, observing almost no change in historic time, that it is insufficiently realized that our

present climatic conditions at higher latitudes are still distinctly Ice-Age-featured. It is difficult to visualize, but nevertheless beyond any reasonable doubt, that the palaeoclimate of the Cretaceous and the large part of the Tertiary up to the Pliocene was very much milder. This must have caused much diminished (or even absent) polar ice caps. At least the borderlands of Antarctica could easily have carried a temperate to cold-temperate forest, suitable to the growth of *Nothofagus*. A climate shift of 15 latitudinal degrees from Fuegia where the deciduous *N. antarctica* is found today, to about 70° S would allow *Nothofagus* to grow on Antarctica. This shift seems to be quite acceptable in view of what we know of the magnitude of Glacial Epoch shifts on the northern hemisphere.

Even today, under the still prevailing Ice Age-featured climatic conditions as compared with those before the onset of the Ice Age in the Pliocene, growth of trees in the Arctic goes as far as 72° N for *Larix* and to 70° for *Juniperus*; for smaller woody plants of *Salix*, *Betula*, and *Vaccinium* even to 77° N. Though their growth must be slow, they get obviously light in sufficient quantity to maintain themselves.

How much better should they be situated under the ameliorated Cretaceous and Tertiary palaeoclimates!

With these northern hemisphere data in mind it seems to me clear that this milder palaeoclimate must have been sufficient, both as to light and temperature, to allow the growth of *Nothofagus* on the borderlands of the antarctic continent.

Mrs. Cranwell (1962, 1964) believed that *Nothofagus* 'could never have maintained itself far southwards outside the temperate belt and cries out for a place in the sun under conditions comparable with those holding between 40° and 50°. How could massive and light-demanding forests have survived long in an Antarctica characterized by a long dark, and inevitably cold polar winter? Antarctica as it is placed today could never have been its cradle.'

My comment on this is firstly, that there is of course no question of a 'cradle', as this would imply an Austral origin in the phylogenetic sense. But surely, Mrs. Cranwell cannot mean to divorce *Nothofagus* from the Fagaceae family and certainly not from *Fagus*? From what ancestors on the southern hemisphere would *Nothofagus* then have emerged, quite independent of the rest of Fagaceae? ¹⁾

In an other place she said (Cranwell, 1963: 396) 'that the highly speculative tropical origins would please some phytogeographers', but it is surely not to please phytogeographers but an utter impossibility for taxonomists to accept a biphyletic origin of the subfamily *Fagoideae*.

Bi-hemispheric ancient counterparts are not restricted to *Fagoideae*, where one genus is northern, the other southern hemisphere. Florin (1963) stressed the early bi-hemispheric geography which he held as most significant in the evolution of the conifer and taxad stocks. I have called attention (van Steenis, 1962: 285) to a similar tendency still discernible among various Phanerogams at different levels (family, tribe, genus). Such 'pairs' are for example: *Staphyleaceae-Cunoniaceae*, *Magnoliaceae-Winteraceae*, *Ericaceae-Epacridaceae*, *Cyperaceae-Restionaceae*, *Poterium-Acaena*, *Carex-Uncinia*, *Dillenia-Hibbertia*, *Veronica-Hebe* complex, and to a fairly large extent *Umbelliferae-Araliaceae* and *Cruciferae-Capparaceae* of which the two members (or at least one of them) are largely developed on one hemisphere. Many more examples can be unearthed, but this requires a separate study. In my

¹⁾ A similarly erroneous premise is the basis of the phytogeographical analysis of a certain number of taxa which would all have extended their ranges from the temperate zones into the tropics including *Nothofagus*, by Bader (1960: 79, 81, 463). Many of them must stem initially from the tropics and have but later extended to higher latitudes.

opinion these pairs still reflect signs of early phylogenetical differentiation from common tropical, tropical-montane, or subtropical matrices.

My second comment is, that even today *N. antarctica* and *N. pumilio* grow profusely as far as 55° S and further that nobody suggested that in Antarctica 'big massive forests' occurred, nor that *Nothofagus* is a distinctly light-demanding plant for which the summer at 70° S would not provide sufficient light to grow. The latter assumption is certainly in correct with the data known from the northern hemisphere even of today. And it is most peculiar that Mrs. Cranwell completely neglects the significant fact that no less than 4 species are dominants as the most advanced woody plants at the tree limit, viz. *N. antarctica* and *N. pumilio* in Fuegia and *N. cliffortioides* and *N. menziesii* in New Zealand. And they belong to both sections, the first two are deciduous, the latter two evergreen. They all are perfectly adapted to grow at a tree limit in Antarctica at 70° S. And as many fossils are described there may well have been other species adapted to cold-endurance which are now extinct.

Mrs. Cranwell's additional hypothesis, necessary to explain the fossil finds of *Nothofagus* on Antarctica under her assumption, namely a close proximity of Antarctica and New Zealand in the Upper Cretaceous and early Tertiary by which *Nothofagus* was able to grow in Antarctica, and then a southward drift of Antarctica by which *Nothofagus* got there extinct, appears to be a completely unnecessary complication. That towards the end of the Tertiary, with the onset of the Glacial Epoch, the borderland antarctic *Nothofagus* forests were wiped out, is of course clear. Everywhere in the South Pacific the Ice Age must have taken a heavy toll of the flora of southern latitudes, probably even more severely than in the northern, because of the then already existing lack of escape possibilities. Mrs. Cranwell (1964: 90) rejects the possibility of long-distance dispersal in *Nothofagus*, unfit to cross salt water.

Concluding this subject, it seems beyond doubt that *Nothofagus* could have grown on the antarctic borderland under present physiographic conditions but under a mild Cretaceous and Tertiary climate.

I will not reject Mrs. Cranwell's reference to Irving's palaeomagnetic data, indicating that Antarctica and Australia were close together in the early Tertiary, swinging down by the Miocene, and that Antarctica and New Zealand were separated later.

What I wanted to show is that *also without continental drift hypothesis* the borderland of Antarctica as it is situated today would allow for *Nothofagus* to grow under a milder climate.

10. THE FOSSIL RECORD. Table 1

There is, fortunately, a profuse trustworthy fossil evidence of *Nothofagus*. This consists partly of macrofossils, partly of pollen. In passing it may be remarked that curiously the pollen of *Nothofagus* is very distinct from that of other *Fagaceae* and had it been known only from the fossil state its correlation would not have been possible, I am told by palynologists.

Among the macrofossils Von Ettingshausen (1888) claimed to have found various species of *Fagus* and also *Betula* in Australian Tertiary fossils. There seems, however, no doubt that these are all *Nothofagus*.

As to the pollen it should be explained in advance that there are three pollen types, the *fusca* and *menziesii* types and the *brassii* type. These coincide only partly with the taxonomy of the genus, which is first subdivided into two sections, evergreen *Calusparassus* and deciduous *Nothofagus*. The *fusca* and *menziesii* types occur in both sections. However,

stratigraphical record of NOTHOFAGUS pollen	NEW GUINEA			NEW CALEDONIA			AUSTRALIA			NEW ZEALAND			Mc MURDO SOUND			SEYMOUR I.			FUEGIA			
	b	f	m	b	f	m	b	f	m	b	f	m	b	f	m	b	f	m	b	f	m	
RECENT																						
PLIOCENE																						
UPPER MIOCENE																						
LOWER MIOCENE																						
OLIGOCENE																						
EOCENE																						
PALAEOCENE																						
UPPER CRETACEOUS																						

Table 1. *Nothofagus*, recent and fossil as yet known from the pollen record (after Cookson, 1959; Couper, 1960; Dettmann & Playford, 1968); those of McMurdo Sound unspecified as to type (b = *brassii* type; f = *fusca* type; m = *menziesii* type). For emendation see Postscript p. 97.

the *brassii* type is amongst living species strictly confined to subsect. *Bipartitae* of *Calusparassus*, comprising the New Guinean and New Caledonian species. Precisely as in the case of *Metasequoia*, *Nothofagus* subsect. *Bipartitae* was described as pollen before botanists described the living plant. Cookson & Pike (1955), who studied the pollen of the species of this subsection, stated that different species can not always be discriminated by their pollen. Among the fossils there may have been consequently far more 'botanical species' than 'pollen species'!

