THE LAND-BRIDGE THEORY IN BOTANY
with particular reference to tropical plants

by

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Contents

1. INTRODUCTION

This essay was primarily made as a background study for a lecture on 'Transpacific Floristic Affinities, particularly in the Tropical Zone' in a symposium on 'Pacific Basin Biogeography: Tropical Relationships' at the 10th Pacific Science Congress, Honolulu, August 1961 [1]).

The occasion was a welcome challenge to crystallize my knowledge and views on the fascinating subject of the Indo-Pacific plant geography which has occupied my thoughts for several decades. Besides, as a corollary of plant-geographical studies on the Malaysian flora, my interest in it was distinctly restimulated by the compilation of maps of Pacific plants for the work 'Pacific Plant Areas'.

I was of course aware that this study could not be restricted to tropical relationships and would involve a scrutiny of extra-tropical Pacific distribution. Furthermore it was clear that the problems of transpacific distribution found a counterpart in problems of transatlantic distribution and that both ranges are specialized cases of pantropical distribution. More and more I realize that *pantropical distribution represents the main problem of historical plant geography.* Its wide scope and intriguing implications bring us to the relation between distribution and dispersal.

The problem before us consists of the correlation of three features. First, the botanical affinities show an essential *latitudinal zonation,* running East—West, *vice versa,* in all zones, tropical, subtropical, warm-temperate, and temperate. This zonation is not only physiognomical but especially taxonomical, and concerns almost all families of both Gymnosperms and Angiosperms. Second, these latitudinal zones of affinity are intersected *longitudinally* by two oceans, mainly the Atlantic and Pacific running North—South, *vice versa.* Third, under the present distribution pattern of the land surface all continents are — or at least were before the Ice Age — connected through two wide terrestrial land-bridges and one very wide insular isthmus, *viz* the Panama isthmus linking the Americas, Beringia connecting North Asia and North America, and the Malaysian Archipelago joining Asia and Australia.

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[1]) An extremely curtailed abstract was published in Abstr. Symposium Pap. 10th Pac. Congr. 228—229, 1961.

Antarctica is an exception; its connection with South America and Australia respectively required a separate temperate land-bridge, but this seems to have been broken up already in early Tertiary times. The continental and oceanic islands excepted, *the entire land surface thus forms a terrestrial continuum, or almost so.* Consequently, in the near past the major part of the land surface of the globe was available for dispersal. Obviously ecological factors prevented a free exchange, resulting in the latitudinally zoned affinity. Therefore, it appeared of vital interest to examine the *thermo-ecological range of genera and families,* a subject familiar to me from my studies on the origin of the Malaysian mountain flora. As according to the fossil record the genesis of the present plant world has taken an immense time, it was also of vital interest to know as much as possible about climatic conditions and about palaeogeographical conditions in the past ages. Besides the reconstruction of the history of the continental floras, the problem of *origin of the island floras* is an inevitable corollary of the synthesis. For this latter problem it has appeared prominent to devote great attention to the reach and probabilities of dispersal (accessibility) and to the efficiency of the means of dispersal.

Furthermore, in arranging the botanical facts it could not be avoided to correlate their evaluation and interpretation with data, theories, and hypotheses of other disciplines of the natural sciences. I have therefore not refrained from venturing on the fields of palaeoclimatology, phytopalaeontology, geomorphology, and geophysics. I have freely borrowed from them in the discussions following the presentation of the botanical facts and not refrained from making critical remarks if I found discrepancies with botanical facts or deductions. It is of course clear that in the other disciplines I could cover only a small, or even very small, part of the vast literature and that even in the botanical discussion I had to set a limit to the digest of plant-geographical literature and discussion of the often controversial opinions. I have tried to cover the essential literature and hope not to have omitted vital information or to have made erroneous conclusions from disciplines in which, as a layman, I have insufficient faith in my judgement.

The general policy of the reasoning has been to fathom solutions offered in the past and to test them with evidence from other sources and, furthermore, to separate negative and positive evidence.

I have also tried to invent new data or dig out neglected facts and I have used some methodologies which were not or little used in plant-geographical discussion.

A careful weighing of the arguments has led me to become an adept of the land-bridge theory which seems to provide the only satisfactory explanation of the genesis of the present angiosperm plant world.

I have tried to fathom the minimum amount of land-bridges required for a reasonable reconstruction of the major features of plant geography through the ages. Three of them still exist in the recent geological age, *viz* Panama, Beringia, and Malaysia. Three others seem essential to understand the past, presumably that of the Mesozoic, *viz* a transoceanic tropical bridge in both the Pacific and Atlantic oceans, and a temperate one in the Pacific Antarctic. A fourth one, between Madagascar and Ceylon, is adopted provisionally; this connection might possibly be explained otherwise.

Naturally these land-bridges have not been synchronous and they must have had a chequered history. The problem of their age and duration has been very tentatively approached by judging the nature of the affinities and the palaeontological record. I have framed the tentative schematic reconstruction on four maps, 21—24, which must be regarded with great caution; they will serve as a basis but will need to be amended in future.

A special chapter is devoted to the discussion of the functioning of such land-bridges and the question whether terrestrial isthmuses are compulsory or that it would be sufficient to have had broad oceanic rises crowned by broad arcs of islands which served as ancient pathways. The conclusion is reached that the latter kind is only acceptable if it offers sufficient wide and high land separated by distances not exceeding a few dozens to at most a few hundreds of kilometres. Though recent geomorphological research has yielded some promising results it is admitted that geomorphology does not provide as yet convincing evidence for such large land surfaces required by the land-bridge theory.

It is clear that if there have been land-bridges in the past they have been used by both plants and animals. For that reason a succinct comparison has been made with Darlington's zoogeography of the Vertebrates. It has appeared that the main aspects of this work concern the Tertiary in which the Beringian and Panama isthmuses have been extremely important path ways. For the Mesozoic a tropical transatlantic and South Pacific land-bridge are envisaged as possible. There appears to be no serious discrepancy between plant-geography and his zoogeography as far as most main lines are concerned.

As to the illustrations I have restricted the reproduction of plant-geographical maps to those which are illustrative for the types.

I express my sincere thanks to several friends and colleagues who improved the text with their criticism and advice, in particular to Dr. P. W. Leenhouts, J. H. Kern, and Dr. J. van der Vecht, and for checking of data to Mr M. J. J. van Balgooy, all at Leyden. To Mr. D. H. Nicolson I owe unpublished data on *Spathiphyllum* in Melanesia, to Mr. E. J. H. Corner on *Moraceae*.

Just before this essay was going to the press it was read by Prof. Dr. R. Florin, Stockholm, whose criticism I sollicited. He did me the great favour in studying it extremely carefully and thus added to the polishing. Furthermore, I enjoyed the privilege of reading the final copy MS of his plant-geography of conifers and taxads in time and space, to which I have been allowed to refer where necessary; see further in the footnote on p. 341. We are both extremely pleased that these two plant-geographical studies, which were composed entirely independently and based on different sources — Florin's on a limited group of plants but inclusive of detailed fossil data, mine largely on the ranges of the recent Angiosperms — have led to a remarkably similar trend of thought, judgement, and conclusion. Mutually we agree "in all essentials" and we find it fortunate that our essays will appear almost simultaneously.

TERMINOLOGY. — I have already used here some terms, amphi-Pacific, trans-Pacific, *etc.* and to avoid confusion it seems useful to define these terms as used here as follows:

pantropical — throughout the tropics, that is at least in three stations, *viz* in America, Indo-Australia, and Africa.

sympatric — genera or species which have, at least essentially, the same pattern of distribution. Their ranges are usually equiform. Generally such plants also have a comparable ecology and not seldom belong to the same major type of vegetation. It is mostly assumed that these unrelated plants attained their distributional area together.

gravity centre — the area in which a taxon is best represented, either by number of species or by presence of higher taxa carrying weight by morphological diversity.

trans-Atlantic — occurring on both sides of the Atlantic, either disjunct or sometimes also found on stepping stones in it, irrespective as to whether represented also elsewhere or not.

amphi-Atlantic — confined to continental parts of the Americas and Europe and/or Africa (sometimes also present on interjacent islands), but absent from Asia and Australia.

amphi-transatlantic — the same as amphi-Atlantic, but in at least two disjunct areas on both sides of the Atlantic.

trans-Pacific — occurring on both sides of the Pacific, either disjunct or sometimes also found on stepping stones in it, irrespective as to whether represented also elsewhere or not.

amphi-Pacific — confined to continental parts of the Americas and/or East Asia, Malaysia, and Australia, or at least represented on islands adjacent to these continents (those west of the Andesite Line, and Galapagos, Desvanturades, Juan Fernandez), sometimes also present on interjacent islands, but not in Africa, Europe, and the Near East.

amphi-transpacific — the same as amphi-Pacific, but in at least two disjunct areas on both sides of the Pacific.

circum-Pacific — occurring in various places around the Pacific basin, not in Africa or Asia.

isthmus — properly a continuous, or almost continuous (Beringia) land-connection between two continents, also designated as a *terrestrial isthmian connection* to distinguish it clearly from an

insular isthmus — an island arc or other discontinuous land which represents plant-geographically an isthmus as the islands are situated close enough to each other to permit a certain degree of plant exchange by dispersal.

thermo-ecological terms — the following very approximate figures are attached to the terms with the altitudinal equivalent in the equatorial zone, according to *fig. 1:*

tropical — between 0—25° L; lowland and colline, 1—1000 m.
subtropical — 25—35° L; submontane, 1000—1500 m.
warm-temperate — 35—45° L; montane, 1500—2400 m.
temperate — 45—60° L; subalpine, 2400—4000 m.
cold — beyond 60° L; above 4000 m.

Terms which are used for an approximate indication of thermo-ecological behaviour of taxa (families, genera, species) are:

microtherm — adapted to a cold and/or temperate a climate.
mesotherm — adapted to a warm-temperate or subtropical climate.
megatherm — adapted to the tropical climate.

2. THE FIVE AMPHI-TRANSPACIFIC TYPES

Transpacific affinities fall roughly into five categories, corresponding with the five major climatic zones, temperate in the North and South, and subtropical on both sides of the equatorial belt. These zones are characterized by temperate, subtropical and tropical plants, which we can conveniently term microterm (or temperate), mesotherm and megatherm plants. It should be emphasized, however, that these terms refer to their ecological potentiality, *not to their geographical distribution.* Genera confined to the tropical zone have frequently produced microtherm species (*e.g.* the genus *Pandanus,* Pand.) or are even restricted to tropical-subalpine altitude (*e.g. Papuzilla,* Cruc. and *Monostachya,* Gram.). Besides, both microtherm and mesotherm plants from extra-tropical higher latitudes are capable to invade the warmer zones by ascending the mountains. Thus it is found that species of the typically microtherm genus *Drapetes,* Thym., which is characteristic of the cold South-Pacific Subantarctic, grow at alpine height on tropical mountains of New Guinea and Borneo. *Araucaria* is much less microtherm than *Drapetes* and consequently this mesotherm genus is not found in the temperate Subantarctic but in the subtropical South Pacific. Its species also ascend the mountains in the tropics but only to montane altitude in agreement with their latitudinal ecological behaviour.

(i) North Temperate

This type of distribution concerns the temperate and cold-temperate boreal plants. Although naturally the Pleistocene Ice Age — with its oscillations — made it possible for this flora to extend and retreat, and to radiate from refugia, this type does not show disjunctions which could not be explained by the geologically recent past. In the cold-temperate and arctic flora Bering Straits and its surrounding regions (Beringia) has, according to the many important contributions by Hultén, been a very important focus of distribution (1937, a), especially as it was a Glacial refuge (1958).

For our subject the North Temperate type is not of great interest as it can almost be explained by the present-day geographical situation. Therefore it has not been attempted to compile a list of species. In scanning Hultén's lists it is clear that hardly any representative of this type extends towards the equator, but there are some curious exceptions. Hultén (1959) agreed that *Trisetum spicatum* (L.) Richt. occurs on the summit of Mt Kinabalu, North Borneo, in its var. *alaskanum* (Nash) Hultén. I have recorded from the Papuan mountains *Drosera rotundifolia* L. subsp. *bracteata* Kern & Steen. (1955) in an entirely isolated position, as the nearest station of the species is in Japan.

(ii) North Warm-Temperate and Subtropical — *Maps 1—3*

This is the element or type which is in a disjunct way represented in both East Asia (mainly Japan and China) and North America, with very few areas which extend as far south as to cross the tropic of Cancer in both the Old and New Worlds. In that case the species mostly start to ascend the mountains and become montane or even subalpine in proportion to the degree of their approach to the tropical zone.

In North America this element is usually found in the southeastern United States though before the Ice Age it has also been present in the western lands, at least in part, according to the fossil record. There is no doubt whatever that the present disjunction is largely brought about by the wide influence of the Glacial Epoch over very large surfaces of the North American continent.

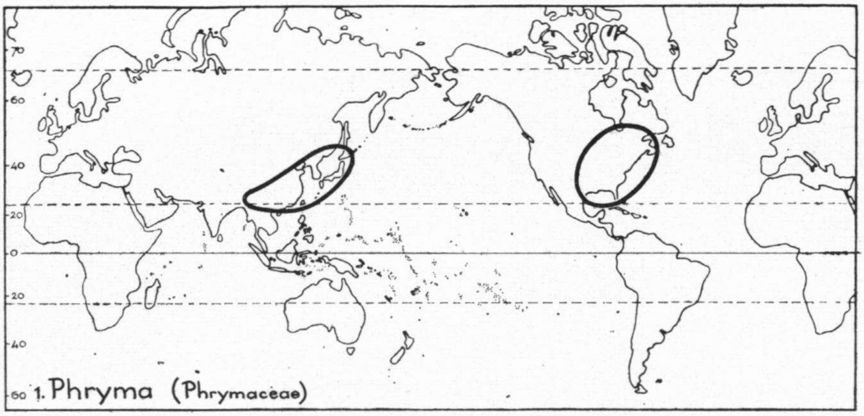
A direct former connection between East Asia and North America is not always the only solution to explain the present disjunction, as in some cases the fossil record — as far as we can trust it from fruits and pollen — seems to indicate that such genera were in pre-glacial time also represented through Asia and Europe, for example *Nyssa,* Nyss., *Engelhardia,* Jugl., *Carya,* Jugl., *etc.,* but were wiped out over the European-Siberian area during the Glacial Epoch. The former distribution of the Arcto-Tertiary relicts could therefore also be understood through a connection between the eastern United States via Europe and Siberia to China and Japan, to span Holarctis, the entire northern hemisphere in the (now temperate) zone. This explanation of the generic similarity of the Sino-Japanese and SE. North American floras would be less satisfactory than a direct former North Pacific connection, notwithstanding the fact that the American section of the Sinojapanese-North American disjunction is largely confined to the *southeastern* United States, that is, the Atlantic side of North America. It would of course infer a former North Atlantic land-connection between Eastern North America and Western Europe and this is less obvious from zoogeographical and zoopalaeontological data. Moreover, geological and palaeogeographical evidence is in full accordance with a wide, continuous Beringian isthmus perpetuated at least from the Upper Cretaceous through the Tertiary. It must be added that the Beringian isthmus was not quite continuous through Tertiary times, but became broken now and then and later re-established, but these brief interruptions will hardly have hampered plant dispersal.

As a matter of fact the continuous (or almost continuous) distribution over the temperate or warm-temperate northern hemisphere is still maintained in far more genera than are now disjunct, *e.g.* in *Streptopus,* Lil., with one widely distributed species, 2 others confined to North America, 2 more Sino-Himalayan, *Cercis,* Leg.-Caes., in North America, East Asia, Central and West Asia, and S. Europe, *Liquidambar,* Hamam., with three species, one in North to Central America, one Sino-Himalayan, one in West Asia, *Aesculus,* Hippocast., with *c.* 25 species mostly in temperate East Asia and North America, and 1 in the Balkan; *Taxus,* Taxac., *Staphylea,* Staph., and *Juglans,* Jugl., behave similarly.