For reasons that will appear later I will now review the fossils along the total range, country by country, going from New Guinea along the South Pacific arc. Table 1.

New Guinea. — About 15 living species, all with *brassii* pollen type. Fossil pollen of this type has been found in SE. New Guinea from the Upper Miocene (A. M. Khan, in litt.). No older records known; it should be realized that the fossil record of New Guinea is extremely poor.

New Caledonia. — At least 5 living species. No fossil records known to me.

Australia & Tasmania. — There are 3 living species, one deciduous (*N. gunnii* in Tasmania). Fossil pollen of both the *fusca* and *menziesii* types occur in abundance in Australia. In 1946 Cookson described fossil pollen from SE. Australia from strata dated as from Oligocene to probably Miocene. Later she compared the pollen types with that of the living New Guinea species (1952) and concluded that one of the Australian pollen types was very much similar to the *brassii* type (Cookson & Pike, 1955).

We have now a recent record of an Upper Cretaceous (Santonian to Uppermost Cretaceous) pollen by Dettmann & Playford (1968) of the *brassii* type from the Otway Basin in Victoria. This was expected by me in the light of the Upper Cretaceous findings

in New Zealand. It is most important to note that during the Tertiary Period the *brassii* type was the commonest and widely distributed pollen found in East, South, and also West Australia (Cookson, 1954). From this follows that in the Tertiary *Nothofagus* must have been one of the most important genera of Australian forests, obviously wiped out by the onset of the continental desiccation following the disappearance of the epeiric seas which caused the earlier pluvial climates. As all three pollen types are represented, and 'pollen species' may have represented more than one or even several 'botanical species', Australia must in the past have been a country rich in *Nothofagus*, possibly some 10—20 species.

New Zealand. — There are 4 living species, all evergreen. As early as 1887 von Ettingshausen had described fossil leaves from New Zealand which he attributed to *Fagus* (4 species), *Quercus*, *Alnus*, and *Ulmus*. In my opinion the larger part of these, if not all, must belong to *Nothofagus*. Oliver (1936, 1950) described macrofossils from the Upper Cretaceous to Miocene and assigned them partly to *Nothofagus*, partly to *Fagus*, and partly to a new genus *Parafagus*. He was only well acquainted with the living species from New Zealand and was not aware of the existence of large-leaved species belonging to subsect. *Bipartitae* from New Guinea and New Caledonia, and obviously inadequately informed about the South American species. The characters he used to distinguish the three genera he mainly derived from the venation patterns and leaf margin. In my monograph (van Steenis, 1953: 322, fig. 1) I have shown that all the venation and leaf-margin structures described by him are also present in living species of *Nothofagus* and I concluded that all, or almost all, his fossil leaf material must be referred to *Nothofagus*.

Fortunately there is a profuse fossil pollen record of *Nothofagus* in New Zealand. This knowledge started with a paper by Mrs. Cranwell (1939) who recorded fossil pollen from Tertiary lignites, in conjunction with a study of the pollen of all living species of *Nothofagus* then known. This fossil pollen was later named *N. cranwellae* Couper (1953), representing the *cranwellae* pollen type.

The oldest pollen record was described by Te Punga (1947) as *N. kaitangata* from the Lower Coal Measures of the Lower Cretaceous. Couper (1952a) reinvestigated these coal measures and confirmed this record. Later Couper (1960a) corrected the dating to Upper Cretaceous (Senonian, l.c. p. 6), adding that in other Upper Cretaceous coal measures the same species occurs abundantly. In the Upper Eocene to Lower Oligocene deposits pollen of four other species was discovered and in some places this makes up 80 % or more of the forest pollen. Their pollen was first considered as belonging to the *cranwellae* type, but this was later found to belong to the *brassii* type.

The great importance of these data is that the *brassii* type is by far the oldest. In fact *Nothofagus* ranges among the earliest generically identifiable fossil Angiosperm pollen types of the world.

The *brassii* type is perpetuated during the Tertiary till the Pliocene, but already in the Upper Cretaceous it is joined by the *fusca* type; the *menziesii* type appears later, in the Oligocene, as recorded by Couper (1960a).

It is tempting to derive data on the New Zealand palaeoclimate from the occurrence of fossil *Nothofagus* and other fossils found with it. In the Miocene (or \pm younger) *Cocos* and ?*Avicennia* are among the latter. Couper (1952) in reviewing *Nothofagus* as a climate indicator concluded that the occurrence of *Cocos* together with *Nothofagus* is 'anomalous'. But at that time he could not know that some *Nothofagus* species of the *brassii* pollen type still grow in New Caledonia under tropical conditions almost to sealevel. Besides, it should be observed that one cannot simply infer that a fossil *Cocos* must have possessed the

same restricted thermo-ecological range as the present *Cocos nucifera*. Furthermore, *Avicennia* is even at present growing in the northern tip of New Zealand. Finally, the Tertiary climate of New Zealand must have been distinctly warmer than it is at present. So I feel that with our increased knowledge the term 'anomalous' is no longer justified.

According to the pollen record many species of *Nothofagus* existed in the New Zealand Tertiary, but not all are found throughout this period.

According to Couper (1953a, 1953b) and Couper & Harris (1960), all species of the *cranwellae* group—*brassii* type became extinct before the Pliocene, or latest in the Upper Pliocene; none is ever found in the Pleistocene.

The *fusca* and *menziesii* types were perpetuated in the fossil record up till the Recent.

A noteworthy remark by Couper (1953b) is that in comparing fossil New Zealand pollen types with Australian ones he found some 'pollen species' very similar. This does not prove that New Zealand shared 'botanical species' with Australia, because we have seen that a pollen species may cover more than one botanical species, but it probably indicates close affinity.

I may add that in scanning the lists of fossils found together with *Nothofagus* in New Zealand and Fuegia, there appears to be a striking homogeneity in this part of the Sub-antarctic, and this affinity is still expressed generically in the present flora, pointing to a great common floristic affinity, hence common history, at least onwards of the Upper Cretaceous.

Concluding, New Zealand must have harboured a large number of *Nothofagus* species, maybe some 20—30; in the Cretaceous mainly of the *brassii* pollen type with one late record of the *menziesii* type, in the Tertiary of all three pollen types. Several species lived only for a certain period in the Tertiary. There was a good similarity with Australian 'pollen species'.

Antarctica. — The first fossil records were from Seymour Island, from where Dusén (1908) attributed macrofossils to species of *Fagus*, from Oligocene deposits, mentioned by Cranwell (1963: 395) also from the Upper Cretaceous. In part they were correlated with some other fossil species from Fuegia. There is no doubt that all these belong to *Nothofagus*.

Mrs. Cranwell (1959) was the first to describe microfossils from Seymour I. situated on the tip of Antarctica (64° W, 57° S) opposite Fuegia, and among them are pollen of *Nothofagus*. She could correct Dusén about the age of the strata which is Early Miocene. In a very recent paper (1969) she corrected the age of the Younger Seymour material which is probably older, viz. Paleocene (Maastrichtien); the Snow Hill samples and Older Seymour material is Upper Cretaceous (Campanian) and contains the *fusca* type. The dominants among the pollen were Conifers and *Nothofagus*, a striking parallel with New Zealand! The pollens belong to the *brassii* and *fusca* types; surprisingly, the *menziesii* type which is so abundant in living South American species was not found.