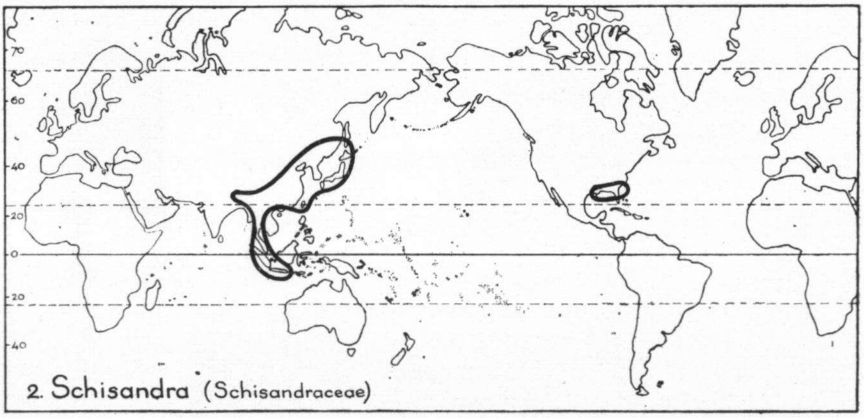
Obviously many of such northern hemisphere areas have crumbled down during the Glacial Epoch and could in Europe and northern Asia only either escape towards or maintain a relict safehold in the southern parts (Mediterranean, Balkan, Persia, and Sino-Himalaya) or the milder parts (Formosa, Japan).

I have enumerated 115 cases of sections, genera, pairs of genera, or tribes, which show the disjunction between East Asia and America.

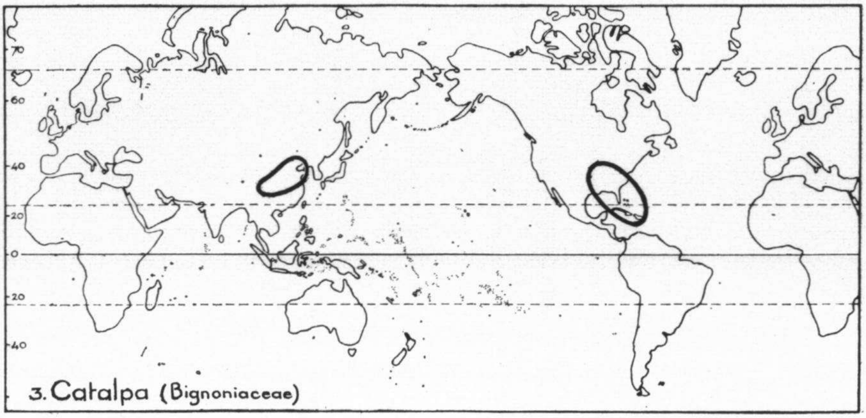
The number of such taxa *strictly* confined to East Asia and eastern North America under temperate conditions is of course smaller and Li (1952) enumerated only 37 of them.



1. Phryma (Phrymaceae)



2. Schisandra (Schisandraceae)



3. Catalpa (Bignoniaceae)

It is questionable to what extent the fossil record will in future show an increase of finds of these genera in the European-Siberian Tertiary.

In 1846 A. Gray first pointed to the similarity of the Japanese flora and that of the Eastern United States and since that year he (1859) and many others have provided contributions on the subject. A digest about the present state has been given in an important survey by Li (1952).

It is difficult to separate this element from the tropical one, because, as has been alluded to above, several species and genera which are typically East Asian—East American overstep the tropic of Cancer towards the tropical zone by ascending the tropical mountains. This difficulty has no bearing on the essence of the problem, it refers only to the numerical exactness of the two types.

The two counterparts of the element, in Asia and North America respectively, do not always agree in their latitudinal distribution, for instance *Pyrularia,* Sant., as mapped by Li, is in Asia found north of the tropic of Cancer but also south of the equator, whereas the American representatives keep much more north in Virginia and South Carolina and do not enter Mexico or other parts of Central America. In other words *Pyrularia* is in Asia subtropical and tropical but in North America warm-temperate. It should be kept in mind that in this case, the Malaysian tropics harbour another very closely allied genus, *Scleropyrum,* Sant., which is even doubtfully distinct. In such cases the ecological potentiality for standing warm-temperate climates is obviously present within a genus, and its former active distribution through warm-temperate regions is, hence, not liable to hypothesis. Therefore, such a genus should be ranged with the subtropical and warm-temperate type; consequently I have excluded it from the tropical type.

On the other hand a genus as for example *Mitrastemon,* Raffl., which occurs in equatorial Sumatra but also in S. Japan, and in the Americas (as far as known only in Mexico and Guatamala), I have reckoned to the tropical element, as South Japan has by virtue of its situation within the ameliorating influence of the warm Kuro Shio drift a very soft climate notwithstanding its latitude, as recently clearly summarized by Tuyama (1957).

There are, however, admittedly border cases with a transitional climatic response, some more tropical, some more subtropical, in which it is difficult to decide whether they should be incorporated in the tropical or subtropical type. Their number is not particularly large. Moreover it does not make much difference for the discussion in which type they are included. If desired they all could be included in the subtropical type in order to give the necessary margin and release any doubt about my intention to keep strictly to the device that wherever we can we should correctly read the ecological thermometer of present plant genera in order to be free to apply it to the past distribution.

In the following approximate list of the subtropical and warm-temperate

Maps 1—3 illustrate the disjunction commonly shown by subtropical to warm-temperate (mesotherm) north amphi-transpacific genera of which the American area is almost always found on the *eastern* side of North America. The counterparts behave sometimes slightly different, for example: *Catalpa* enters the tropics only in America; *Schisandra* enters the tropics only in Malaysia, but is there only found above 1000 m altitude.

type of recent distribution of amphi-Pacific taxa there are but a few species which are common to both Asia and America; an example is *Polygonum virginianum* L., Polygon. The species may be closely related, however, as for instance in *Campsis,* Bign., in which *C. grandiflora* (Thunb.) Loisel. and *C. radicans* (L.) Seem. are capable of hybridizing and apparently produce a fertile progeny.

The bulk of the list consists of genera with a set of species on each side of the North Pacific. The affinity is also found in the higher ranks, in which an East Asiatic genus is represented in America by an other allied genus — here called a "pair" — or is represented by a section or subgenus different from that in Asia.

Sometimes there is a pair of related genera, and as sections are sometimes raised to generic rank one can quibble about the exact status of such taxa; thus I find that *Photinia,* Ros., is sometimes taken apart from *Heteromeles* or united with it into one genus with two sections.

It may also occur that a whole tribe is amphi-Pacific, as for example *Liliaceae* trib. *Melianthoideae-Helonieae, Papaveraceae-Bocconieae,* and *Rosaceae-Kerrieae.*

There are even 7 families which I regard as amphi-transpacific, *viz: Diapensiaceae* with 6 genera of which only *Diapensia* is circumpolar, the others amphi-Pacific, *Illiciaceae* (one genus only), *Clethraceae* (one genus only), *Nyssaceae* (3 genera), *Phrymaceae* (one genus only), *map 1, Saururaceae* (4 genera), *Schisandraceae* (2 genera) *map 2,* and *Lardizabalaceae.* The last one comprises 7 genera, 5 in East Asia and 2 in South (!) America. A similarly remarkable E. Asia—S. Chile distribution is found in *Osteomeles,* Ros.

If in either Asia or America the genus enters the tropical zone — and that almost always in ascending the mountains — this has been indicated in the following list by "Tr+".

As far as possible I have approximately indicated on which side of the Pacific the greater number of species is found.

LIST OF AMPHI-TRANSPACIFIC GENERA AND OTHER AFFINITIES: NORTH WARM-TEMPERATE AND SUBTROPICAL

	East Asia	America
CONIFERAE		
Chamaecyparis	+	+
Pair	*Glyptostrobus,* 1 sp., Tr +	*Taxodium,* 3 spp., Tr +
Calocedrus (Heyderia)	2 spp.	1 sp.
Torreya	4 spp.	2 spp.
APOCYNACEAE		
Amsonia	1 sp.	16 spp., Tr +
AQUIFOLIACEAE		
Ilex subg. Prinus	3 spp.	3 spp.
ARACEAE		
Arisaema	*c.* 100 spp. (2 spp. in Abyss., 1 sp. in trop. Afr.), Tr +	2 spp.
Symplocarpus	2 spp.	1 sp.
ARALIACEAE		
Aralia	*c.* 25 spp., Tr +	4 spp.
Dendropanax (Gilibertia)	*c.* 20 spp., Tr +	*c.* 50 spp.
Oplopanax	2 spp.	1 sp.

Panax	3 spp.	2 spp.
Pentapanax	10 spp.	2 spp.
BERBERIDACEAE		
Achlys	1 sp.	1 sp.
Berberis	∼ spp. (1 sp. in Europe), Tr +	∼ spp., Tr +
Caulophyllum	1 sp.	1 sp.
Diphylleia	3 spp.	1 sp.
Jeffersonia	1 sp.	1 sp.
Mahonia	∼ spp., Tr +	∼ spp., Tr +
Podophyllum	3—4 spp.	1 sp.
BIGNONIACEAE		
Campsis	1 sp.	1 sp.
Catalpa (map 3)	4 spp.	5 spp., Tr +
BUXACEAE		
Pachysandra	3 spp.	1 sp.
CALYCANTHACEAE		
Pair	*Chimonanthus*, 3 spp.	*Calycanthus*, 5 spp.
CAPRIFOLIACEAE		
Abelia	25 spp.	2 spp. (Mex.), Tr +
Symphoricarpos	1 sp.	17 spp., Tr +
Triosteum	6 spp.	4 spp.
Pair	*Weigela*, 12 spp.	*Diervilla*, 3 spp.
CELASTRACEAE		
Celastrus § Paniculati	6 spp.	1 sp.
Pair	*Tripterygium*, 5 spp.	*Wimmeria*, 10 spp. in Mexico
CLETHRACEAE		
Clethra 1)	∼ spp., Tr +	∼ spp., Tr +
CORNACEAE		
Cornus § Macrocarpium	+	+
CRASSULACEAE		
Penthorum	1—2 spp.	1 sp.
CYPERACEAE		
Scirpus § Trichophorum	1 sp.	*c.* 4 spp.
DIAPENSIACEAE		
Shortia	2 spp. (+ *Schizocodon*)	1 sp.
DIOSCOREACEAE		
Dioscorea § Stenophora	∼ spp.; fossil in Europe	1 sp.
ERICACEAE		
Chiogenes	1 sp.	1 sp.
Epigeia	1 sp.	1 sp.
Lyonia	*c.* 15 spp.	*c.* 15 spp., Tr +
Pieris	*c.* 10 spp.	*c.* 3 spp., Tr +
Pair	*Elliottia*, 2 spp.	*Tripetaleia*, 1 sp.
FAGACEAE		
Castanopsis	∼ spp., Tr +	1 sp.
Lithocarpus	∼ spp., Tr +	1 sp.
GRAMINEAE		
Diarrhena	2 spp.	1 sp.
Muehlenbergia	few spp., Tr +	∼ spp., Tr +
Schizachne (1 sp.)	+	+
Zizania (*aquatica* L.)	+	+
GUTTIFERAE		
Ascyrum	1 sp.	5—6 spp., Tr +
HAMAMELIDACEAE		
Hamamelis	6 spp.	3 spp.
Liquidambar	2 spp., also Asia Minor	1 sp., Tr +
Triad	*Parrotia*, 1 sp. & *Parrotiopsis*, 1 sp.	*Fothergilla*, 4 spp.

1) *Clethra* is dubiously native in the Azores.

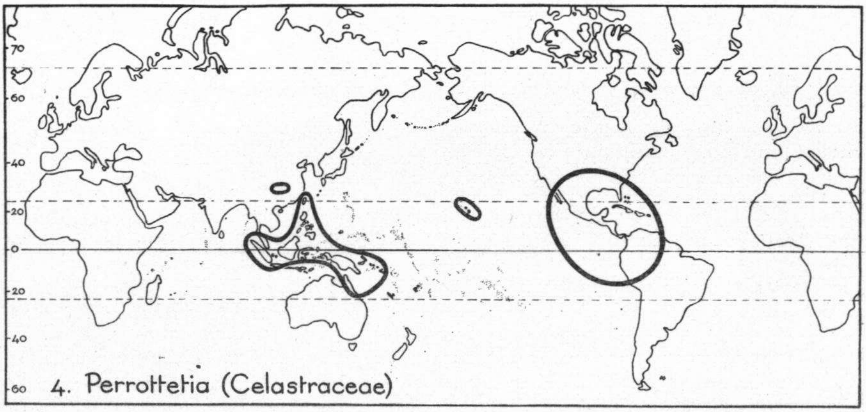
ILLICIACEAE		
Illicium	37 spp., Tr +	5 spp., Tr +
JUGLANDACEAE		
Carya	4 spp.	20 spp., Tr +
LARDIZABALACEAE		
7 genera	5 spp.	2 spp. (Chile)
LAURACEAE		
Sassafras	2 spp.	1 sp.
LEGUMINOSAE		
Amphicarpaea	*c.* 8 spp., Himalaya to Japan	*c.* 7 spp., Peru to E. Canada
Apios	6 spp.	2 spp.
Cladrastis	4 spp.	1 sp.
Gymnocladus	1 sp.	1 sp.
Lespedeza	*c.* 15 spp., India to Manchuria, Malaysia (2 spp.), and Australia (1 sp.), Tr +	*c.* 10 spp., Mexico to S. Canada
Thermopsis	*c.* 7 spp., India to Japan and Manchuria	*c.* 4 spp., U.S.A.
Wisteria	7 spp.	2 spp.
LILIACEAE		
Aletris	6 spp., Tr +	2 spp.
Clintonia	2 spp.	4 spp.
Disporum	several spp., Tr +	few spp.
Melianthoideae-Helonieae	3 genera	3 genera
Nothoscordum	1 sp.	~ spp., Tr +
Smilacina	7 spp.	8 spp., Tr +
Trillium	few spp.	*c.* 25 spp.
MAGNOLIACEAE		
Liriodendron	1 sp.	1 sp.
Magnolia	*c.* 30 spp., Tr +	*c.* 8 spp., Tr +
MENISPERMACEAE		
Menispermum	1 sp.	1 sp.
NYCTAGINACEAE		
Mirabilis (incl. *Oxybaphus*)	1 sp. in Himalaya and SW. China	60 spp., N.M.S. America
NYMPHAEACEAE		
Nelumbo	1 sp., Tr +	1 sp.
NYSSACEAE		
Nyssa	2 spp., Tr +	3 spp.
OLEACEAE		
Chionanthus	1 sp.	1 sp.
Osmanthus	20 spp., Tr +	3 spp., Tr +
ORCHIDACEAE		
Arethusa	1 sp.	1 sp.
Pogonia	uncertain, Tr +	many spp., Tr +
Tipularia	1 sp.	1 sp.
PAPAVERACEAE		
Stylophorum	2 spp., and 3 allied genera	1 sp.
Trib. Bocconieae	*Mackleaya*	*Bocconia*
PHRYMACEAE		
Phryma (*leptostachya* L.) (*map 1*)	+	+
POLYGONACEAE		
Polygonum (*Tovara*) *virginianum*	+, Tr +	+
RANUNCULACEAE		
Trautvetteria	1 sp.	2 spp.
Pair	*Anemonopsis,* 1 sp.	*Xanthorrhiza,* 1 sp.
Pair	*Glaucidium,* 2 spp.	*Hydrastis,* 1 sp.