A second record, remote from the above, was published by Cranwell, Harrington & Speden (1960), viz. from the McMurdo Sound District, Grahamland, Ross Sea (c. 165° E, 77° S), opposite New Zealand, supposed to be late Cretaceous to Oligocene. These are now by Mrs. Cranwell (1969) believed to be Upper Eocene. Among the pollens, none of which was found identical with those of Seymour I., *Nothofagus* predominates, pollen of conifers being in smaller quantity with palmoid and proteaceous types.

Summarizing on Antarctica: though data are yet few, there appears to be an astounding parallelism between the fossil evidence with that of New Zealand. It is of eminent value that the *brassii* type was found so early and so close to South America.

Southern South America. — Ten living species, of which 3 evergreen and 7 deciduous. Dusén (1899), Gothen, and others described various macrofossils, attributed to *Fagus* etc. They are certainly *Nothofagus* species.

According to Archangelski (1970) no *Nothofagus* fossils are recorded from the South American (Argentine) Cretaceous. In the Eocene flora of Rio Turbia (Santa Cruz Province), at 52° S *Nothofagus* is dominant (leaf impressions, wood). It was said that *Fagus* wood occurs here, but no pollen records sustain this.

In the Oligocene floras of Rio Pichileufí (Rio Negro Province) at 41° S in Argentina, and the similar one at Concepción-Arauco, at 37° S in Chile no *Nothofagus* was found.

Recently Cookson & Cranwell (1967) have published the first *Nothofagus* pollen records from the Fuegian mainland in the valley of the Río Leña Dura at c. 53° S. The age of these strata is Eo-Oligocene (probably Eocene) and they contain pollen of the *brassii* and *fusca* types.

Summarizing this chapter, the main results are:

- (i) *Nothofagus* species of the *brassii* pollen type existed in Australia, New Zealand, and Antarctica (Seymour I.) already at least from the Upper Cretaceous.
- (ii) This pollen type was abundantly perpetuated and is known in the Tertiary from New Guinea (onwards of the Upper Miocene), Australia, New Zealand, Seymour Island, and Fuegia.
- (iii) *Nothofagus* species of the *fusca* pollen type: the oldest occurrence is known from the Upper Cretaceous in Seymour I. (Antarctica); it occurs further widely distributed all over Australia, New Zealand, ?McMurdo Sound, and southern South America. The earliest record of the *menziesii* pollen type is as far as we know of less wide distribution, dating in New Zealand from the Eo-Oligocene; older records from New Zealand are as yet uncertain.
- (iv) The impression is that there must have been many dozens of botanical species.
- (v) The impression is further that if more places were as intensely searched as New Zealand, similar abundances will be found and gaps filled in the pollen record.
- (vi) Including the fossil records there is thus a tolerably complete, continuous range from New Guinea, through Australia, New Caledonia, Tasmania, New Zealand, northern Antarctica to southern South America.

The summary on this impressive pollen record should include a statement on the records of *Nothofagus* pollen from the northern hemisphere. It is curious that claims of fossil *Nothofagus* pollen from the northern hemisphere keep appearing, even in the past decade, e.g. by Potonié (1960), Ma Khin Sein (1961), Ames & Riesel (1962), Kedves (1964), Ramanujam (1966), and Kuprianova (1967). This is also the case for *Podocarpus* pollen. Significantly, they represent rare occurrences and identifications are debatable or definitely erroneous. If some are genuine I feel inclined to attribute their occurrence to long-distance dispersal from the south at a time when the *Nothofagus* forests were far more extensive, especially in Australia, than they are at present. Such long-distance dispersal has, admittedly in the southern zone of the roaring forties, been found to occur, notably in recent peats on Gough I. by Hafsten. Such accidental occurrences can, however, certainly not be taken as an indication for the existence of *Nothofagus* or *Podocarpus* trees growing on the northern hemisphere. This conclusion is agreed on by the great *Nothofagus* pollen specialist Couper (in litt.) and by Mrs. Cranwell (1963) and reflects also the opinion of Muller (personal communication).

11. PHYLOGENY OF NOTHOFAGUS, IN TIME AND SPACE

An interpretation of the origin and spread of the southern hemisphere genus *Nothofagus* cannot be divorced from considering that of the northern hemisphere genus *Fagus*, the pair forming together the subfamily *Fagoideae*. At present the smallest distributional gap between these two genera is *Fagus* in Formosa and southern China and *Nothofagus* in New Guinea.

In this connection it is noteworthy to observe that within this same area, ranging from the Sino-Himalayan area to New Guinea and Queensland all 5 other genera of *Fagaceae*¹⁾ are represented. Four of them occur in profusion in Malesia, viz. *Lithocarpus* and *Castanopsis* of the *Castanoideae* and *Quercus* and *Trigonobalanus* of the *Quercoideae*, only *Castanea* (a close ally of *Castanopsis*) being Sino-Himalayan-Japanese.

Thus at present the entire major morphological diversity is represented in the area between Yunnan and Queensland.

This leads to the question whether this centre is of secondary origin or whether it is a Fagaceous cradle-area persisting to the present day.

Besides the fact that in this region almost the entire gene pool of the family is concentrated, there are two important additional arguments for accepting it as the cradle-area of the family.

In the first place it is argued that, though pre-Tertiary fossils are not recorded yet, the indubitable Upper Cretaceous fossils of *Nothofagus* in the southern Pacific sites prove that the tie of *Nothofagus* with *Fagus* must date from even before that time; the ancient ancestral Fagaceous matrix from which they differentiated must have existed in the present transtropical disjunction of *Fagoideae* between southern China and Queensland.

Secondly, there is the remarkable genus *Trigonobalanus*, of which one species, *T. verticillatus*, is endemic on the Sunda shelf (Malaya, NW. Borneo) and the other, *T. doichangensis*, in N. Thailand. This genus is remarkable in several aspects, in the first place as the vegetative morphology of the two species is rather different, and in the second place because its more essential generic characters (floral structure, wood anatomy, pollen) show partly Fagoid and partly Quercoid affinity or features. Even so much that, whereas Forman (1964) reckons *Trigonobalanus* to *Quercoideae*, Soepadmo is inclined to find its affinity somewhat more with *Fagoideae*.

An other recently found significant aspect of *Trigonobalanus* is, that *T. verticillatus* has 42 ± 2 chromosomes²⁾ in the diploid and *c.* 21 in the haploid fase. This strongly contrasts with chromosome counts in other *Fagaceae* where the numbers 20 and 24 in diploid fase prevail. Obviously, *Trigonobalanus* is an ancient (? dysploid) palaeo-allotetraploid, virtually a relict which could well stem from an ancient Fagaceous matrix.

Finally the fact that the genus *Trigonobalanus* consists of two rather different local species point also to the relict character of both. This conclusion has received recent support by Mai (1970) who accepts that several species of *Trigonobalanus* occurred in the European Lauro-Fagaceous mesophytic forest climax from the mid-Eocene to the mid-Miocene as important dominants or co-dominants, associating the cupules and nuts with leaves of a fossil genus of *Fagaceae*, described as *Dryophyllum*.

The above-mentioned three arguments represent, I believe, convincing evidence that

¹⁾ Even if an 8th genus, *Chrysolepis*, is admitted, as is done by Forman (1966), of which one species occurs in California, this seems to be represented in the cradle-area, as Dr. Soepadmo communicated to me that if this genus is recognized a second species occurs in Indo-China.

²⁾ I owe this vital information to Dr. Ding Hou who is preparing a paper on this subject.

the region where the present concentration of Fagaceous morphology is found, broadly ranging from Yunnan to Queensland, must be the cradle-area of *Fagaceae* where the ancestral matrix to the present genera was located.

Only in passing I remark that for the possibility of a neotropical Fagaceous lineage across the tropics there are no such valid arguments; this neotropical origin can be eliminated with confidence.

It is then obvious that for *Nothofagus* ancestry we must also search for its real cradle somewhere in the Indo-Malesian region. One needs not to pin this down in New Guinea or any other single island, but consider the entire region from Yunnan and Indo-China through Malesia to Queensland as the matrix area of the ancestral stock of which we have no fossil material. And if this was found it would not even be certain that we should be able to recognize it. In this connection I might point in passing to the fact that if *Nothofagus* were entirely extinct, the pollens would have been described as some 'Stephanopores', but not referred to *Fagaceae*¹). We can also not hypothesize about the question whether *Nothofagus* split off from a sort of primitive *Fagus* or the reverse. It would be more reasonable to assume a common ancestral generic stock, distributed from Yunnan to Queensland, in the more northern, southern Chinese part of which a genus emerged which led to present northern hemisphere *Fagus* and independently in the more southern part somewhere in the New Guinea - Queensland area of which emerged what we now know as the southern hemisphere *Nothofagus*.

The assumed cradle-area of *Fagaceae* coincides in a marked way with the gradually developed idea that this Yunnan-Queensland area could well have been the critical theater in which Angiosperms evolved. This has been stressed recently by Takhtajan (1969) and by A. C. Smith (1970), the latter also defending my steady state concept as far as evolution of Phanerogams is concerned, saying that: 'After establishment and initial diversification in this' (Indo-Australian cradle-) 'area, they spread over the rest of the world's surfaces, which in configuration were not vastly different in the Middle and Late Cretaceous Period than they are today'. Though I do not wish to make any suggestion about the absolute age of Amentiferous orders, their fossil record is among the earliest known, though their ancestry is possibly not so old as that of *Ranales*.

I believe it is futile to speculate beyond the general importance of this cradle-area. It might be tempting to derive from table 1, from which appears that as far as known the *brassii* pollen type is the only type among fossil and living *Nothofagus* in New Caledonia and New Guinea, that *Nothofagus* arrived there later, after having evolved in northern Australia. This could then also lead to the view that the lowland occurrence of the *brassii* type in New Caledonia would be a secondary megatherm extension of the generic ecology.

About *Fagaceae* on the northern hemisphere, and *Fagus* in particular (see map 1) a few words first. There are abundant macrofossils on the northern hemisphere, and it seems certain according to Kirchheimer (1957) that they partly belong to several genera of

¹) As regards pollen morphology, Soepadmo (1968: 362) stated that the pollen of *Castanopsis* and *Lithocarpus* belong to one pollen type, that of *Fagus*, *Quercus*, and *Trigonobalanus* to a second type, while *Nothofagus* stands quite apart with a third distinct type. The close affinity of *Lithocarpus* and *Castanopsis*, therefore, does show up in the pollen morphology. On the other hand, the difference between the pollen of *Fagus* and *Nothofagus* does not reflect their taxonomic affinity and their forming together a distinct subfamily of the *Fagaceae*.

For establishing systematic affinity, pollen morphology is often, necessarily, less valuable than complete macrofossil material, because the latter possesses far more criteria for the interpretation of morphological structure of the complete plant.

Fagaceae, but some to other groups (*Alnus*). Unfortunately the pollen of the northern hemisphere *Fagaceae* gives no clue and possesses no peculiar features as *Nothofagus*. Anyway indubitable *Fagus* is found in amber of Oligo-Miocene age. Weyland (1964) admits *Fagus* also for the Tertiary and possibly also for the Cretaceous, saying that such forms cannot immediately be tied up with recent species (which is not surprising). There are for these uncertain fossils of the Upper Cretaceous and Tertiary form genera (*Dryophyllum*¹) and *Quercophyllum*) which could well belong to an ancient matrix which became largely extinct but from which modern *Fagus* emerged. Summarizing: *Fagus* obviously became clear in the Oligocene, but had then already a lineage in the warm-temperate to temperate northern hemisphere behind it. There remains a good chance that it dates back from the Upper Cretaceous.

Although *Nothofagus* occurs at present in the supposed cradle area only in New Guinea and a few adjacent islands, its ancestors might have occurred in other Malesian islands or North Queensland as well, but there is as yet no fossil pollen to sustain this.

No *Nothofagus* pollen has been found during the extensive research done in Sarawak and Brunei in strata ranging from the Middle Cretaceous to the Pliocene according to Muller (1968, and pers. comm.).

Also in NW. New Guinea the fossil *Nothofagus* pollen record is meagre and only located as far down as the Upper Miocene. But it would be too rash to conclude from this hitherto negative evidence that *Nothofagus* migrated into the Arfak Mountains only in geologically recent time. Far more data are needed from other strata in New Guinea to give evidence pro or con of its early history in this huge island.

In passing I may remark that one could hypothesize that the upland growth of *Nothofagus* in New Guinea (c. 750—3100 m) could have been responsible for the absence of pollen in marine sediments and that the upland deposits have been destroyed. Such reasoning has sometimes even been made to explain the sudden origin of Angiosperms thought to be originally an upland development which only later replaced the gymnospermous lowland forests, an idea repeatedly advanced by Axelrod (1970). From research done with recent pollen and experience with fossil pollen this is, however, untenable: most pollen gathered by montane river systems, by direct catchment or by soil erosion is transported downstream and incorporated in deltaic and offshore sediments. Also a considerable part of the pollen production, especially of anemophilous trees like *Nothofagus*, is directly transported to the sea and settles in the marine sediment. In Venezuelan marine sediments mangrove pollen and pollen from montane plants is consequently found together.

Anyway New Guinea occupies together with New Caledonia certainly a key position in that they harbour species belonging to subsect. *Bipartitae* of which all species are characterized by one of the two most ancient and most widespread types of pollen, the *brassii* type.

It is therefore reasonable to assume that New Guinea formed at least part of the region of the ancient Fagaceous matrix from which *Nothofagus* emerged.

From the fact of the Upper Cretaceous occurrence of *Nothofagus* pollen in Australia, New Zealand, and Seymour I., the conclusion is that the cradle of *Nothofagus* must date at least from pre-Upper Cretaceous time. And this was probably Early Cretaceous in view of the time needed to obtain the wide distribution already present in the Upper Cretaceous and the inevitable conclusion that it must have been tied up and sprung from an early

¹) This leaf type has quite recently been tied up by Mai (1970) with *Trigonobalanus* in an extremely interesting publication which came into my hands while the MS was already in press.

Fagaceous matrix which — if not on the northern hemisphere — must have been at the closest distance at least in the Malesian (montane) tropics.

To regard the present species array as representative of the ancient stock is very unlikely, but there is reason to assume that species with a well-developed lamellar cupule containing three nuts and male flowers in triads are morphologically undoubtedly more primitive than species with an elamellate or even ecupular nut and solitary male flowers.

Species of this primitive category are found in New Guinea, and also in New Caledonia, the land crowded with ancient primitive plants.

It could well be supposed that the gene pool of the New Caledonian species approaches a slightly more ancient condition, because of the more varied ecology (both lowland and mountains) as compared with the New Guinea assemblage which lacks the capacity to grow in the proper lowland, and the less strict phyllotaxis.

It may be that the original stock of ancient *Nothofagus brassii* type in New Guinea developed the *fusca* and *menziesii* types, it may be that this occurred in ancient Queensland.