ROSACEAE		
Osteomeles	1 sp. in E. Asia, Hawaii, and Polynesia	10 spp. in S. America
Photinia	14 spp. (§ *Photinia*)	3 spp. (§ *Heteromeles*)
Physocarpus	1 sp.	13 spp.
Trib. Kerrieae	*Rhodotypus* & *Kerria*	*Neviusia*
RUBIACEAE		
Mitchella	1 sp.	1 sp.
SANTALACEAE		
Buckleya	3 spp.	1 sp.
Pyrularia	2 spp., Tr + (Mal. *Scleropyrum* closely allied)	1 sp.
SAURURACEAE		
Saururus	1 sp., Tr +	1 sp.
Pair	*Houttuynia,* 1 sp., Tr +	*Anemopsis,* 1 sp.
SAXIFRAGACEAE		
Astilbe	10—20 spp., Tr +	2 spp.
Boykinia	3 spp.	7 spp.
Decumaria	1 sp.	1 sp.
Hydrangea	∼ spp., Tr +	∼ spp., N.—S. America, Tr +
Itea	10 spp., Tr +	1 sp.
Mitella	3 spp.	9 spp.
Philadelphus	1 sect.; 33 spp. (1 in Balkan and Caucasus)	8 sect.; 38 spp.
Tiarella	1 sp.	6 spp.
Pair	*Deutzia,* ∼ spp., Tr +	*Neodeutzia,* 2 spp., Tr +
SCHISANDRACEAE		
Schisandra (*map 2*)	26 spp., Tr +	1 sp.
SCROPHULARIACEAE		
Veronicastrum	1 sp.	1 sp.
SOLANACEAE		
Capsicum	1 sp. (§ *Tubocapsicum*) in Japan	*c.* 30 spp. (§ *Capsicum*), Central to S. America
STEMONACEAE		
Croomia	2 spp.	1 sp.
STYRACACEAE		
Halesia	1 sp.	3—4 spp.
THEACEAE		
Cleyera	1 sp.	16 spp. & *Symplococarpon*
Stewartia	6 spp.	2 spp.
UMBELLIFERAE		
Glehnia	1 sp.	1 sp.
VITACEAE		
Ampelopsis	*c.* 23 spp.	2 spp., Tr +
Parthenocissus	6 spp.	3 spp., Tr +

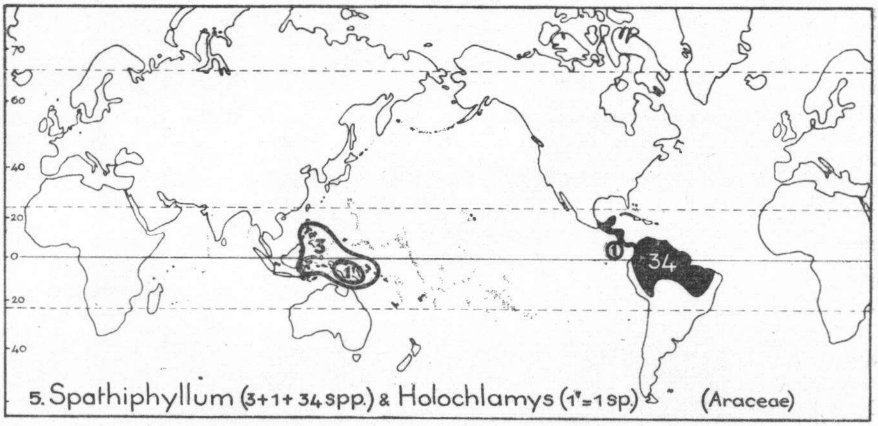
(iii) Tropical — *Maps 4—7*

In scanning the tropical list it appears significant that on the Asiatic side it is composed preponderantly of Indo-Malaysian distributions of which not a few have only very limited areas in the *southern* Malaysian equatorial region (*Batis,* Batid., *Corsia,* Cors., *Annesijoa,* Euph., *Heliconia,* Musac., *Eriandra,* Polygal.). Most of the other genera possess also representatives in Australia, at least in Queensland. This slight discrepancy of symmetry in relation to the equator is possibly due to the relative scarcity of rain-forest in present day Australia.

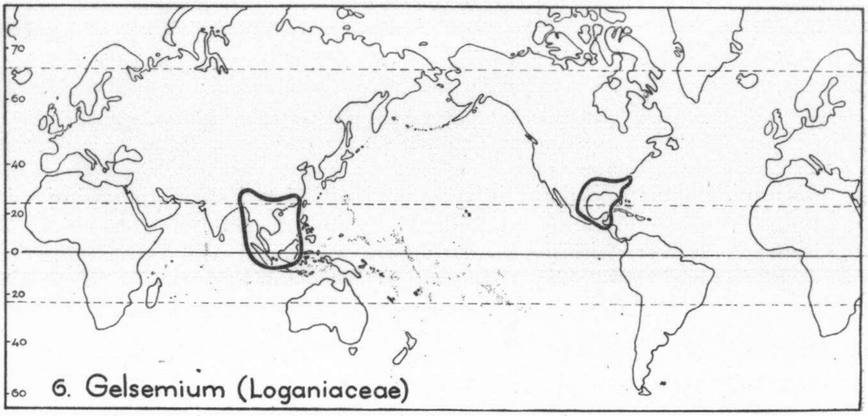
It will, I believe, not escape attention that the major portion of the



4. Perrottetia (Celastraceae)



5. Spathiphyllum (3+1+34 spp.) & Holochlamys (1'=1 sp.) (Araceae)



6. Gelsemium (Loganiaceae)

genera on the list are rain-forest trees or herbs. There is no savannah or open land genus among them, save for *Cynoctonum,* Logan. See *map 7.*

In contrast with the south temperate type there is only one species (*Cynoctonum mitreola* (L.) Britt.) common to both hemispheres, but there are several instances in which species of one section of a genus are represented on both sides of the Pacific, *e.g.* in *Burmannia,* Burm.

An example of such a typically tropical amphi-transpacific genus is for instance *Spathiphyllum,* Arac., with 34 species in tropical America, one species in Cocos I. (500 km off the coast of Costa Rica), and one species in East Malaysia (Philippines, Moluccas) and Micronesia (Palau), and at least 2 other species in New Guinea, Fergusson I., New Britain, and the Solomon Is. (Bougainville). See *map 5.* The Malaysian species, that of Cocos I., and the widest distributed American species (*S. cannaefolium*) are intimately allied and form a separate section of the genus. A related monotypic genus *Holochlamys* occurs in New Guinea. The genera *Hedyosmum,* Chloranth., *Guadua,* Bambus., and *Heliconia,* Musac., show a similar range. *Homalomena,* Arac., has, conversely, *c.* 70 spp. in Indo-Malaysia and 6, representing a separate section, in tropical America. *Schismatoglottis* has 80 spp. in Asia and a monotypic separate sect. *Philonotion* in tropical America (*cf.* Jonker-Verhoef, 1953); other examples are *Microtropis, Perrottetia* (*map 4*), *etc.*

Examples on the tribual level are for example the *Bonnettieae,* Theac., of which *Ploiarium* is Malaysian and *Archytaea* and *Bonnettia* tropical American, the *Moutabeae,* Polygal., of which *Moutabea, Barnhartia,* and *Diclidanthera* are tropical American and *Eriandra* Papuan, tribe *Joannesieae,* Euph., of which *Hevea* and *Joannesia* are tropical American, but *Annesijoa* Papuan and *Deutzianthus* Indo-Chinese, *Araceae-Spathiphylleae* with *Spathiphyllum* American and Malaysian and *Holochlamys* Papuan, *Araceae-Monstereae* (9 genera), *Euphorbiaceae-Omphaleineae* (3 genera concerned), *Meliaceae-Cedreleae* (2 genera), and *Saxifragaceae-Hydrangeeae* (8 genera).

An example on the subfamily level is that of the *Balanophoraceae-Helosioideae* of which 2 genera occur in Indo-Malaysia and 3 in America.

Finally the small families *Batidaceae* (1 genus), *Trigoniaceae* (3 genera, a fourth in Madagascar), *Corsiaceae* (2 genera), and *Saurauiaceae* (1 genus) possess amphi-transpacific distribution or almost so.

The delimitation of the tropical type against the warm-temperate — subtropical type is of course not easy and in some cases the Indo-Malaysian representatives overstep the tropic of Cancer to occur in South Japan. As was clearly demonstrated by Tuyama (1957) such genera as a rule occur in China only in the southern provinces but can occur in Japan at much higher latitude because of the milder climate caused by the warm Kuro Shio current, as is found in the genera *Mitrastemon, Turpinia,* and others.

On the southern hemisphere there is a similar difficulty in its delimitation against the southern subtropical — warm-temperate type, as certain typically

Maps 4—6 illustrate tropical amphi-transpacific generic distribution. *Perrottetias* occur from the lowland into the hills, *Spathiphyllum* and *Holochlamys* (together forming the tribe *Spathiphylleae*) are restricted to the tropical lowland, *Gelsemium* occurs in the lowland and the hills. *Perrottetia* is the only of the three with intermediate stations in Polynesia.

tropical genera may occur in North New Zealand, for example *Tecomanthe*, Bign., in a stray station on the Three King's Islands, at the most northern corner of that country.

LIST OF AMPHI-TRANSPACIFIC GENERA AND OTHER AFFINITIES: TROPICAL

	West Pacific (Indo-Malaysian)	East Pacific (tropical American)
AMARANTHACEAE		
Gomphrena	few spp. in Australia and E. Malaysia	centre; also Galapagos
Iresine	some spp. in Australia	centre; also Galapagos
Philoxerus	some spp. in Australia	centre; also Galapagos
ANACARDIACEAE		
Spondias	*c.* 3 spp.	*c.* 3 spp.
ANNONACEAE		
Anaxagorea	§, 7 spp.	§, 21 spp.
AQUIFOLIACEAE		
Ilex Reihe D. Thyrsoprinus	2 sect.	3 sect.
ARACEAE		
Homalomena	*c.* 70 spp. + *Diandriella*	6 spp. (§ *Curmeria*)
Schismatoglottis	*c.* 80 spp.	1 sp. (§ *Philonotion*)
Trib. Monstereae (10 genera with 170 spp.)	4 genera (a 5th with 2 spp. in W. Africa)	5 genera
Trib. Spathiphylleae (*map 5*)	*Spathiphyllum* 3 sp. *Holochlamys* 1 sp.	*Spathiphyllum* 35 spp.
BALANOPHORACEAE		
Subfam. Helosioideae	2 genera (a 3rd in Madagascar)	3 genera
BATIDACEAE		
Batis	1 sp. (New Guinea)	1 sp. (Galapagos and Central America)
BURMANNIACEAE		
Burmannia § Foliosa	1 sp.	4 spp.
Thismia	2 sect., 17 spp.	2 sect., 6 spp.
[*Thismia § Rodwaya*	1 sp. in Tasmania and New Zealand	1 sp. in N. America]
CELASTRACEAE		
Celastrus	*ser. Axillaris* (also Madagascar)	*Celastrus subg. Racemocelastrus*
Microtropis	25 spp.	2 spp.
Perrottetia (*map 4*)	China to Malaysia, 5 spp. (also in Hawaii and Solomons)	8 spp.
CHLORANTHACEAE		
Hedyosmum	1 sp. Hainan, W. Malaysia (montane)	*c.* 20 spp. Mexico to Brazil
CORSIACEAE		
Corsiaceae	*Corsia* (New Guinea)	*Arachnites* (Chile)
CUNONIACEAE		
Weinmannia	~ spp. (throughout the S. Pacific, Madagascar)	~ spp.
Pair	*Geissois*	*Belangera*
CYPERACEAE		
Machaerina	~ spp. in Asia, Malaysia and Australia; 1 sp. in Madagascar; through the Pacific	a few spp. in Central and S. America

ELAEOCARPACEAE		
Sloanea	spp.	∼ spp.
EUPHORBIACEAE		
Trib. Joannesieae	*Deutzianthus* (Indo-China) *Annesijoa* (New Guinea)	*Hevea, Joannesia*
Subtrib. Omphaleineae	*Omphalea* (1 sp. Madagascar) & *Neomphalea*	*Omphalea*
FLACOURTIACEAE		
Xylosma	9 spp.; in Micronesia, Polynesia & Melanesia 24 spp.	68 spp.
GESNERIACEAE		
Rhynchoglossum	10 spp., Ceylon to Papua	3 spp., Mexico to Columbia
GRAMINEAE		
Guadua (*Bambus.*)	1 sp. (Philippines)	*c.* 15 spp.
Ichnanthus	few spp.	*c.* 30—40 spp.
HAMAMELIDACEAE		
Distylium	10 spp.; N to Japan	2 spp.
ICACINACEAE		
Citronella	§ *Euchariessa*	§ *Citronella*
Pair	*Nothapodytes,* 5 spp., Ceylon to Ryukyu and Malaysia	*Mappia,* 3 spp., Mexico and Greater Antilles
JUGLANDACEAE		
Engelhardia	5 spp.	2—3 spp.
LAURACEAE		
Cinnamomum	many spp., Formosa to trop. Australia and Fiji	Central America, few spp.
Endiandra	Malaysia, Australia	equatorial America
Lindera	over 60 spp.	2 spp., South U.S.
Litsea	Japan to Fiji, ∼ spp.	Central America, South. U.S.
Persea	Formosa to Malaysia	South. U.S. to N. Chile
LEGUMINOSAE		
Ormosia	*c.* 50 spp.	*c.* 40 spp.
LINACEAE		
Pair	*Indorouchera*	*Roucheria*
LOGANIACEAE		
Cynoctonum (map 7)	3 spp. (2 spp. only in Madagascar)	2 spp.
Gelsemium (map 6)	1 sp.	1 sp.
MAGNOLIACEAE		
Talauma	∼ spp.	∼ spp.
MELIACEAE		
Cedreloideae-Cedreleae	*Toona, c.* 10 spp. (?)	*Cedrela,* 7 spp.
MORACEAE		
Ficus subg. Pharmacosycea	*sect. Oreosycea* (1 sp. in Madagascar)	*sect. Pharmacosycea*
Trophis	*Calpidochlamys, Paratrophis philippinensis,* (and *Maillardia* of Madagascar) congeneric with *Trophis*	*Trophis*
Affinity	*Antiaris, Antiaropsis,* and *Sparattosyce*	*Olmedieae*
MUSACEAE		
Heliconia	1 sp. (cult. in Pacific?)	several spp.
OCHNACEAE		
Pair	*Neckia, c.* 3 spp.	*Pocillandra,* 1 sp.
OLACACEAE		
Schoepfia	2 sect. (to S. China & Japan)	1 sect.

ORCHIDACEAE		
Tropidia	*c.* 35 spp., Indo-Malaysia to Japan, Fiji, and New Caledonia	1 sp. from Florida to Central America; also Galapagos
Erythrodes (*Physurus*)	few spp., Indo-Malaysia, also in New Caledonia & Samoa	many spp., Central to S. America
POLYGALACEAE		
Trib. Moutabeae	*Eriandra* 1 sp. (New Guinea)	*Moutabea, Barnhartia, Diclidanthera*
PROTEACEAE		
Oreocallis	3 spp.	2 spp.
RAFFLESIACEAE		
Mitrastemon	? 2 spp.	1 sp.
RHAMNACEAE		
Berchemia	*c.* 12 spp.	1 sp. (warm temp. N. America)
Colubrina[1])	*c.* 10 spp. (also in Pacific!)	*c.* 20 spp.
Sageretia[2])	*c.* 8 sp.	*c.* 5 spp.
SABIACEAE		
Meliosma	*c.* 50 spp. from Ceylon to Korea, Formosa and New Guinea	*c.* 12 spp. from Mexico to Brazil
SAPINDACEAE		
Sapindus	11 spp., Indo-Malaysia throughout trop. Pacific, not in Australia	3 spp. from South U.S.A. to S. America
SAURAUIACEAE		
Saurauia	many spp. (also Fiji)	many spp.
SAXIFRAGACEAE		
Subtrib. Hydrangeeae (without *Hydrangea*)	6 genera E. Asiatic, 1 genus warm-temperate in Asia and N. America; 1 genus in Hawaii; Tr +	
SIMAROUBACEAE		
Picrasma	2 spp.	6 spp.
Simaba	1 sp.	22 spp.
Pair	*Eurycoma,* 2 spp.	*Simarouba,* 9 spp.
STAPHYLEACEAE		
Turpinia	*c.* 20 spp.	*c.* 6 spp.
STEMONACEAE		
Croomia	2 spp.	1 sp.
STERCULIACEAE		
Helicteres	many dozens in Indo-Australia; also Palau I.	many dozens in Central & S. America
SYMPLOCACEAE		
Symplocos	§ *Cordyloblaste*	§ *Ciponima*
TACCACEAE		
Tacca § *Ataccia*	11 spp.	1 sp.
Tacca § *Palmotacca*	5 spp.	2 spp.
THEACEAE		
Eurya	many spp. (also Hawaii)	*Freziera, Killipiodendron*
Gordonia	many spp.	1 sp. in SE. U.S.A. (aff. *Franklinia*)
Laplacea	*c.* 10 spp.	*c.* 20 spp.
Ternstroemia	25 spp. (also Fiji; 1 sp. in Africa)	60 spp.
Trib. Bonnettieae	*Ploiarium* 3 spp.	*Archytaea* 2 spp. *Bonnettia* 6 spp.

[1]) *C. asiatica* Brongn., a beach plant from E. Africa to Hawaii, not included.

[2]) One species from Arabia to Eritrea.

THYMELAEACEAE		
Subtrib. Linostomatinae	*Linostoma, Enkleia*	*Lophostoma*
TRIGONIACEAE		
Trigoniaceae 1)	*Trigoniastrum*	*Trigonia, Euphronia*
VERBENACEAE		
Callicarpa	*c.* 60 spp., Indo-Australia, Japan, and China; also in Micronesia and Solomons	some spp. in trop. America

(iv) South Subtropical and Warm-Temperate — *Map 8*

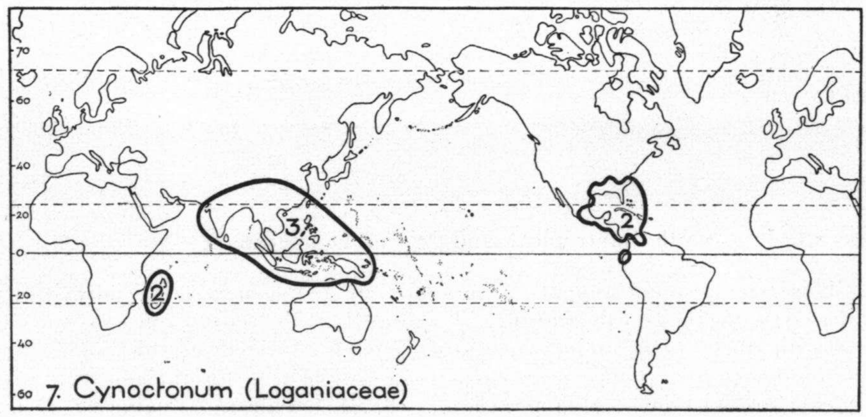
This type is proportionally represented by few genera, especially if it is compared with the north subtropical type. This is remarkable, as through the Pacific the largest archipelagos are precisely situated in this zone where one would expect stepping stones, as is for example true for the representatives of the genus *Nicotiana,* Solan. See map 8. The bad functioning of former connections is more especially true for transpacific plants, as conversely the genera of the Malaysian-Australian element extend far towards the east into the Pacific beyond the Andesite Line, as has been shown by Van Balgooy (1960). Evidently many of these occurrences are due to later eastward migration. For the transpacific types the bad functioning of connections is apparently in particular due to early breaking up of such connections in the far East Pacific, except for the south temperate type. This is also expressed in the fact that of the south subtropical type no species is common to the West Pacific and the Americas, whereas of the south temperate type several species are distributed from S. Australia to Patagonia.

The subtropical type is difficult to separate from the south temperate and I have segregated the genera mainly on the ecological behaviour of their tropical representatives, if these are extant, and the degree of their distribution towards the south. *Araucaria,* Conif., goes for example not as far south as New Zealand, and in New Guinea it is montane, descending almost to the tropical lowland; consequently I find it subtropical rather than temperate. On the other hand *Dacrydium,* Conif., shows in the Malaysian tropics a similar behaviour but has produced subalpine and nearly alpine species; besides it occurs in New Zealand and even on islands south of it, showing that its ecological potentiality is wider than that of *Araucaria* and extends to microtherm conditions. A similar case is that of *Discaria,* Rhamn. *Nothofagus,* Fagac., behaves similarly as *Dacrydium,* but is more temperate in character in that it is not found below 2000 m in New Guinea, although in New Caledonia, near the Tropic of Capricorn, it is said to descend to only 500 m.

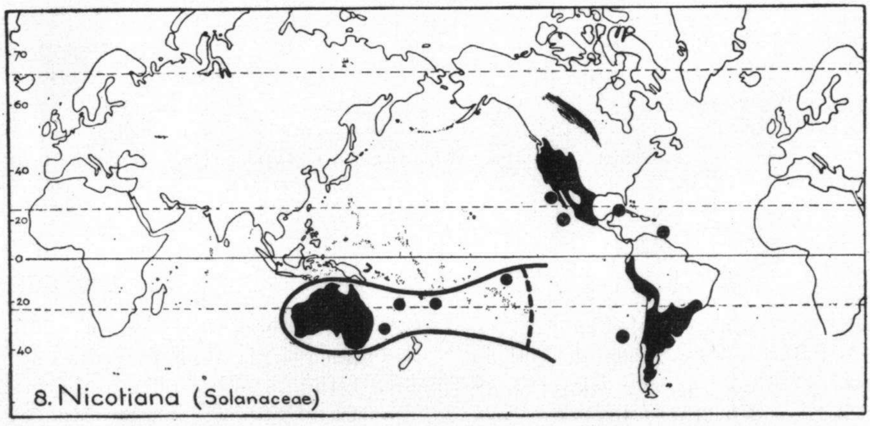
The genera of the south temperate type behave essentially subalpine to alpine in the tropics, for example *Oreobolus (map 13), Uncinia,* Cyp., *Libertia,* Irid., *Gaultheria,* Eric., *Oxalis,* Oxal., *Drapetes,* Thym., *etc.*

A remarkable case which is difficult to place is that of *Thismia,* Burm., all species being typically tropical save the two species forming the sect. *Rodwaya,* which are restricted to such far-flung places as Tasmania and New Zealand in the SW. Pacific and the Chicago area in North America.

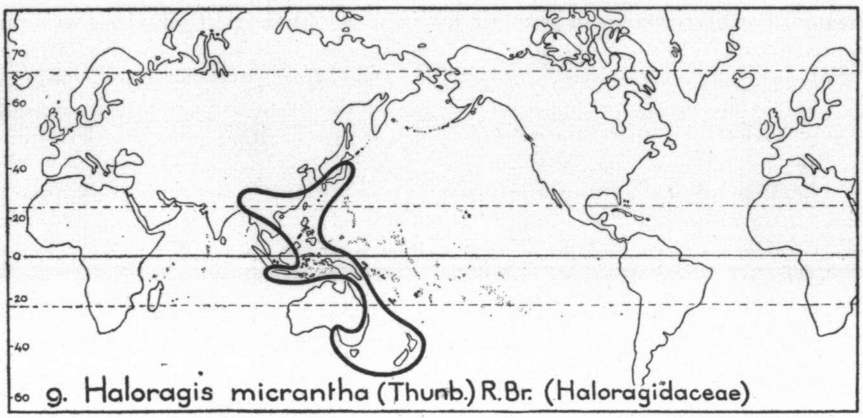
1) One genus in Madagascar, *Humbertiodendron* Léandri.



7. Cynoctonum (Loganiaceae)



8. Nicotiana (Solanaceae)



9. Haloragis micrantha (Thunb.) R.Br. (Haloragidaceae)

In the south there are again a few extensions of areas westwards to the islands of Amsterdam, Réunion, *etc.*, for example *Sophora* § *Edwarsia*, Leg.-Pap.

I have included two genera in this type which are not known to occur native in South America proper, but which occur in Juan Fernandez close to the S. American coast, *viz Santalum*, Sant., and *Haloragis*, Halor.

Preponderance on the west as well as on the east of the Pacific occurs but is not very common in this type. *Araucaria, Haloragis*, and *Muehlenbeckia*, Polygon., are largely developed in the West Pacific, *Discaria*, Rhamn., and *Nicotiana* in the Americas.

From the list it is clear that hardly any typically tropical Indo-Malaysian genera are involved (*Thismia*); the majority of the western-centred genera are Australian.

But several genera extend their area towards Malaysia, *e.g. Haloragis, Santalum*, Sant., *Phrygilanthus*, Lor., *Muehlenbeckia*, Polygon., and *Gevuina*, Prot., the latter three all to New Guinea, and *Santalum* as far as Central Celebes.

Five genera extend their area even far into the northern hemisphere, *Haloragis* (1 sp.) to S. Japan and *Santalum* to the Bonin Is., and in the Americas *Thismia, Nicotiana*, and *Calandrinia*, Portul., to North America.

LIST OF AMPHI-TRANSPACIFIC GENERA AND OTHER AFFINITIES: SOUTH SUBTROPICAL AND WARM-TEMPERATE

	West Pacific (Indomalaysian or/and Australian	South America
BIGNONIACEAE		
Affinity	*Tecomanthe, Pandorea*	*Campsidium* (Chile)
CONIFERAE		
Araucaria	14 spp.	2 spp.
Podocarpus § *Polypodiopsis*	4 spp., Moluccas to Fiji, not in Australia; fossils in N. S. Wales & Tasmania	2 spp., Andine Venezuela to Peru; fossils in Chile
Affinity	*Libocedrus, Papuacedrus*	*Pilgerodendron, Austrocedrus*
CUNONIACEAE		
Caldcluvia	Malaysia, Solomons, E. Australia, New Zealand	1 sp. in S. Chile
GRAMINEAE		
Distichlis	1 sp. in N. S. Wales to Tasmania	4—8 spp. in trop. America
HALORAGIDACEAE		
Haloragis	Centre in Australia; NW. to China; also in Pacific	East to Juan Fernandez

Maps 7—9. Cynoctonum shows characteristic amphi-transpacific distribution but is also represented in Madagascar.

Nicotiana illustrates subtropical to warm-temperate south amphi-transpacific distribution.

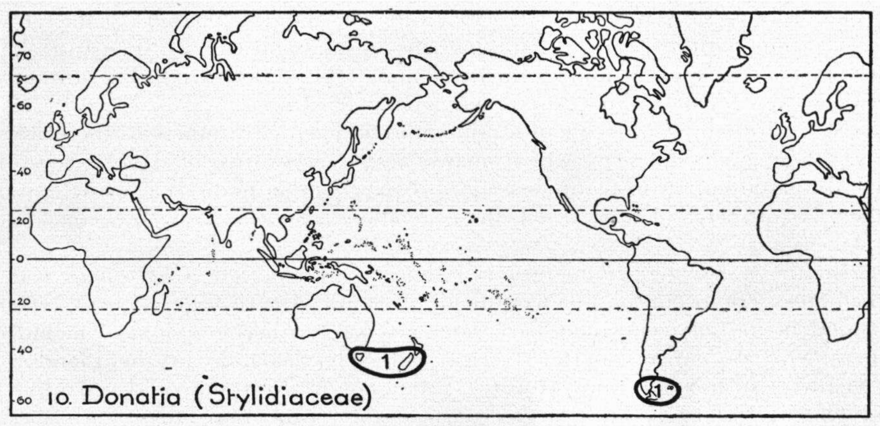
Haloragis micrantha (Thunb.) R. Br. is a strictly microtherm species of an otherwise characteristic Australasian centred eurytherm genus; this species has reached a remarkably symmetrical area in relation to the equatorial zone; in the tropics it is only found at high altitudes.

IRIDACEAE		
Orthrosanthus	5 spp., S. Australia	3 spp., trop. America
LEGUMINOSAE		
Sophora § Edwardsia	S. Pacific and Hawaii (not in Australia); also in Réunion and Gough I. (? India)	2 spp. in S. Chile; 2 spp. in Juan Fernandez
LILIACEAE		
Cordyline	Indo-Pacific, 5 spp. in New Zealand, 20 spp.	1 sp.
LORANTHACEAE		
Loranthoideae subtrib. Gaiadendrinae	*Atkinsonia* 1 sp. in N. S. Wales	*Gaiadendron,* 4 spp. Costa Rica to S. America, Tr +, *Desmaria,* 1 sp., Chile
Phrygilanthus	3 sect.; in Pacific only New Zealand and Juan Fernandez; N to Philippines	4 sect.
MYRTACEAE		
Pair	*Metrosideros,* Tr +, also in Pacific	*Tepualia* (monotypic)
ORCHIDACEAE		
Epistephium	1 sp. New Caledonia	6 spp.
POLYGONACEAE		
Muehlenbeckia	centre in Australia	to Central America
PORTULACACEAE		
Calandrinia	*c.* 60 spp. in Australia & Tasmania	N.—S. America
PROTEACEAE		
Gevuina	2 spp.; and *Kermadecia,* 7 spp. in Melanesia	1 sp.
Lomatia	+	+
Orites	+	+
ROSACEAE		
Licania	6 spp. New Caledonia	~ spp. Andine S. America
RUBIACEAE		
Lindenia	1 sp., Fiji; New Caledonia	2 spp.
SANTALACEAE		
Santalum (incl. *Mida*)	to Celebes & Bonin; many in Polynesia; also New Zealand	East to Juan Fernandez
SOLANACEAE		
Nicotiana subg. Petunioides (*map 8*)	also in Polynesia: New Caledonia, Lord Howe, Loyalty, Tonga, and Marquesas Is., 21 ssp. in Australia; § *Suaveolentes*	generic centre in America; § *Suaveolentes* not in America

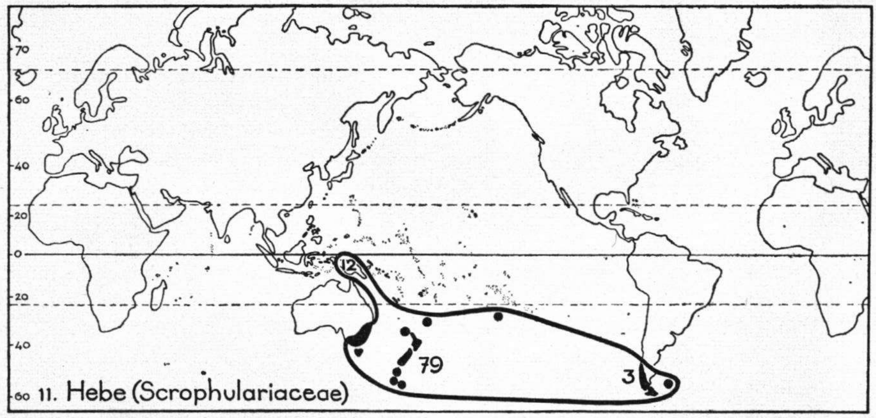
(v) South Temperate — *Maps 10—15*

This distributional type is as showy as its north Pacific counterpart. It is, after all, far more astonishing and conspicuous, because of the fact that in contrast to the site of this northern counterpart which at present shows geographical "insular-isthmian" connections (Beringia), the Pacific Ocean between New Zealand and South America is between 40° and 60° SL entirely

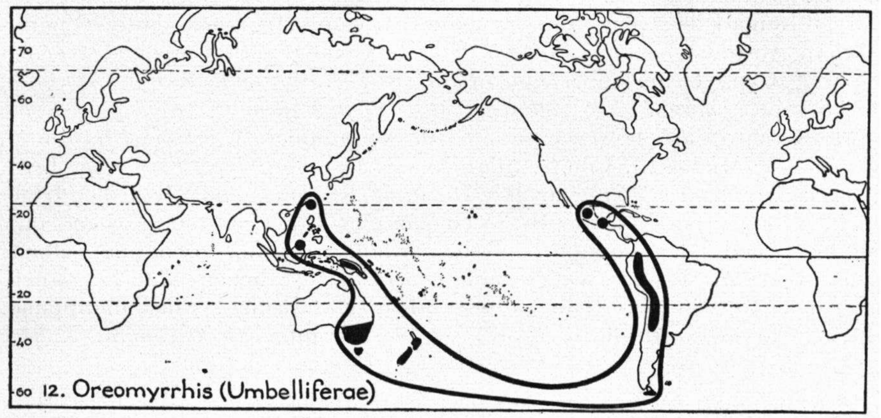
Maps 10—12 illustrate temperate south amphi-transpacific distribution. *Donatia* keeps strictly to the Subantarctic, others of these temperate genera extend their area towards or over the equator in ascending the mountains as for example can be observed in the areas of *Hebe* and *Oreomyrrhis.* See also maps 13—15.