The great fact is that *Nothofagus brassii* ancestors succeeded in spreading (almost) throughout Australia and to New Zealand, and onwards to Seymour Island and Fuegia.

Whether this was by way of Tasmania or by way of New Caledonia is questionable. Tasmania harbours *N. gunnii*, a characteristic deciduous species of sect. *Nothofagus*, which is absent from New Zealand, but reappears in southern South America, where is found its nearest congener *N. antarctica*. *N. gunnii* is certainly a primitive species in sect. *Nothofagus*, by its 4-valved cupule with entire lamellae and containing three nuts.

The pollen of *N. antarctica* and *N. gunnii* belong to the *fusca* type, which is, according to the fossil record, precisely the second-oldest pollen type as recorded by Couper for the Upper Cretaceous.

In Australasia and South America the *fusca* pollen type occurs among the living representatives of both evergreen and deciduous species. It is likely that the deciduous habit already developed in Australia. It may well be that it already existed in the ancient *brassii* matrix; unfortunately, the pollen can give no clue about this character for the fossils.

As to New Caledonia, it is curious that no *fusca* and *menziesii* types occur. It might point to an early distribution of the *brassii* type in the Cretaceous, but later isolation (with New Guinea) from the Australian speciation centre where the *fusca* and *menziesii* types developed. In this trend of thought it would appear that New Caledonia did not serve as a post-Cretaceous pathway of *Nothofagus* towards New Zealand. The New Hebrides mountains must be still explored.

In Australia recently the fossil record was extended to the Upper Cretaceous in Victoria. The further story in Australia is rather simple: the warm, moist Tertiary abounded with species of all three pollen types; the onset of the desiccation and the Ice Age were responsible for a wholesale extinction in the Pliocene, from which the most temperature and moistness-sensitive species of the *brassii* type fell a victim and suffered entire extinction. A meagre triplet survived in extremely restricted places, one of the *fusca* type (*N. gunnii* in Tasmania), two of the *menziesii* type (*N. moorei* and *N. cunninghamii*), vestiges of a glorious past.

As to New Zealand, at least a Cretaceous land connection with Australia or Tasmania must be suggested, because in the first place the oldest *brassii* type reached it in the Upper Cretaceous, but besides the *fusca* and *menziesii* types were there in profusion in the Upper Cretaceous and Early Tertiary respectively. And as Couper remarked some of the Tertiary New Zealand pollens are very similar to Australian ones, which includes the possibility that they had species in common on this Australasian continent. There is of course no necessity to assume this 'continental land' to have been intact all through this epoch, but

there must have been periods of intense contact to allow dispersal of these southern beeches.

In the New Zealandian Cretaceous region which must have had land connections with Antarctica as well, at least both in the Early Cretaceous and in the Early Tertiary as testified by the finds of the *brassii* type in Seymour Island and the occurrence of the *menziesii* and *fusca* types in South America, there must have been a profuse speciation as shown by the many fossil species described and occurring throughout the Tertiary. Not all species survived this whole period, some became extinct in the Miocene, or even Eocene. And there was an abrupt end to all of the *brassii* type and most of the other two types in the Lower Pliocene, an extinction doubtless due to the onset of the Ice Age.

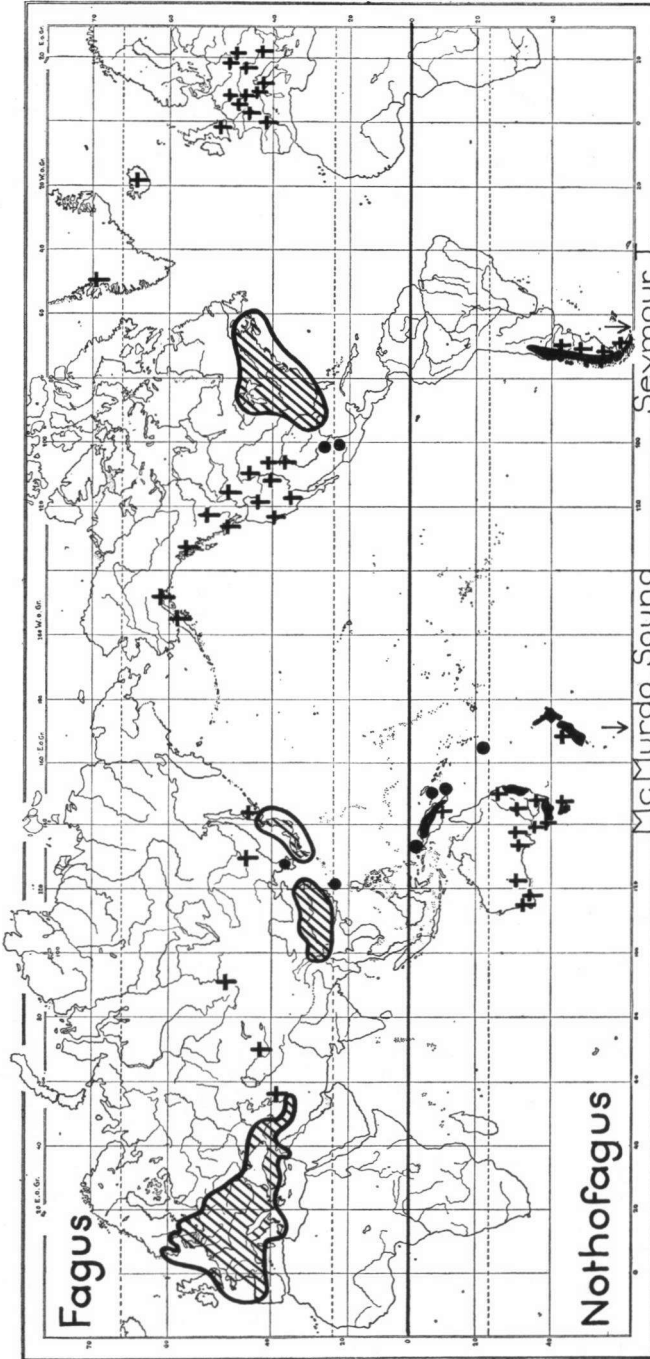
Whether there have been in the Australasian region very primitive species with more than 3 nuts per cupule (as in the South American *N. alessandrii*) or derived types with cupules adorned with an intricate pattern of appendages, such as are still living in South America, is of course unknown. But the gene pool carried by the representatives which contained all three types and spread along the borderland of Antarctica must have been distinctly richer than is reflected by the two extremely meagre but most important fossil finds at McMurdo Sound and Seymour Island. In both places, however, the accompanying fossil assemblage is similar to that found in New Zealand at comparable geological age, giving this assumption a not unreasonable background.

The Cretaceous-Tertiary borderland antarctic Nothofagetum will have allowed only for hardy species, evergreen and deciduous, similar in ecology to *N. antarctica*, *N. pumilio*, and *N. cliffortioides* which also now grow to the tree limit at 55° S. The antarctic tree limit conditions at c. 70° S will have been similar to those in the northern hemisphere, with denser, higher forests along the coastal regions, and more stunted, gradually dwarfing and spaced to the tree limit.

As we have seen there are from southern South America Eocene records of the occurrence of the *brassii* and *fusca* types and there are living species with the *menziesii* and *fusca* pollen types. Though the record is very incomplete, through the meagre research as yet performed, it is reasonable to expect that the situation in Fuegia will not have differed from that in Australia and New Zealand. This means that it can confidently be expected that there will be a continuous record for the *fusca* type till the present, and probably also of the *menziesii* type, while it can be expected that the *brassii* type will be found up till the Pliocene. There is also good reason to assume, judging from the abundance of macrofossils and the similarity of accompanying trees, and comparison with the finds on Seymour I., that the *Nothofagus* assemblage must have been very much richer in the Tertiary than it is at present. The deterioration of the climate through the Tertiary, initially slow, but gaining strength towards the end of the Tertiary, came to a climax with the Pleistocene Ice Age which played havoc with much of the austral mesophytic forest¹).

¹) The destructive influence of the deteriorating climate on the 'Arcto-Tertiary' Fago-Lauraceous mesophytic forest on the northern hemisphere resulted in a reflected image of the same process of gradual extinction, finally accelerated towards the end of the Tertiary with the onset of the Ice Age in the Pleistocene. Except in China and local areas in West Asia most of this mesophytic forest became extinct, because the east-west directed mountain massifs did not allow for escape possibility southward, except for a few genera, e.g. *Liquidambar*, *Platanus*, etc., which managed to survive as local relicts in the subtropics. In China the mesophytic forest zone could move southward with the southward latitudinal move of the warm-temperate and subtropical climate zones, and furthermore maintain its footholds in Japan and Formosa thanks to the ameliorate oceanic climate of these West Pacific lands.

This broad explanation is, however, in my opinion not sufficient for the whole story of extinction of this mesophytic forest, as several of these relicts are now so very much restricted — as for example *Sequoia*, *Sequoiadendron*, the primitive *Platanus kerrii*, *Metasequoia*, *Trigonobalanus*, and many more — that additional



Map 1. Distribution of *Fagus* and *Nothofagus*; fossils indicated by crosses.

It could be questioned why *Nothofagus*, which is now found living to 33° S in S. America, as far as the meagre fossil record goes is absent in the Oligocene at 41—37° S. Especially if one takes into consideration that it must have had time to spread during almost the entire Tertiary.

A reasonable explanation for this could be that by the passage eastwards along the borderland of Antarctica, only species succeeded which could stand a temperate to cold climate, and in this way the ancient capacity of the ancestral stock to produce more megatherm species was underway eliminated from the gene pool by selection.

This microthermic ecology must also have been shared by species of the *brassii* type. This is still present among living species of this subsection; several species are in New Guinea only found in the subalpine zone, for example *N. resinosa* and *N. pseudoresinosa* (2300—3100 m), token of hardiness. They are not microphyllous, which agrees with the Fuegian macrofossils. In living *Nothofagus* leaf-size itself is not a measure for hardiness.

12. BI-HEMISPHERIC RANGES HOMOLOGOUS WITH THAT OF FAGOIDEAE (Maps 1 & 2)

Ranges matching or approximating that of *Nothofagus* are in the southern Pacific not rare. Ranges similar to that of *Fagus* are common on the northern hemisphere.

But there are very few which show a similar pattern of an undoubtedly genealogical lineage, that is of a higher order, such as *Fagoideae*, the ranges of *Fagus* and *Nothofagus* combined into a characteristic bi-hemispherical range, 'hour-glass-shaped' narrowed in the Malesian tropical middle. See map 1.

In chapter 9 I have already referred to the fact that there are, at several levels (genus, subfamily, and family) bi-hemispheric relationships, in which one counterpart is northern and the other southern. Obviously such affinities are lineages sprung from a common ancestral matrix which is likely to have been situated halfway, that is, in the tropical and subtropical zone.

It is not surprising that not all taxa of higher order which occur on both hemispheres still exhibit this picture in a very clear and distinct way. Starting from these ancient matrices it will usually not have occurred that the gene pool was sharply divided into two distinct parts; this might occur but would seem the exception rather than the rule. Thus we find that for example *Ericaceae* and *Epacridaceae* are not sharply counterparts, as for example *Gaultheria* is found both northern and southern. It can be expected, therefore, that sharply separated complements are rather rare.

Such distributions are found in all sorts and to various degree. They have often been obscured by later deviating evolution in the counterparts and become then no longer recognizable. Evolutionary trends and speed, and rate of spread, have been very different for various groups, and extinction as well. The term 'random' is here not well in place, one could better call the situation 'erratic', by which I mean that there is no single rule about this for all groups. Each group behaved, according to its capacities and potentialities, in an opportune way. One can simply not imagine, let alone explain, why certain taxa

explanation has to be called for, the deterioration of climate (cold or drought) being insufficient as a single factor. This touches the general problem of extinction, I am afraid, which is still very much obscure. Possibly, biotic factors may play a more important role in this than is presently understood. I think in this matter of viruses, bacteria, and fungi in plants, as suggested by the elm and chestnut diseases, and the large-scale extinction of *Zostera marina*. Also in the fauna colossal shifts seem to occur by biotic factors as shown by the recent destruction of corals in the Pacific.

differentiated to a large degree and why form-making was poor in others. It goes beyond our comprehension why certain taxa developed a large number of species or genera, and others did not, and especially why some diverged and others kept their precise identity for very long geological epochs, similar as *Gingko*, *Araucaria*, etc. Whether we will ever be able to dig such secrets out of the genome structures where they must be seated, remains questionable.

However, *Fagoideae* is a remarkably good illustrative example of 'keeping identity', as its genealogical lineage cannot be doubted, and the ranges of *Fagus* and *Nothofagus* are exemplary complementary. See map 1.

Both *Fagus* and *Nothofagus* are not especially microtherm, but they are certainly largely mesotherm to temperate. *Nothofagus* has the largest eco-climatical amplitude of the pair by growing at present in the tropics besides montane and subalpine montane also with some New Caledonian species in the tropical lowland.

Therefore, it is reasonable to assume that mesotherm and microtherm groups are the most likely to show a similar bi-hemisphere distribution through the Malesian montane pathway connecting the two hemispheres.

Here, again, we will have to face an erratic array, 'virility', keeping identity, extinction, etc. Some of these genera or species will show to have been able to maintain themselves on single tropical montane stations, others became extinct in the tropical zone. They are then expected to represent equiformal or homologous ranges to various degree.

Besides, within this group of mesotherm to temperate taxa, they vary in thermophilous response and capacity, and none can be expected to be exactly identical in this respect to an other. They have behaved as an assemblage varying from tropical montane to alpine.

In my treatise of the flora of Mount Kinabalu (1964) I have called attention to this most interesting group of plants and given examples of ranges which appear almost intact, as that of *Euphrasia*, but added others which have only still a few stations: *Poa* with 3 (Kinabalu, Central Celebes, New Guinea), *Oreomyrrhis* with 2 (New Guinea and Kinabalu), *Trisetum* with 1 (Kinabalu), *Eryngium* with 1 (Ceram), *Centunculus* with 1 (Timor).

But there are numerous others which have no present tropical-montane station in the Malesian tropics although their range extends over it, for example: *Aphanes*, *Asperula*, *Barbarea*, *Caltha*, *Capsella*, *Centaurium*, *Eritrichum*, *Erodium*, *Gypsophila*, *Lepidium*, *Limosella*, *Linum*, *Lotus*, *Lythrum*, *Mentha*, *Myosurus*, *Papaver*, *Prunella*, *Samolus*, *Scleranthus*, *Thlaspi*, *Tillaea*, *Trigonella*, etc. etc.

The range of such genera can no longer be called bi-hemispheric, but has become bipolar when their stations in the tropical and sometimes adjacent subtropical zones have disappeared and their northern and southern partial ranges are separated by a considerable transtropical disjunction.

It is also to be suspected that sometimes ancient or aberrant species are found in the isolated tropical montane stations, and in this respect I remind of the rather aberrant features of *Eryngium moluccanum* and of *Ranunculus fasciculiflorus*, both alpinics of Mount Binaya in Ceram I. (Moluccas).