10. Donatia (Stylidiaceae)



11. Hebe (Scrophulariaceae)



12. Oreomyrrhis (Umbelliferae)

devoid of islands over about 100° longitude or about 7200 km as the crow flies at that latitude, not calculating the distance between SE. Australia-Tasmania and New Zealand which is also 1400—2000 km. The distance between New Zealand and Antarctica is c. 2500 km.

Notwithstanding this gigantic subantarctic-Pacific disjunction there is a series of fine examples to which many authors onwards of Hooker's work have drawn attention in plant-geographical papers or in maps (*e.g.* Hutchinson, 1926). Skottsberg (1915) listed these relations between New Zealand and S. America.

In the following enumeration I have also inserted *Coprosma,* Rub., which does not occur on the continent of South America proper but which is found in the adjacent Juan Fernandez group. Furthermore I have included genera which occur in South America and New Zealand (or the islands of Kermadec, Norfolk, or Lord Howe) — but not in Australia or Tasmania — and which thus bridge the largest part of the disjunction; these have been marked with an asterisk (*). They are: *Pseudopanax,* Aral., *Tetrachondra,* Borr., *Griselinia,* Corn., *Sicyos,* Cuc., *Marsippospermum, Rostkovia,* Junc., *Fuchsia,* Onagr., *Hoheria-Gaya,* Malv., *Laurelia,* Monim., and *Jovellana,* Scroph.

I have not included species of large genera which show the south temperate distributional pattern, *e.g. Oxalis magellanica* Forst. f. *sens. lat., Sicyos angulata* L., *Myriophyllum elatinoides* Gaud., Halor. (Australia to Mexico!), *Gratiola peruviana* L., Scroph., *Taraxacum magellanicum* Comm. ex Schultz, Comp., *etc.*; they are often replaced by pairs of vicarious species (see list in Hooker, 1859, p. xc—xci).

The Tasmanian flora I have considered as making part of that of Australia.

The gravity centres may be situated either in Australia, New Zealand, or South America. Families or genera centering in Australia are *e.g. Epacridaceae* (only 1 genus in Patagonia), *Centrolepidaceae* with 1 species in S. America, *Stylidiaceae* with 2 species in S. America, and *Goodeniaceae* with 1 species in S. America if we discard the two pantropical *Scaevolas* from the beach; *Compositae* to wit: *Abrotanella, Brachycome,* and *Vittadinia*; further *Winteraceae* (but these mostly in New Guinea and in New Caledonia rather than in Australia proper).

It is remarkable that New Zealand harbours far more centres of this type than Australia, *viz: Pseudopanax,* Aral., *Colobanthus,* Caryoph., *Uncinia* (in part), Cyp., *Geum* subg. *Oncostylus,* Ros., *Coprosma,* Rub., *Euphrasia, Hebe,* Scroph. (*map 11*), *Stylidiaceae* trib. *Phyllachneae.*

Many centres are, however, situated in South America, *viz* of: *Erechthites, Lagenophora, Microseris,* Comp., *Sicyos,* Cuc., *Uncinia,* Cyp., *Pernettya,* Eric., *Deyeuxia,* Gram., *Fuchsia,* Onagr., *Discaria,* Rhamn., and *Azorella,* Umb.

Numerous genera of the list occur also at lower latitudes where they generally ascend the mountains, mostly reaching subalpine to alpine habitats in the tropics¹). In this way several genera have reached Malaysia where some occur only in New Guinea but others go as far as the Philippines, Mt Kinabalu in North Borneo, or even North Sumatra (*Oreobolus,* Cyp.),

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¹) As in List II genera which are also found in the mountains of the tropics have been marked with "Tr +".

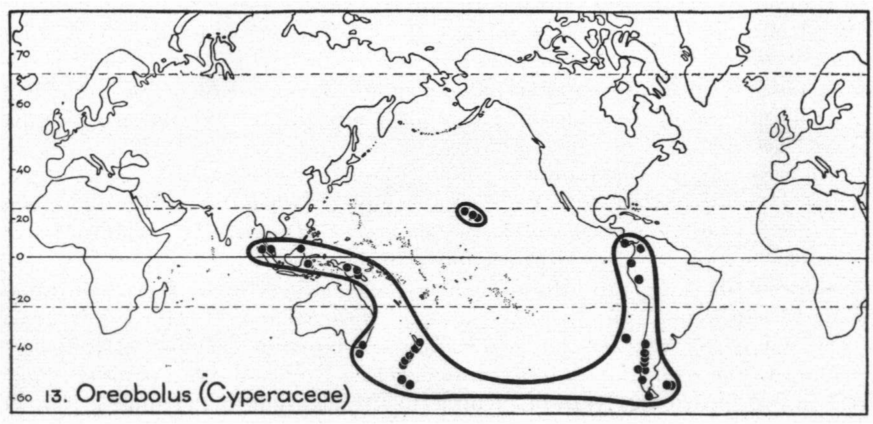
for example: *Gaimardia,* Centrol., *Abrotanella, Erechthites, Brachycome, Vittadinia,* Comp., *Oreobolus, Uncinia,* Cyp., *Aristotelia,* Elaeoc., *Nothofagus,* Fagac., *Selliera,* Good., *Deyeuxia,* Gram., *Libertia,* Irid., *Astelia,* Lil., *Oxalis* (*magellanica*), Oxal., *Muehlenbeckia,* Polygon., *Acaena,* Ros., *Coprosma,* Rub., *Hebe,* Scroph., *Drapetes,* Thym., *Azorella,* Umb., and *Winteraceae.* Compare *maps 11—15.*

Some are moreover found in other islands of the Pacific or have even reached Hawaii and/or SE. Asia, for example: *Lobelia* sect. *Pratia,* Camp., *Dacrydium,* Conif., *Gaultheria,* Eric., *Liliaceae-Dianellinae, Nertera,* Rub., *Euphrasia,* Scroph., *Oreomyrrhis,* Umb. (to Formosa). *Maps 12, 14—15.*

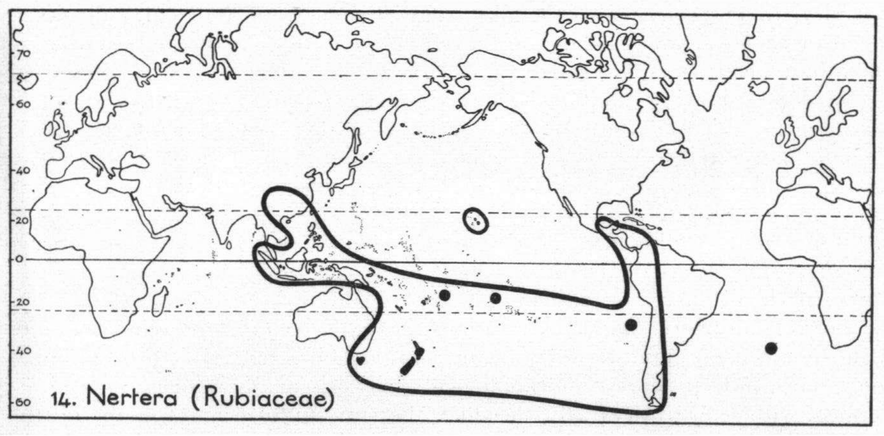
Some of the latter are also known to have outliers in southern hemisphere Indian Ocean relict stations, for example: *Brachycome,* Comp. (S. Africa), *Carpha,* Cyp. (S. Africa), *Astelia* (Réunion, Mauritius), *Dianella,* Lil. (1 sp. extending to the Malagasian area), *Leptocarpus,* Rest. (also S. Africa), *Acaena,* Ros. (also S. Africa), *Nertera,* Rub. (to Malagasian area and Tristan da Cunha). See *map 14.*

It is remarkable that with three exceptions, *viz Eucryphia,* Eucryph., *Nothofagus* § *Calucechinus,* Fagac., and *Bredemeyera,* Polygal., all taxa of the list occur in New Zealand or have representatives in the adjacent islands (Chatham, Kermadec, Norfolk, Lord Howe, and often also in Rapa or Juan Fernandez), showing that this land served as an essential part of the plant geographical pattern of these genera in the past. They have in New Zealand not rarely centres of endemic speciation. The relicts of the assumed former land-bridge are in this type better represented than in any of the other zones. See also *maps 10—14.*

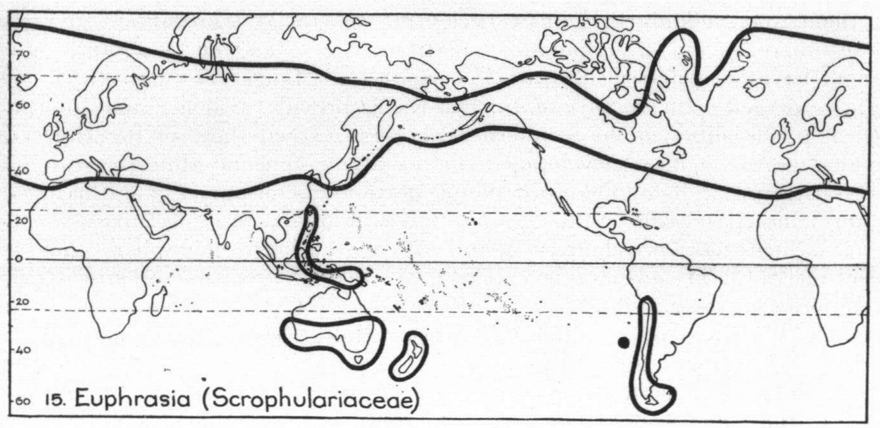
One genus represents a very remarkable case, *viz Euphrasia,* Scroph. See *map 15.* Von Wettstein (1896, 48—52) argued that this genus is of northern hemisphere origin and dispersed in the geological past to the southern hemisphere, and later authors have, I believe, unanimously agreed with him. There are, however, some serious objections to this opinion, as the genus finds it largest morphological diversity in New Zealand and New Guinea, with semi-frutices, *etc.,* to which the very uniform habit of the northern hemisphere species stands in marked contrast. The fact that from the northern hemisphere a host of species have been described does mean little; many of them are, undoubtedly, microspecies due to racial segregation. It is far more important in my opinion that from New Zealand two other allied genera have been described, *viz Siphonidium* and *Anagosperma* which, though rightly merged with *Euphrasia* by Du Rietz, provide evidence that morphological potentialities in the southern hemisphere exceed those of the Holarctis; besides there is a large development in the alpine zone of Malaysia with subligneous forms, a habit unknown in the northern hemisphere. For this reason I am tempted to believe that *Euphrasia* is originally a *South West Pacific* genus which has spread from there to the northern hemisphere and has been successful because of its capacity to create hardy, microtherm species, even more successful than *Nertera,* Rub. (*map 14*), which goes only as far north as Formosa and Szechuan, *Haloragis,* Halor., which has reached Japan (*map 9*), and *Gaultheria,* Eric., which is only absent from Europe and Siberia in the northern hemisphere. Why *Euphrasia* has not produced more species along the Andes and does not reach lower latitudes is of course a



13. Oreobolus (Cyperaceae)



14. Nertera (Rubiaceae)



15. Euphrasia (Scrophulariaceae)

mystery, and that holds also for *Nertera, Coprosma,* Rub., *Haloragis,* Halor., *etc.*

This is closely connected with another problem, *viz* the occurrence in Patagonia of a few genera which have unquestionably migrated from North America southwards along the Andes (*e.g. Primula,* Prim., *Empetrum,* Empetr., *Koenigia,* Polygon., *Littorella,* Plantag., *Saxifraga, Chrysosplenium,* Sax., but which show large disjunctions between their North and South American ranges. The examples given by Du Rietz (1940) are rather few but striking. Could it be that, by the time they were on their way towards Patagonia, the isthmian links had already broken up, preventing their further subantarctic distribution? In that case precisely such plants would be extremely valuable as "age indicators" of the links.

It is significant that these Andine-spread genera which reached a bipolar distribution are represented in Patagonia almost always by only one "macrospecies" which has only developed some microspecies of racial rank. Obviously the gene pool carried was of limited potentiality. Genera which are more or less an exception to this rule are *Caltha, Anemone* and *Geum.* The last one is in many respects a counterpart of *Euphrasia.* It is widely distributed in the northern hemisphere but crossed the tropics towards the extremities of the southern hemisphere in Africa, and along the Andes to Tierra del Fuego, New Zealand, Tasmania, and the Auckland Is. In the latter four subantarctic countries 9 species occur which belong to a separate subg. *Oncostylus* (Schlecht.) ... Obviously *Anemone, Caltha* and *Geum* have not followed the transtropical Sunda Bridge and are absent between Japan and Australia.

In the case of *Anemone, Caltha,* and *Geum* a special section was involved. For *Anemone* Parkin & Sledge (1935) have clearly drawn the consequences, *viz* that it is unavoidable to explain the occurrence of the two species in New Zealand and Tasmania by a former land connection along the Antarctic continent, from subantarctic South America westwards, under milder climatic conditions.

This view holds for several other genera of which no special section is involved, but in which the affinities between Tasmania/New Zealand and temperate S. America are perfectly clear, sometimes through one species which is found on both sides of the South Pacific. Properly they are as significant as the former. Examples are the following:

AIZOACEAE. *Tetragonia.* S. hemisphere, centres in S. America and S. Africa; one species, *T. tetragonoides* (Pall.) O.K. (*T. expansa* Murr.) from Chile via New Zealand and other S. Pacific islands to Tasmania and Australia, also in S. Japan and Bonin.

CARYOPHYLLACEAE. *Scleranthus.* Two species occur in Victoria, Tasmania, and New Zealand; genus also in S. America.

COMPOSITAE. *Taraxacum.* New Zealand species allied to those of S. Chile.

Maps 13—15 show a similar distribution pattern as *Oreomyrrhis,* but both *Oreobolus* and *Nertera* occur in the Hawaiian Is. and *Nertera* has a remarkably short extension northward in the Andes but is reaching high northern latitude in East Asia. *Euphrasia* is absent in Hawaii but extends via East Asia to northern Asia and Europe.

CRASSULACEAE. *Tillaea.* Tasmania, Australia, New Zealand, one species common to New Zealand and Tierra del Fuego.

CRUCIFERAE. *Cardamine.* One species is common to New Zealand and S. Chile.

GERANIACEAE. *Geranium.* One species is common to SE. Australia and Chile.

OXALIDACEAE. *Oxalis* § *Acetosellae.* One species common to New Guinea Alps, New Zealand, and S. Chile.

PORTULACACEAE. *Claytonia.* Victoria, Tasmania, New Zealand.

RANUNCULACEAE. *Myosurus.* The New Zealand species allied to the S. American *M. apetalus* Gay.

Ranunculus. R. biternatus Sm. occurs in SE. Australia, New Zealand, and Chile; *R. acaulis* Banks & Sol. in New Zealand and Chile.

SCROPHULARIACEAE. *Gratiola.* One species common to S. Australia, New Zealand, and S. America.

Limosella. One species (*L. lineata* Glück) *i.a.* in New Zealand and Patagonia.

UMBELLIFERAE. *Apium.* One species in New Zealand (*A. australe* Thouars), genus also in Chile and Hawaii.

Daucus. One species (*D. glochidiatus* (Lab.) Fischer) in Australia, New Zealand and Chile, recently found in Timor.

Other genera which may have reached Australasia along the same route are for example: *Barbarea, Eryngium, Hymenolobus, Lepidium, Linum, Mimulus, Sisymbrium,* and *Sium.* It would require a comprehensive taxonomical investigation to verify this in detail. It is entirely clear, however, that temperate South America has been a substantial source area for Andine-spread holarctic genera towards New Zealand, Tasmania and South Australia, some of which have also proceeded with a single species to the Alps of New Guinea, Ceram, *etc.*

There is no case comparable with the transoceanic tropical pattern where largely taxa of higher rank are concerned. This must certainly be an indication that the latter are more ancient than the Andine-spread taxa. This fits well in with the relatively young age of the Andean Range.

LIST OF AMPHI-TRANSPACIFIC GENERA AND OTHER AFFINITIES: SOUTH TEMPERATE

	West Pacific (Indo-Malaysian and/or Australian)	South America
ARALIACEAE		
*Pseudopanax**	8 spp. (New Zealand and Chatham I.)	2—3 spp.
BORRAGINACEAE		
*Tetrachondra**	1 sp. (New Zealand)	1 sp. (Patagonia)
CAMPANULACEAE		
Hypsela	2 spp. in SE. Australia, 1 sp. in New Zealand	1 sp.
Laurentia § Isotoma	8 spp. (Australia, New Zealand)	1 sp.
Lobelia § Pratia	also in Pacific and New Zealand, Tr +	Andes & Falkland Is.