Imagining the vicissitudes of the geographical physiography of Malesian tropics during the huge period from the Cretaceous to the present and the unknown biogeographical role played by the Tethys Sea, it is clear that only by exception representatives of such taxa, mostly genera, could maintain themselves. They lived a precarious life. With mountain ranges dwindling down by tropical erosion footholds were lost, and by migration others were gained; for all it was: to spread or die.

Spreading in a geological period means inevitably jumping from one decaying mountain to another coming up. Hence, I have emphasized (van Steenis, 1967) that many plants will be older than the mountains they grow on at present; they may even be endemic and nonetheless not have had their cradle on the mountain on which they are now endemic. This will be clear to any chorologist who wants to get some insight by thinking in historical terms necessary to get at least some faint idea of the implications of the time dynamics of plant wandering.

It is therefore not likely that species, for example of Mount Kinabalu, originated there; the occurrence of *Euphrasia* certainly must be ascribed to a later accession. It is more likely that mountain species of lowland genera are real neo-endemics. Mountains rising in lowland countries or penepains with no neighbouring mountains with a mountain flora available for exchange, will develop and carry only a mountain flora recruited from the lowland genera, say of *Lauraceae*, *Symplocos*, *Ericaceae*, *Theaceae*, *Myrtaceae*, etc. Such a situation is of course seldom found, especially in the Malesian tropics with their widespread active orogeny, present and past. But it would account for instance for the almost absence of true mountain plants in Guadalcanal, which developed obviously without access of such alpine within effective dispersal distance.

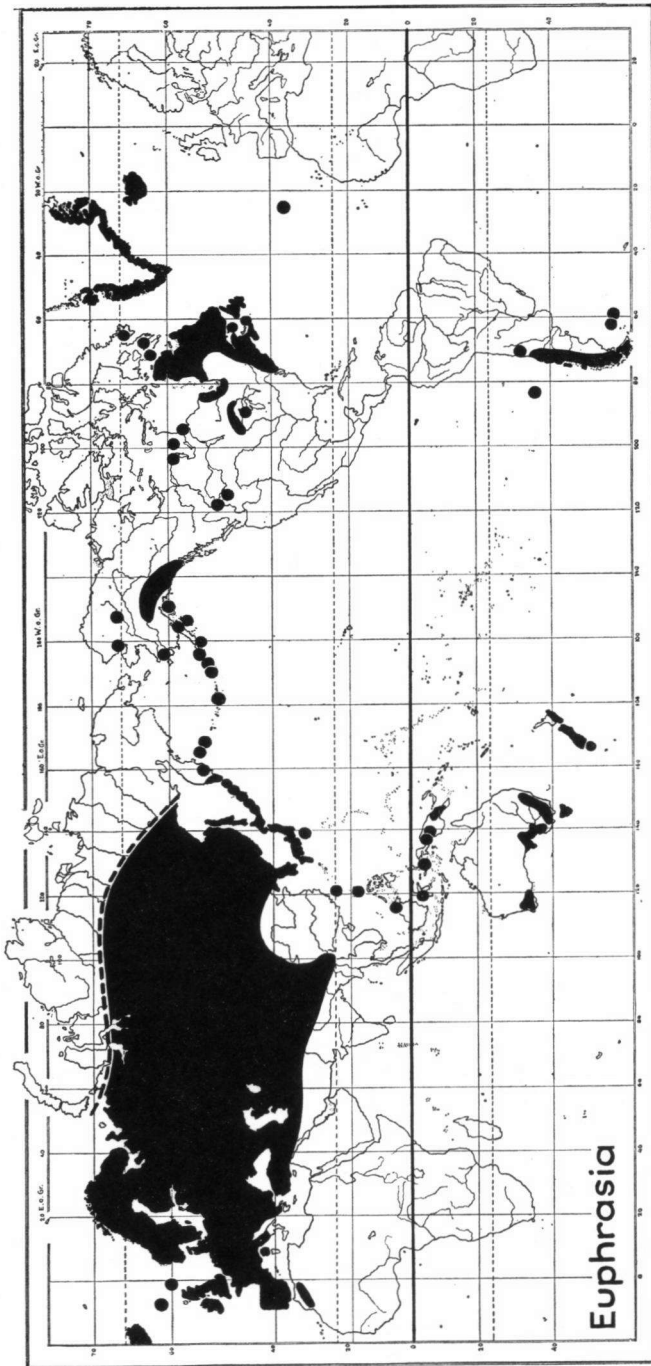
I have put forward these considerations for a better understanding of the generic range of *Euphrasia* (*Scrophulariaceae*) which is in my opinion a remarkable example of a range which is homologous with that of the *Fagoideae*. It is also ecologically comparable with the understanding that it is eco-climatically somewhat more temperate to cold fashioned. Therefore it occurs in the tropics at somewhat higher elevation than *Nothofagus*, viz. from 2000—4000 m. Consequently its range on the northern hemisphere goes farther north and is more extensive than that of *Fagus*. Probably it suffered also less from the Pleistocene Ice Age than *Fagus*, and spreads furthermore more rapidly than *Fagus*. See map 2.

A significant point of further agreement between the ranges of *Fagoideae* and *Euphrasia* is that, similar to the situation in *Fagoideae*, at present the greatest morphological diversity of *Euphrasia* is found on the southern hemisphere. In New Zealand even two endemic entities, obviously representing specialisations, are sometimes regarded as closely allied, but separate genera, viz. *Anagosperra* and *Siphonidium*.

An other parallel with the Fagoid range may be represented by the *Veronica-Hebe-Parahebe-Dezneria* complex. This also shows a most remarkable form-making in the austral region. One would even be inclined to parallelize the position of *Hebe* in this complex with that of the *Bipartitae* in *Nothofagus*, that is, the most ancient type.

It is easily understood that many of the 'hour-glass-shaped, bi-hemispheric, trans-Malesian-tropics ranges' (see p. 77, 89) or sometimes bipolar ranges (see p. 90) have come into being by means of land areas along the western side of the Pacific ranging from the Siberian shield to Antarctica, not necessarily continuous land *all* the time, as some unimaginative opponents of the landbridge, better 'land theory' in plant-geography, sometimes unreasonably have deduced.

It also involves to accept the steady state principle in geomorphology, at least as far as Conifers, Taxads, and Angiosperms are concerned, that is at least from the Cretaceous. There can be no question to explain such ranges by a southern Gondwana land origin, as correctly pointed out by Diels (1928) in his classic critique of the continental drift theory in its original concept for the Australian-Papuan flora. Anyway, it requires a close contact between northern and southern land masses (of Asia and Australia) in the Early Cretaceous.



Map 2. Distribution of *Euphrasia*.

And may be even in the Upper Jurassic¹⁾, because we must be well aware that all fossil finds give a minimum age, not an absolute age. And experience has taught that with progress of research in palaeontology hitherto almost all groups appear to be older than considered half a century ago.

It stands to reason that the 'phylogenetic chorology', that is phylogenetic development and range extension in time and space, of *Fagoideae* and *Euphrasia* and many other taxa of their distributional type (see pp. 77, 90) must have gone synchronously. If the *Fagoideae* range dates from the Upper Cretaceous, so must that of *Euphrasia*, and the other taxa.

It is also clear that bi-hemispheric ranges of this kind must be of high antiquity.