CARYOPHYLLACEAE		
Colobanthus	centre in New Zealand	Patagonia
CENTROLEPIDACEAE		
Gaimardia	1 sp. (New Zealand to New Guinea), Tr +	1 sp.
COMPOSITAE		
Abrotanella	13 spp., also in Fiji (?), centre in New Zealand, Tr +	2 spp., also Falkland Is.
Brachycome	centre in Australia, 3 spp. in New Zealand, also in Hawaii, 1 in S. Africa, Tr +	+
Erechthites	rather large genus, Australia, 8 spp. in New Zealand, W. to E. Java, an allied genus *Arrhenechthites* in the mountains of New Guinea, Tr +	∼ sp.
Lagenophora	rather large genus, also in Polynesia, 4 spp. in New Zealand, 1 sp. through Malaysia to China, Tr +	+
Microseris	1 sp. in Australia and New Zealand	36 spp.
Vittadinia	centre in Australia also in New Caledonia and New Guinea, 1 sp. in New Zealand, Tr +	+
CONIFERAE		
Dacrydium	to SE. Asia, also in New Zealand and New Caledonia, Fiji, Tr +	S. Chile
CORIARIACEAE		
Coriaria group C	probably only 1 polymorphous species; from New Guinea via New Hebrides, Fiji, and Samoa to New Zealand, Tahiti, and S. America, Tr +	
CORNACEAE		
Griselinia	2 spp. in New Zealand	6 spp. in Chile
CUCURBITACEAE		
*Sicyos**	Australia, 1 sp. in New Zealand, also in Hawaii and many other Polynesian Is.	centre in the Americas
CYPERACEAE		
Carpha	1 sp., also in New Zealand and in S. Africa, Tr +	1 sp.
Oreobolus (map 13)	? 5 spp., also in New Zealand and Hawaii, Tr +	1 sp.
Uncinia	? 10 spp., centres in New Zealand and S. America and Malaysia, also 1 sp. in Kerguelen and Tristan da Cunha, Tr +	? 10 spp.
DROSERACEAE		
Drosera § *Psychophila*	1 sp. in Australia, 2 spp. in New Zealand	1 sp.
ELAEOCARPACEAE		
Aristotelia	4 spp. in Australia, 5 in New Zealand, *Sericolea* in Papua and N. Queensland, Tr +	2 spp.

EPACRIDACEAE		
Trib. Prionoteae	*Prionotis* (Tasmania), other genera in New Zealand	*Lebetanthus* (Patagonia)
ERICACEAE		
Gaultheria	from New Zealand N to Japan, Tr +	S.—N. America
Pernettya	4 spp. (Tasmania, New Zealand)	15 spp., also in Galapagos and Juan Fernandez Is.
EUCRYPHIACEAE		
Eucryphia	2 spp. (S. Australia, Tasmania), not in New Zealand	2 spp. (Patagonia)
FAGACEAE		
Nothofagus	New Zealand and E. Australia to New Guinea and New Caledonia, both sections present on both sides of the S. Pacific, Tr +	
GOODENIACEAE		
Selliera	2 spp., 1 sp. also in New Zealand	1 sp.
GRAMINEAE		
Deyeuxia	centre in S. America, also in New Zealand and Hawaii; also in Malaysia, Tr +	∼ spp.
IRIDACEAE		
Libertia	few sp., also in New Zealand	? 4 spp.
JUNCACEAE		
*Marsippospermum**	1 sp., New Zealand	2 spp.
*Rostkovia**	1 sp. from New Zealand to Patagonia	
LILIACEAE		
Astelia	New Zealand, Tasmania, Victoria, also in New Guinea, Polynesia, 1 sp. in Patagonia, Réunion and Mauritius, Tr +	
Subtrib. Dianellinae	2 genera, 1 wide species also Malagassian, Tr +	2 genera
Triad	*Eustrephus* and *Geitonoplesium**, Australia, Melanesia, also New Zealand, Tr +	*Luzuriaga*
MALVACEAE		
Pair	*Hoheria,* endemic in New Zealand	*Gaya,* 10 spp.
MONIMIACEAE		
*Laurelia**	1 sp. in New Zealand	1—2 spp. in Chile
ONAGRACEAE		
*Fuchsia**	3 spp., in New Zealand and Tahiti, Tr +	*c.* 60 spp.
PLANTAGINACEAE		
Plantago § Oliganthos	3 spp. in all, Australia, Tasmania, New Zealand, also in New Guinea, Tr +	
POLYGALACEAE		
Bredemeyera	*c.* 60 spp. (not in New Zealand)	few
POLYGONACEAE		
Muehlenbeckia	∼ spp., Australia, also New Zealand and in New Guinea, also in Pacific, Tr +	∼ spp.
RANUNCULACEAE		
Anemone § Rivularidium	1 sp. in Tasmania, 1 sp. in New Zealand	11 spp. in America and Asia

Caltha sect. Psychrophila	a few peculiar spp., 2 spp. in New Zealand	∼ spp.
RESTIONACEAE		
Hypolaena	centre in S. America, smaller in Australia; also in New Zealand	
Leptocarpus	also ∼ in S. Africa, Tr +, Australia and New Zealand 12 spp.	1 sp.
RHAMNACEAE		
Discaria	1 sp. in SE. Australia, 1 sp. in New Zealand	8 spp.
ROSACEAE		
Acaena	14 spp. in New Zealand, also in Hawaii, 1 sp. also in S. Africa, Tr +	∼ spp.
Geum subg. Oncostylus[1]	Tasmania, Auckland I., New Zealand, 7 spp.	Tierra del Fuego, 2 spp.
RUBIACEAE		
Coprosma	through Pacific, centres in New Zealand and Hawaii, E to Juan Fernandez, N to Mt Kinabalu (N. Borneo), Tr +	
Nertera (*map 14*)	also New Zealand and Hawaii, Madagascar, Tristan da Cunha, N to Central China and Formosa, Tr +	Central to South America
SCROPHULARIACEAE		
Euphrasia (*map 15*)	centre in New Zealand to New Guinea, northward through Malaysia to entire N. hemisphere, Tr +	1 sp.
Hebe (*map 11*)	centre New Zealand, northward to New Guinea, also in Kermadec and Rapa, Tr +	
*Jovellana**	New Zealand, 2 spp.	few spp., aff. *Calceolaria*
Ourisia	4 spp. in Tasmania, 10 spp. in New Zealand	+
STYLIDIACEAE		
Donatia (*map 10*)	2 spp., Tasmania, New Zealand	1 sp., Fuegia
Trib. Phyllachneae (2 genera)	centre in New Zealand, both genera (*Forstera* and *Phyllachne*) in Tasmania, New Zealand, Fuegia	
THYMELAEACEAE		
Drapetes	Australia, New Zealand, N to Mt Kinabalu in N. Borneo	a few spp. in Fuegia
UMBELLIFERAE		
Azorella	1 sp. in Macquarie and Kerguelen Is.	centre, *c.* 70 spp.
Lilaeopsis	monotypic[2], SE. Australia, Tasmania, New Zealand	Central to South America
Oreomyrrhis (*map 12*)	N to Formosa, Tr +	few spp., Mexico to Fuegia
Schizeilema	1 sp. in SE. Australia, centre in New Zealand	1 sp. (Patagonia), also Falkland Is.
WINTERACEAE		
Winteraceae (*Belliolum, Bubbia*[3], *Drimys, Exospermum, Pseudowintera. Zygogonum*)	*c.* 80 spp., Tr +, N to Luzon, Tr +, in New Zealand only the endemic *Pseudowintera*	4 spp., Tr +

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[1] The generic name *Oncostylus* (Schlechtend.) Bolle, 1933, seems a later homonym of *Oncostylis* Nees.

[2] Some authors distinguish some 15 spp.

[3] One species of *Bubbia* in Madagascar (Capuron).

3. SUMMARY OF AMPHI-TRANSPACIFIC DISTRIBUTION

From Chapter 2 it must be concluded that there are 5 distinct though grading types of amphi-transpacific distribution in the temperate, subtropical and tropical zones, with the following number of cases to which I have added for comparison the number of cases from Engler's account of tropical transatlantic distribution.

	Number of cases	Number of supra-specific affinities
(i) North Temperate and Arctic	many, but not specified here	
(ii) North Warm-Temperate and Subtropical	115	17 = 15 %
(iii) Tropical	80	39 = 49 %
(iv) South Subtropical and Warm-Temperate	23	6 = 24 %
(v) South Temperate	62	4 = 6½ %
Tropical Transatlantic (after Engler) ...	81	

These latitudinal zones of affinity are intersected longitudinally by two oceans, the Atlantic and the Pacific.

Only the Arctic and North Temperate types can approximately be explained by the present distribution of land and sea and climate in the Beringian area.

During the warmer Upper Cretaceous and Tertiary when Beringia was a wide continuous isthmus enabling an exchange of the North Warm-Temperate and possibly (least subtropical) part of the North Subtropical element between East Asia and North America, the frigid and microtherm element could be assumed to have survived by retreating on the mountains of Beringia. It seems not disputable that the Glacial Epoch destroyed the mesotherm element in Beringia and in the adjacent very large continental areas of Asia and North America, enabling the microtherm element to descend and take the place it occupies today.

The Glacial Epoch cannot bring any solution for the other four types (North Subtropical sensu stricto, Tropical, South Subtropical, and South Temperate), however, which show immense disjunctions in distribution coinciding with disjunctions in the occurrence of land. It must be observed, however, that where there *is* some land, in islands in Polynesia, in New Zealand *etc.* in the South Pacific, many genera have stray representatives in the smaller islands, or even centres (New Zealand, Fiji, Hawaii, Rapa, *etc.*).

4. THE AMPHI-TRANSPACIFIC ELEMENT IN THE PACIFIC ISLAND FLORAS

It is not my intention to give here a full account of all aspects of the Pacific island flora. My purpose is to confine this chapter to some essential points and an account of the representatives of the amphi-transpacific taxa on Pacific islands.

First, it should be stressed that in proportion to the amount of land the number of representatives increases in all of the five transpacific zones. This would appear to be natural in the West Pacific islands situated west of the Andesite Line which is supposed to be of old subcontinental character, but it holds also to some degree for the truly oceanic basalt islands in the Central Pacific.

This is in line with the fact that the western two thirds of the Pacific has a preponderantly Indo-Malaysian flora, a thesis I believe first pointed out by Hooker (1859), later stressed by Skottsberg and by Merrill, and recently confirmed with great detail by Van Balgooy (1960).

Second, as is pointed out elsewhere in this essay, the amount of land in the Pacific has been much greater in the past of which the atolls and undersea mounts and guyots bear testimony, representing fully convincing evidence for Darwin's hypothesis of submergence. From this follows again that in the past the amount of land must have been larger and the flora richer, because notwithstanding a certain amount of subsidiary dispersal should be admitted, foci must have disappeared with the vicissitudes of time.

For the North warm-temperate to subtropical Type II hardly any island surfaces are available in the North Pacific but what there is, the Bonins, have this type, as their flora is almost entirely Japanese.

Of the tropical Type III almost all groups are represented in the Pacific in certain localities west of the Andesite Line, either in Micronesia or Melanesia and/or in the coastal islands of Pacific America, as for example *Spathiphyllum,* Arac. (*map 5*). East of the Andesite Line, in Polynesia proper, the number of genera is decidedly small but still significant, *viz Perrottetia,* Celastr. (*map 4*), *Weinmannia,* Cunon., *Xylosma,* Flac., *Heliconia,* Mus., *Colubrina,* Rhamn. (inland spp.!), *Sapindus,* Sapind., *Saxifragaceae* subtrib. *Hydrangeeae* (an endemic genus in Hawaii), *Eurya* and *Ternstroemia,* Theac.; several are represented there by a number of species.

For the south subtropical Type IV, which is small in numbers, the same picture is obtained. Almost all occur on islands not far from the continents (Melanesia, Fiji, New Zealand, Juan Fernandez) and three are even found in the Central Pacific, either Hawaii and/or other Polynesian islands, *viz Nicotiana,* Solan. (*map 8*), *Sophora* § *Edwarsia,* and *Metrosideros,* Myrt.

For the south temperate Type V the amount of land is of course very large through the presence of large islands of New Zealand, and it is remarkable that of the 62 odd cases all except two (*viz Eucryphia* and *Bredemeyera*) are found in New Zealand and mostly also in Tasmania, sometimes also in the islands surrounding New Zealand (Norfolk, Lord Howe, Chatham, Campbell, or Kermadec). See *maps 10—14.*

5. PANTROPICAL MEGATHERM FAMILIES AND GENERA

Judged from the present geographical situation, and from the fact that it has been almost axiomatic in historical geology that transverse transpacific land connections were impossible to envisage and never existed in the past, I am aware that the lists of tropical transpacific and South transpacific taxa are to botanists, palaeobotanists, palaeogeographers, and geologists a hair-raising challenge, to say the least.

And the figures of the amphi-transatlantic and amphi-transpacific plant distribution represent still only part of the story, and a small part indeed. The most formidable body of facts is concealed in the *pantropical families, tribes, genera, and sections,* which are for the major part megatherm. See *maps 7, 16—18.*

The following pantropical larger megatherm families are exclusively found in the tropics or almost so:

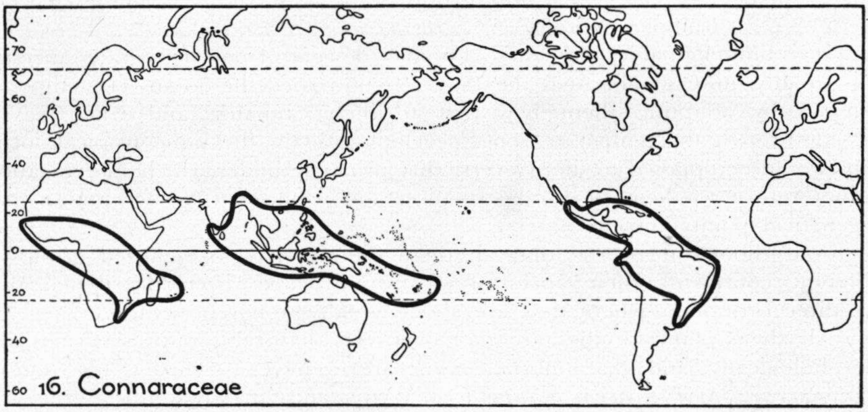
Annonaceae
Bombacaceae
Burseraceae
Cannaceae
Cochlospermaceae
Combretaceae
Connaraceae (map 18)
Cyperaceae-Mapanioideae
Dichapetalaceae
Dilleniaceae
Erythroxylaceae
Flagellariaceae
Guttiferae s.str.
Hernandiaceae
Hippocrateaceae
Lecythidaceae
Malpighiaceae
Marantaceae
Musaceae
Myristicaceae
Ochnaceae
Opiliaceae
Pandanaceae
Rhizophoraceae
Taccaceae
Triuridaceae
Zingiberaceae

The following are almost tropical or can be considered tropical *pro majore parte,* that is with subtropical and a few stray temperate outliers:

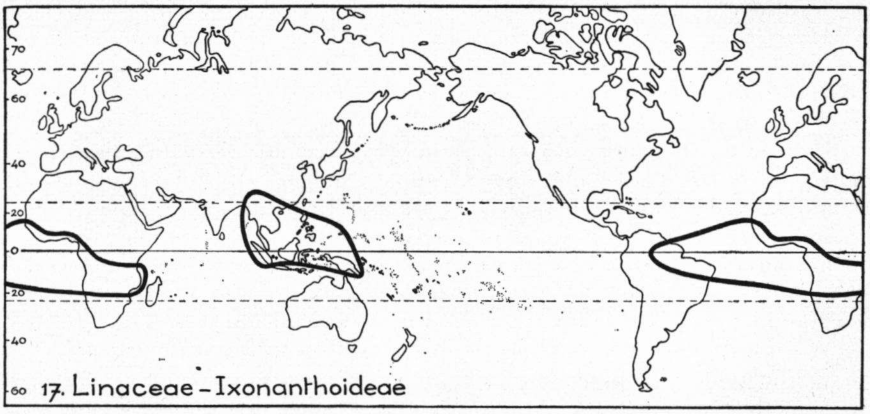
Acanthaceae
Anacardiaceae
Apocynaceae
Araceae
Asclepiadaceae
Begoniaceae
Bignoniaceae
Burmanniaceae
Capparidaceae
Chloranthaceae
Commelinaceae
Cucurbitaceae
Cunoniaceae
Dioscoreaceae
Ebenaceae
Elaeocarpaceae
Eriocaulaceae
Euphorbiaceae
Flacourtiaceae
Gesneraceae
Haemodoraceae
Icacinaceae
Lauraceae
Leg.-Caesalpinoideae
Leg.-Mimosoideae
Loganiaceae
Loranthaceae
Melastomataceae
Meliaceae
Menispermaceae
Monimiaceae
Moraceae
Myrsinaceae
Myrtaceae
Olacaceae
Oleaceae
Palmae
Passifloraceae
Piperaceae
Podostemonaceae
Pontederiaceae
Rafflesiaceae
Rubiaceae
Rutaceae
Sapindaceae
Sapotaceae
Simaroubaceae
Sterculiaceae
Theaceae
Tiliaceae
Urticaceae
Verbenaceae
Vitaceae
Xyridaceae

If we accept that the climatic zones of the globe have been permanent and the thermo-ecology of these families has not changed, it is clear that the two-ocean disjunction found in these pantropical families represents a formidable body of facts which needs explanation and is of immensely more

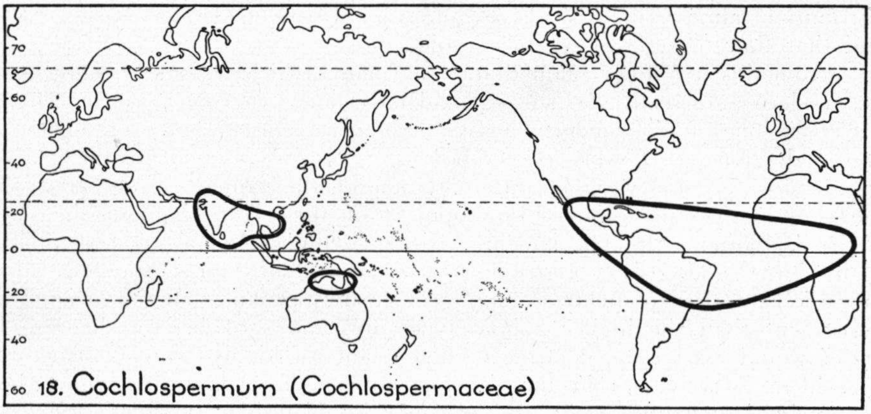
Maps 16—18 are examples of pantropical lowland distribution of the family *Connaraceae,* the subfam. *Linaceae-Ixonanthoideae,* and the genus *Cochlospermum* (16 after Suessenguth, 17—18 after Hutchinson).



16. Connaraceae



17. Linaceae – Ixonanthoideae



18. Cochlospermum (Cochlospermaceae)

weight than the cases of amphi-transpacific distribution enumerated on p. 250—253. Compare *maps 7, 16—18.*

It is unimaginable that these families descend from temperate ancestry. It is equally unimaginable that they have circumpassed the oceans via temperate climates by adapting themselves first to these climates, and when having passed through the temperate zone, developing again the same tropical forms. This would be opposed to the irreversibility principle under which specializations cannot return to their ancestral structure, and would not be acceptable from a genetical point of view.

And though it is true that all these families have specialized groups in different continents their ancestral stock must have been distributed over the three continents where they are about equally well represented.

All these plant families are moreover very natural groups systematically, morphologically, and anatomically. Some are even very compact, for example *Annonaceae, Myristicaceae, Sapotaceae, etc.* and it would be absurd to postulate a three-phyletic origin for their ancestral stock. It would be still more fantastic to assume a three-phyletic origin of the many hundreds of *genera* which have a pantropic distribution.

Map 16 gives an example of a pantropical family, *Connaraceae, map 17* gives an example of the pantropical distribution of a subfamily, *Linaceae-Ixonanthoideae, map 19* that of a single genus, *Cochlospermum, map 7* that of an almost pantropical genus, *Cynoctonum.*

In addition to this imposing number of pantropical families there is among the other strictly megatherm families an equally imposing number of subfamilies, tribes, and genera which are purely pantropical. These families, although largely pantropical, have been omitted, for example *Malvaceae,* which contains a number of pantropical genera, *e.g. Abelmoschus, Abutilon, Gossypium, Hibiscus* (a few stray warm-temperate), and *Pavonia.* Many of these families have representatives on tropical oceanic islands.

We must assume that the *proto-Annonaceae, proto-Bombacaceae, etc.* had in the past full opportunity and time to come across the oceans in some way or other, at least the Atlantic, and that they had time to spread and evolve into new forms in the three main tropical centres of the world.

If our reasoning is correct it follows that at the time of the transoceanic distribution almost all basic types of Angiosperms had already developed, and that they must be very ancient indeed.

From this it follows again that many plants which we superficially define as "modern" are really very ancient and have not changed in essence. Hooker (1859) in one of his wonderful essays — as usual a rich source of suggestions and deductions, preferably in footnotes — already pointed to the marked contrast of the showy, vivid differentiation of the fauna as compared with the conservative, monotonous development of the plant kingdom; he wrote (*l.c.* xii, footnote): "The much narrower delimitation in area of animals than plants, and greater restriction of Faunas than Floras, should lead us to anticipate that plant types are, geologically speaking, more ancient and permanent than the higher animal types are, and so I believe them to be, and I would extend the doctrine even to plants of highly complex structure." The idea that changes in the development of the Angiosperms have been extremely slow was recently stressed anew by Hamshaw Thomas (1960, 3).

6. POSSIBLE EXPLANATIONS OF TRANSOCEANIC DISTRIBUTION IN GENERAL AND IN THE PACIFIC IN PARTICULAR

As far as I can see there can be, or have been, put forward eight alternative explanations for transoceanic plant distribution.

Under all of them changes in the distribution of land and sea in the past have been accepted, even by the most fervent diffusionists.

They are the following:

(i) A former tropical world.
(ii) Polyphyletic origin of transoceanic disjunct taxa.
(iii) Plant taxa as unreliable thermometers for the past.
(iv) Relict hypothesis of formerly pantropical genera.
(v) Active transoceanic dispersal under the steady state.
(vi) Continental drift as opposed to the steady state principle in plant geography.
(vii) Polar shift.
(viii) Transoceanic land-bridges.

The first seven possible explanations will be included in this chapter, the eigth, that of former land-bridges, will form the subject of a separate chapter 7.

I will discuss their merits one by one.

(i) A former tropical world

It has sometimes been assumed that the whole globe was, at some period in the past, tropical and that tropical plant genera could then have freely moved or migrated either along the northern border or southern border of the Pacific basin or along both borders. Even recently to Skottsberg (1956, 274—275) "it would seem more acceptable to fall back on an ancient pantropical flora, spread from pole to pole before any temperate zones had become sharply delimited...; with the appearance of distinct climatic belts a sorting out of meso- and microthermic groups followed...".

Accepting a "steady state" of the crust of the earth, hence of the main situation of the continental (sial) masses, and of the rotation axis of the globe which beyond any doubt remained fixed in space in the solar system, and of the latitudinal climatic zonation, these routes rounding the North Pacific must have run between latitudes 50°—70° N and those rounding the South Pacific between latitudes 40°—60° S. Although these latitudes were admittedly milder in the past — at least in the Tertiary — than they are now, they cannot have had a "tropical" climate, as they must have had alternating warm and cold seasons. They might have been warm-temperate to subtropical and the majority of the trees must have been deciduous.

Kryshtofovich (1929) admirably summarized the significance of the older Tertiary floras of Siberia, together with those of Manchuria, Korea, and adjacent parts of northeastern Asia and concluded that in this region during the Tertiary there were nowhere tropical or subtropical conditions, but that as late as the Lower Miocene it was still occupied by a temperate forest, similar to that of the Eocene of Alaska.

Chaney concluded (1936) "that in the North Pacific the major movement has been southward as a result of a progressive trend toward cooling and aridity since the early Tertiary. This gradual shifting southward of the northern limits of most of the Eocene species has resulted in their restriction to the low latitudes of Asia and America, in the forests of which there is remarkable correspondence of genera on both sides of the Pacific. Following closely behind them the temperate Miocene flora left the northern regions and became widely established in middle latitudes of both continents".

There have been authors who suggested that Spitzbergen and Greenland had a subtropical flora in the Cretaceous. Seward (1927) reported, for instance, on the Cretaceous flora of West Greenland at *c.* 70° NL where he found many Conifers, Pteridophytes and rather large-leaved Angiosperms (almost all leaves only) which he refers to *Menispermaceae, Magnoliaceae, Lauraceae,* and *Platanus.* He referred *Dalbergites* with hesitation to *Leguminosae* and believed, like previously Nathorst, that *Artocarpus* is represented in this flora. He gives, however, no structural characters on which these identifications are based and I believe they are absolutely inadequate as a basis for widegoing speculations. The only general conclusion one could draw from this analysis is the presence of moderate-sized, deciduous temperate forest as now found between 35°—50° NL. This is exactly fitting the conclusions of Kryshtofovich, Berry, and Chaney. Seward's suggestion (1927, 155) that "it was within the Arctic circle that the evolution of deciduous Angiosperms progressed with greater rapidity and energy than in more southern latitudes. A factor concerned in this development may have been the alternation of continuous sunshine and a long period of rest" seems to me untenable as they were at any rate outliers of frontier pioneers of southern-centred groups standing extreme conditions. It led him even to consider the Arctic as the birthplace of the Angiosperms, and consequently to the view (1934, 23) that the London Clay Flora may have been derived from or have made part of a widespread *northern* flora "which in the course of the Tertiary Period suffered progressive reduction and is now represented by enfeebled relicts in Indo-Malaya". As a matter of fact this immensely rich Indo-Malayan flora bears no testimony of being enfeebled and has, as Kryshtofovich (1929, 310—311) correctly stated, remained "unmolested ever since its first descent from its Cretaceous ancestors". It is the tropics which saw the birth and expansion of the Angiosperms, not the Arctis.

It has been claimed that fossil *Palmae* occurred in Greenland, but Kaul (1945, 1960) has found this evidence resting on erroneous identification. As a matter of fact the 40° latitude, both north and south, is at present the extreme frontier of living palms, and according to the trustworthy Cretaceous-Tertiary fossil record palms have never been found beyond about 50° latitude. Their distribution forms a most important argument for the conservative view of only slight climatic changes in the zonation at medium latitudes and a full confirmation of the steady state principle.

The myth of the occurrence of tropical floras in the Arctic has been so frequently disproved by Berry (1930) and others that their supposed climatic implications can be wholly disregarded.

Although superfluous I may add that the distribution of the mangrove genera (Van Steenis, 1962) strongly pleads against a former tropical world.

In the West Pacific they find their most northern stations in the Ryukyus and the southernmost corner of Kyushyu. If the North Pacific, at least the southern shore of Beringia, would have been tropical these mangrove genera would have migrated along these shores; in this way they would have reached the Pacific shores of America and have extended their distribution to Central and South America. With the Tertiary cooling of the climate their North Pacific stations would have disappeared but they would have survived in the southern tropical parts. However, none of the West Pacific genera is found in West America.

According to Brooks (1926) the warmer Tertiary in the boreal zones must have had a peculiar character with a hot summer but on the whole very wet and misty, without glaciers or ice, but with snow in the long dark winter and a temperature not much and not long below zero. Such conditions may at most suit warm-temperate and perhaps a few odd subtropical plants, but would mean a certain death to all tropicals and almost all subtropicals.

Brooks maintains that, for climatological reasons, thermal zonation has persisted throughout the ages, as the amount of solar energy received at different latitudes has always been graded and decreased towards higher latitudes.

It may be true as Steere (1960) says that it is "a misconception that the Arctic is the land of six months of light and six months of darkness" and that photosynthesis is mainly suspended because of the low temperature and less so because of the darkness, twilight and very short intervals of light during the long dormant winter period. The thermo-ecological composition of the luxuriant forests represented by abundant fossils in the Arctic must, however, be the decisive aspect from which we should define the climate under which these forests once thrived in ancient periods, by comparing their composition with vegetation types growing today at lower latitudes. Though at present low temperature is more important than light, increase of the world's temperature will, at arctic latitudes, very soon find its bottleneck in the form of this same light, as part of the amount of solar energy which decreases rapidly at high latitudes. Though the forest limit will have been more north, the rate of growth of conifers and deciduous leafy trees during the short summer must have been very slow.

Even Axelrod (1952, 38), who rather loosely applied the terms tropical, subtropical, and warm-temperate, pinned the warm-temperate zone from the Cretaceous to the Oligocene down to 45°—50° NL and SL, that is the latitude of North Japan and Southern New Zealand.

Reid & Chandler (1933) have in their magnificent study of the Eocene London Clay Flora concluded that this flora must have represented a unique most northern outpost of a *tropical* flora, during a relatively brief "hottest" phase of the Eocene (*l.c.* 84—85) at the "lowest extreme of temperature that would permit its growth" (*l.c.* 74—75). They assume this flora to have been deposited as debris from a large river flowing in the London Clay Sea, communicating with both the Northern Ocean and the warm southern Tethys or Nummulitic Sea, which covered the area where are now the Mediterranean, the Alps, the Carpathians, the Balkans, the Atlas, the Sahara, Egypt, Arabia, Palestine, Persia, and the Himalayas to the farthest confines of India. It was further assumed "that the plants must have grown comparatively near the place of deposition. It is unlikely that in very far transported material so many hundreds of individuals belonging to the same species would be found deposited together. All the families to which the fossils belong are found in the tropics, five even only in the tropics, *viz 'Nypaceae', Burseraceae, Icacinaceae, Flacourtiaceae* and *Sapotaceae* (11 %) and fourteen others are largely tropical at present, *viz Palmae, Olacaceae, Menispermaceae, Annonaceae, Lauraceae, Meliaceae, Anacardiaceae, Sapindaceae, Sabiaceae, Elaeocarpaceae, Sterculiaceae, Dilleniaceae, Myrsinaceae,* and *Apocynaceae* (32 %)". In passing it may be remarked that nobody has ever found a fossil fruit or seed *in situ*; they were collected along the beach; only teredo-bored wood was located in the clay. All plants found were woody except *Protobarclaya,* Nymph., and *Palaeoeucharidium,* Onagr. In comparing the London Clay Flora with younger Tertiary floras it is remarkable that the percentage of woody plants gradually decreases to that in the living flora (17 %). This goes parallel with a cooling of the climate onwards of the Eocene; the first to disappear are *Nypa,* Palm., *Tetrastigma,* Vitac., and *Iodes,* Icac., which are not known from both older and younger deposits. The number of genera of presumably cooler affinity in the London Clay Flora is very small, *viz Petrophiloides,* Jugl., and *Cornus,* Corn. The number of tropical shore genera is very small, besides *Nypa burtinii* there is *Ochrosioidea,* Apoc. Their conclusion is (*l.c.* 88) "that the London Clay Flora was mainly of a tropical rain-forest type, allied principally with the living Indo-Malayan flora, as proved by *Nypa* which was in the Anglo-Belgian basin living at its northernmost range".

Although the London Clay Flora bears a great resemblance to the flora of Madagascar (*l.c.* 58), the immense Tethys made migration difficult from what was then Africa; the London Clay Flora has essential Indo-Malayan affinity (*l.c.* 64).

Through my admiration for the tenacious and careful documentation, argumentation, and reasoning, I am reluctant to oppose the existence of an Eocene *tropical* habitat at 50° N, but cannot refrain from it.