From this follows that such ranges as we find still largely essentially unimpaired in *Fagoideae* and *Euphrasia* must be rare in the present plant world, because to maintain such range and besides maintain taxonomic characters by which we can still with full confidence consider the taxa as representing a true genealogical lineage (a genus as *Euphrasia*, a complex as that of *Hebe-Veronica*, a subfamily as *Fagoideae*) it requires a high taxonomic and ecological stability against evolutionary pressure or tendency towards change, towards diversity and consequent frequent extinction. Most plant groups will have been less stable in these aspects and evolution will have caused a so much chequered phylogeny that taxonomists only very hesitatingly will suggest lineages, or are even not capable to distinguish lineages ('*Sippen*') with any confidence. The uncertainty of discerning such lineages in more rapidly evolving and diverging groups is enlarged by the greater probability that in such groups extinction has been more severe and has led to obliteration of too many affinities and face us with too many missing links.

13. CONCLUDING THESESES

The detailed study of *Nothofagus*, recent and fossil, leads to several conclusions of more general bearing, both for taxonomy and for chorology.

Because of the restricted means of effective dispersal of *Nothofagus* by which long-distance dispersal is indubitably excluded, and because of its wide and well-known distribution and ecology, and an ample trustworthy fossil evidence of great age, it is a pre-eminent example for geobotanical conclusions.

In the preceding chapters I have already alluded to some of the general rules which we can derive from this detailed study, and the corollaries involved. Clearly a 'New Chorology' is needed in plant-geography. I am aware that it will drastically differ from some currently accepted views.

I find it desirable to summarize into a number of theses.

(i) The present centre of morphological diversity of *Fagaceae* where all genera still

¹⁾ Axelrod (1970: 285—290) has convincingly summarized evidence and reasoning for a pre-Cretaceous origin of Phanerogams.

On pollen evidence Muller (1970: 428, 444) concluded that 'except for the possibility that the *Magnoliales* considerably preceded the development of other groups, the palynological evidence does not support the view that the Angiosperms had behind them a long evolutionary history, starting as early as the Permian', as postulated by Axelrod and Eames. He tabulated the plants possibly ancestral to *Polycarpiceae* ('*Clavatipollenites*'), from the Upper Jurassic, but the 'modern' branches of Phanerogams from the Cretaceous. However, Muller (l.c. 429) leaves the door open for presence of their pre-Cretaceous ancestors which could possibly have had primitive pollen types — evolution of pollen types lagging behind morphological evolution — and admitting that palynology has some (regrettable) limitations.

occur, viz. from Yunnan to Queensland, appears to be the 'cradle-area' of the family *Fagaceae* which harboured its ancestral matrix (chapter 11).

In the southern part of this matrix *Nothofagus* differentiated and spread in austral regions, other genera evolved in this matrix spread with the mesophytic forests over the northern hemisphere, westwards towards Europe and eastwards via Beringia to North and Central America.

(ii) A Gondwana Land origin ('cradle') of *Fagaceae* is taxonomically an impossible assumption, a biphyletic origin of *Fagoideae* is still more so.

(iii) The fact that *Nothofagus* occurred already in the Upper Cretaceous in Australia, New Zealand, and Antarctica, and that its birth-place from the ancestral Fagaceous stock can at most have been closest to the fossil sites in the tropics, involves that it must have taken some time to reach New Zealand, which dates the age of the ancestral stock back to the Upper Jurassic, at least Lower Cretaceous.

(iv) As *Fagaceae* themselves are morphologically certainly derived plants which cannot in the least be tied up directly with Pteridosperms or other potential Gymnosperm ancestors, the origin of Angiosperms must be considerably older than the Cretaceous.

(v) The shrinking of the genus *Nothofagus* in space and size is exemplary for extinction brought along by the two major environmental changes affecting the South Pacific at the end of the Tertiary, viz. desiccation of the Australian continent and the Ice Age.

(vi) The ancient range of *Nothofagus* can be explained in an unrestrained way under the steady state theory, provided the filling at some period in the Upper Cretaceous of the present oceanic gaps between the borderland of Antarctica and South America and Australasia before the Upper Cretaceous (allowing the *brassii* and *fusca* types to reach Seymour Island in the Upper Cretaceous and Fuegia in the Early Tertiary).

(vii) If continental drift ever occurred in the austral regions it must have taken place long before the Cretaceous. The Fagaceous matrix can only have developed if already in the (at least) Late Jurassic southern and northern hemisphere continental lands have been in contact in the Malesian tropics.

(viii) The occurrence of ranges which are equiformal (homologous) to that of *Fagoideae* and which show a similar bi-hemispheric affinity either on family level (see p. 77) or on generic level (see p. 90) is assumed to point to an ancient synchronous development of many unrelated groups in the plant kingdom, involving both ligneous and herbaceous plant groups.

(ix) For the cradle of these lineages the Sino-Malesian subtropics and montane tropics represent a crucial region.

Among these lineages *Euphrasia* is exemplary in exhibiting a remarkably unimpaired, ecological similar distribution and speciation pattern to such an extent that it must be concluded that this distribution is as ancient as that of *Fagoideae*, *Magnoliaceae*/*Winteraceae*, and many other groups mentioned (pp. 77, 90, 91.).

(x) Although *Euphrasia* and many other lineages are morphologically far more 'ad-

vanced' in the taxonomic system as compared with *Fagaceae* or *Magnoliaceae/Winteraceae*, they must be of great antiquity and date back to the Cretaceous.

We must obviously abandon the current view that morphologically advanced groups are necessarily of young age.

(xi) We have to abandon the common, light-heartedly accepted view that size and structure of diaspores is necessarily a measure for degree of success of dispersal. Range extension in primary vegetation goes slowly, by plant associations and ecological groups and rather independent of the structure of diaspores.

(xii) The degree of evolutionary development, form making, and extinction is unpredictable and erratic (see p. 75).

Biogeography is, however, not erratic as plants which evolved more or less simultaneously will take (or at least have) the same opportunity to spread according their ecological capacity and the geomorphological future ahead of them, which is the same for all plants spread together.

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POSTSCRIPT

When this paper was in galley proof most important news was communicated by Dr. S. Archangelsky, Divisio Paleobotanica, Museo de Ciencias Naturales, La Plata, Argentina, which he generously permitted me, through Mr. J. Muller, to quote, for which I express my sincere thanks.

1) The oldest pollen record from Patagonia is from Lower Maestrichtian Jaguel Formation, Upper Cretaceous, Prov. Rio Negro. This is of the *brassii* type, which perpetuates in small quantities in the Paleocene. In the Eocene pollen of all three types (*brassii*, *menziesii*, and *fusca*) are abundant, both in Argentina and Chile.

2) Also at present the *brassii* type is still represented in Argentina, as it has appeared that pollen of the very rare, South American living species *N. alessandrii* Espinosa belongs to this type. Pollen of *N. alessandrii* had been described by Miss Cranwell (Rec. Auckl. New Zeal. Inst. 2: 190. 1939) and was attributed by her to the *fusca* type, but this record cannot be checked as no collecting number is given. I am convinced that it is based on erro-

neously identified material supplied to her by Skottsberg from the Arnold Arboretum Herbarium.

3) The *brassii* type is through this no longer bound to the purely tropical West Pacific sect. *Calusparassus* subsect. *Bilamellatae*, as *N. alessandrii* belongs to the leaf-shedding sect. *Nothofagus*. This makes it more comprehensible that the *brassii* type is among the oldest in the genus. Two small gaps in table 1 can now be reduced.

4) This better understanding is strengthened by the morphologically logical deduction which I made formerly (van Steenis, 1953, p. 310, 335; 1954, p. 267, fig. 1e) that *N. alessandrii* is the most primitive among the living species of sect. *Nothofagus* (7 ♀ flowers, a lamellate, 4-partite cupule).

Concluding, the new facts confirm the theory and strengthen it. I hope that the remaining gaps will be filled in future: records of the three pollen types through the Tertiary of Patagonia, further details on the three types in Antarctica, and Upper Cretaceous records from Queensland and possibly New Guinea.