My arguments are:

(a) The authors admit that a comparison with other Eocene floras of West Central Europe, described by Saporta, Crié, and Bandulska, is impossible as these all have in part tropical types but also a considerable intermingling of purely temperate genera (*l.c.* 83—85). They find the London Clay Flora "unique". This is, however, not admissable according to their own reasoning that the "bulk" should be decisive. One cannot neglect the character of adjacent Eocene floras.

(b) They admit (*l.c.* 60) that the marine fauna gives parallel evidence of an intermingling of cooler and warmer types in the Palaeocene and London Clay Flora. The animal remains of the London Clay Flora, apart from the Mollusca, are regarded as showing tropical affinity (*l.c.* 19).

(c) They state (*l.c.* 61): "In any case Vertebrate and Invertebrate palaeozoology are at one in finding that the life in the ocean (Tethys?) was predominantly *tropical or subtropical* during the period of the London Clay.... So that they point to ocean conditions which would accord with the growth of a tropical flora in that period."

There is, however, a great difference between subtropical and tropical and they must have felt the discrepancy; consequently they gave themselves much trouble in advocating on the basis of rather haphazard information (*l.c.* 88—89) that the tropical London Clay flora "was enabled to live because *exceptional climatic conditions* allowed it to *overstep* its norm of temperature. The most important of these conditions probably were: great precipitation, a suitable balance between precipitation and evaporation, a suitable seasonal distribution of rainfall, a uniform climate, and frostless winters." They based these conclusions "on the observed fact that the measure of climate in terms of plant life does not coincide exactly with the measure of climate by temperature." They even went so far as to suggest that the climate in the tropical rain-forest is much cooler than assumed, but their reasoning to meet ends seems here futile. They are here at variance with Brooks who gave as his opinion that the maximum which could be reached at 50° NL under the most favourable conditions would be a yearly average of 65° F, which is a subtropical climate, not more!

Though the ameliorating effect of the Kuro Shio Current in East Asia and the Gulf Stream in W. Europe is well-known, such local effects should not be overrated.

(d) The finding of the (now) American palm species *Sabal palmetto* and *Serenoa serrulata,* and *Eucharidium,* Onogr., which live under subtropical conditions is unexpected, as the Tethys carried an equatorial Asiatic current towards the Atlantic.

(e) They say that, according to Moseley, of the debris in a tropical ocean the leaves drop first to the bottom, wood and fruits will sink farther off land, which does not conform with their conclusion (*l.c.* 65) that the London Clay plants "must have grown comparatively near the place of deposition", but no leaves are found there.

(f) They say that it is impossible to accept transport of the London Clay Flora from some distant tropical region — leaving unconsidered their accepted equatorial Tethys current — amongst others because the flotsam of the Gulf Stream contains always admixture of local forms which outnumber the tropical and this is not the case with the Sheppey Flora.

This is in my opinion no fair comparison, as such debris along the coast of Norway combines two extremes, tropical and fully temperate. But if we suppose, what seems likely, that the climate of the Clay Basin was subtropical we would find the flotsam of the *tropical* South Tethys mingled with *subtropical to warm-temperate local forms,* not with temperate ones. And that seems to me the logical conclusion, as species of almost all genera found in the London Clay Flora could grow in the warmer part of the subtropics and that condition would have been given by the ameliorating effect of the Tethys equatorial current. Such subtropical elements would in species outnumber the proper tropical ones, that is, in fact, solely *Nypa,* Palm., *Iodes,* Icac., and *Tetrastigma,* Vit.

(g) "The key to the solution lies in the presence of *Nypa*" (*l.c.* 61), and this is true since there is, in the London Clay flora, an astonishing absence of other tropical Indo-Malayan shore plants associated with *Nypa, viz Pandanus, mangroves* (two have since been reported!), *beach* *plants, Casuarina,* and further a remarkable absence of inland *Dipterocarpaceae* which were through the Tertiary characteristic of the Indo-Malayan forest. The drifting power of *Nypa* fruits is exemplary and as a large proportion of the specimens in the London Clay Flora are undersized (and possibly barren?), it is not unlikely that they were transported over large distances.

Besides we are very badly informed about the details of actual deposition of debris carried by sea currents and especially about the *sorting* which will take place on the way. We are also unacquainted with the caprices of such currents. Observations in nature are made of material floating on the surface, but what happens to suspended material escapes observation.

(h) *Nypa* belongs to the mangrove and the present distribution of that vegetation type and its constituents provides a formidable argument against the tropical nature of the London Clay Flora, and, besides, against polar shift.

In order to demonstrate this I have given (1962) a short survey of mangrove composition, confining myself to genera of which *all* species belong to that formation. The mangrove or tidal forest is restricted to the tropics and finds its main distribution between *c.* 30° northern and southern latitude. As far as known to me only one species of *Avicennia,* Verb., occurs in North Island, New Zealand, southwards as far as *c.* 38° SL. On the *west coasts* of Africa and of South America the southern latitude is much less, *viz* 4° and 9° SL respectively, correlated with the dry coastal climate, hence lack of silt-bringing rivers needed for mangrove growth. The fruits, seeds, or embryos (in the viviparous genera) are all dispersed by sea-water. As I have explained elsewhere (Van Steenis, 1962) the mangroves are, by their indisputable sea-borne dispersal and megatherm ecology, extremely important as trustworthy botanical indicators for palaeogeographical purposes. Further, their dispersal, although sea-borne, is evidently not effective over large distances, in contrast with dispersal of the strand flora (*Pescrapae* and *Barringtonia* formations).

It appears that the mangrove genera are largely developed in the Old World Tropics (West Africa excepted), and poorly represented in the New World (and West African) tropics.

To this should be remarked that *Rhizophora mangle* L. ranges from New Caledonia through the Pacific to W. America and from the Caribbean to West Africa¹). A similar thing can be said of *Rhizophora harrisonii* which occurs on both sides of the Americas, and of *Laguncularia, Conocarpus*

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¹) A similar distribution pattern is found in the marine Hydrocharitaceous genera *Halophila* and *Thalassia,* found from East Africa through the Indian and Pacific Oceans to the Caribbean (Den Hartog, 1957); they are, however, not found in *West* Africa.

Another exactly similar pattern is shown by the sea-dispersed littoral genus *Batis,* the only genus of the *Batidaceae,* of which one species is known from South New Guinea on clay flats near the mangrove (*B. argillicola* van Royen) and another (*B. maritima* L.) occurs on the shores of the Galapagos Is. (introduced (?) in Hawaii), the Pacific coast of Central America and the Caribbean. This is also not found in West Africa.

DISTRIBUTION AND NUMBER OF SPECIES OF MANGROVE GENERA

Names of families and genera	Total number of species	Indian Ocean to W. Pacific (incl. E. Africa)	Pacific Americas	Atlantic Americas	West Africa
Rhizophoraceae					
Rhizophora	7	6	2	3	3
Bruguiera	6	6	—	—	—
Ceriops	2	2	—	—	—
Kandelia	1	1	—	—	—
Verbenaceae					
Avicennia	11	?6	3	3	1
Meliaceae					
Xylocarpus (incl. *Carapa*)	?10	?8	?	2	1
Combretaceae					
Laguncularia	1	—	1	1	1
Conocarpus	1	—	?	1	1
Lumnitzera	2	2	—	—	—
Bombacaceae					
Camptostemon	2	2	—	—	—
Plumbaginaceae					
Aegialitis	2	2	—	—	—
Myrsinaceae					
Aegiceras	2	2	—	—	—
Palmae					
Nypa	1	1	—	—	—
Myrtaceae					
Osbornia	1	1	—	—	—
Sonneratiaceae					
Sonneratia	5	5	—	—	—
Rubiaceae					
Scyphiphora	1	1	—	—	—
Totals	?55	?45	?6	10	7

(?), *Avicennia nitida,* and *Batis maritima. West* Africa and *East* Africa do not share a single species!

This proves that these genera existed and were already widely distributed at the opening of the Panama isthmus in the Eocene, and that their distribution must have taken place between the Eocene and the late Miocene through an oceanic connection between the two Americas.

The fact that the Atlantic is so poor in mangrove species, although the number of suitable habitats in the Caribbean and Amazon deltas must be plentiful, proves further that the dispersal from the West Pacific to the East Pacific must have offered difficulties, probably by lack of large silt areas in the East Pacific, and further by the relatively short period available and the rather narrow open connection between the Americas.

It is most likely that the origin of the mangroves must have been in the Indo-Malaysian-West Pacific area, from where they spread eastwards to the Americas and westwards to the Malagassian and East African coasts; but they could not round South Africa which is now situated only at 34° SL.

This again implies that a shift of the Pole to the Bering Straits area is most unlikely; it would have brought South Africa full up into the tropical zone and would have permitted mangroves to creep around it and reach the Atlantic.

Originally only *Nypa burtini* was reported as the single mangrove plant in the London Clay Flora, but later Chandler (1951) has found also petrified mangrove hypocotyls, which had previously been held to be pieces of wood, of *Bruguiera* and *cf. Ceriops.*

For the London Clay Flora the distribution of the mangroves as outlined above under the steady state of the pole defeats a tropical climate at 50°, because though Reid & Chandler's assumption was that *Nypa* could only thrive there at a brief hottest phase of the Lower Eocene, the *southern* shore of the Tethys, which communicated with the Atlantic where now is Morocco would anyway have been distinctly tropical, and would have been fringed with at least an interrupted mangrove (including also *Nypa*) from the Indian Ocean area to the Atlantic and would easily have reached the West African Atlantic coast. However, *there is not a single species of mangrove common to the Indian and Atlantic basins,* but all the West African species are again found in the Caribbean! Furthermore the genera *Bruguiera* and *Ceriops* are not known from the shores of the Atlantic Ocean. From this it can be concluded that even Morocco did not have a tropical climate suited to mangrove conditions, let alone the London Clay Sea.

The only likely thing emanates, *viz* that *the European Eocene deposits got their truly tropical component from allochthonous drift material carried by the Tethys.* The alternative explanation, that the mangroves now centering in Indo-Malaysia had then not yet developed (*Nypa* excepted), is not acceptable from the botanical point of view, and from the fact that they had by that time already spread from the Indian Ocean eastwards to Panama.

In addition to the estimation of the thermo-ecology of fossil species and fossil biota (see *fig. 1*) — which must remain a guess in case of totally extinct groups or species which we are unable to compare with living groups or species — great attention should be given to the origin of fossilized material, whether it is allochthonous or autochthonous or partly so. This is particularly important as the conditions under which fossilization takes place varies enormously and the effect of many of these conditions escapes observation. In respect to shelf areas it is not difficult to conclude that the majority of the fossils will give an exact reflection of the coastal flora with a probable contamination of species of the upland region behind. But in the case of drift and wide-reaching sea-currents it is not clear what happens to this large amount of material which is brought to distant shores where coastal deposition may follow at much higher latitudes than its origin. Caprices of currents and favourable sedimentation conditions cannot always be assumed to have been local or exceptional.

It would be highly desirable that a sufficiently subtle and practical objective method could be found to establish the temperature under which sedimentation has taken place, for example by the mineralogical or crystallographic composition of the sediment. A rather rough method has recently been found for limestone deposits. Otherwise a rather safe indication of autochthonous deposits is when leaves are found together with wood and/or fruits, as it is unlikely that leaves will travel over large distances. A deposit of wood and/or fruits without leaves seems much less safe.

If in a deposit mixtures are found of species which partly suggest a warm climate but partly a cold climate the decision will depend on the proportion of both components and whether there is a distinct discrepancy in the composition. If the majority is indicating a cold climate and a few a warm climate, the latter component is obviously allochthonous. Conversely, if the majority is indicating a warm climate and the minority a cool climate, it may be that the contamination is due to plants of adjacent high mountains of which diaspores have come down with rivers. In that case also diaspores of warm-temperate intermediate altitudes must be found mixed as an intermediary connecting the warm and cool indicators.

If there is a distinct discrepancy of tropical and temperate elements, the tropical element will probably be due to allochthonous tropical material, as must be the case for instance in the Northeast Atlantic where Gulf Stream material is brought together with that of the native temperate to cold element of Scandinavia.

The amber flora of the Baltic, of which Mrs Czeczott (1961) gave a concise, provisional summary, is an example of such a mixed flora, of which the thermo-ecological spectre, judging from family names, runs from *Connaraceae* and *Palmae* to almost temperate families. In my opinion this flora had thermo-ecologically a mesotherm character (see p. 287—288).

In general, I believe, the cooler element will, in mixtures, be decisive for temperature indication of the autochthonous element.

The pollen testimony, originally designed for recent or subrecent sediments, must be handled with extremely great care when applied to older deposits, as allochthonous sedimentation of pollens, either by wind or by water, must be the rule rather than an exception. Recently Hafsten (1951, 1960) reported subfossil pollen of *Nothofagus,* Fagac., from a recent bog in the island of Tristan da Cunha at 4500 km distance from the nearest living source in South America. He found also pollen of *Ephedra* and *Polemonium* which must have been windborne over large distances. And wind-dispersed pollen may well be the source of the few allochthonous grains which have been reported from Europe.

Besides by wind, pollen may be carried by sea-currents, and herewith we come again to the ticklish question of transport over large distances and distant sedimentation. I asked Prof. Knut Faegri, Bergen, whether any tests have been made in Gulf Stream water before the Norwegian coast, but he wrote me that no such observations are available. He agrees that some pollens float very well, *Pinaceae* above all, and that drifting masses of pine pollen are sometimes observed far from land. Most ordinary pollens (without air-sacs) sink, however, rather rapidly and are very soon incorporated in the bottom sediment. He drew my attention to the fact that oil-geologists are much interested in this question and that a friend of his has even a patent for finding old shore-lines by means of pollen-analysis. Correspondence with Dr. J. Muller, Brunei, brought to my knowledge that he has made a study of recent pollen transported by sea-currents in the Orinoco delta and shelf sediments (1959).

In this study it is stated that water-dispersed pollens of *Alnus* spp., Betul., have been found in the Orinoco delta at a distance of 800 km from their site of origin at 2000—3000 m altitude in the Andes. Dr. Muller thinks this is exceptional, because *Alnus* is both a prolific pollen producer and occupies a riverine habitat.

Among his other conclusions it is important to note that seaward transport from the delta shows a certain degree of size selection, the smallest grains being relatively concentrated the farthest seaward. In addition air-borne supply is apparent, but is outnumbered by water-borne pollen. The total pollen content offshore is shown to reflect the hydrographic current pattern. In his letter Dr. Muller assumed that water-borne pollen is generally deposited within a radius of a few hundred kilometres from the coast, but is not transported by sea-currents further to an appreciable quantity. Hereby it is left open what quantity.

This brings me again to the London Clay Flora which is now under palynological observation for a thesis by Miss Ma Khin Sein (Mrs Kyin Swi) at University College, London. The provisional list which she kindly forwarded me is a baffling one, as it shows an unimaginable spectrum from temperate (*Betulaceae, Coniferae*) to tropical (*Sapotaceae, Palmae*), and also with southern hemisphere *Restionaceae, Proteaceae,* and *Nothofagus* (Ma Khin Sein, 1961).

Although I am rather well acquainted with vegetation types and floristic botany, I cannot correlate this floristic spectrum with present plant geography in any of these two fields if it is conceived that all the plants which have delivered these pollens throve within a radius of a few hundred kilometres of the London Clay Sea. This leads me to suspect that either the identifications are not trustworthy¹) or that the pollen is, at least in part, an allochthonous assemblage, assuming the samples are of the same age (stratum).

Concluding, my impression is that in the Eocene there was a distinctly warm-temperate to slightly subtropical flora in Europe to about 45°—50° N,

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¹) The slides of "*Nothofagus*" have been examined by Dr. R. A. Couper but have appeared not to belong to *Nothofagus* (Dr. J. Muller, *in litt.*); plant-geographically it is impossible that this genus occurred on the northern hemisphere.

possibly somewhat warmer than could be expected from the latitude, but definitely not tropical.

The tropical aspect of the fossil London Clay Flora is due to a few tropical and many subtropical fruits transported from lower latitude by the equatorial Tethys current. There was no overstepping of the norm of temperature and among the Eocene floras of Central Europe the London Clay Flora is only unique because of the low percentage of temperate forms, for which I can give no other explanation than suggest a local caprice of deposition of debris sorted in that way by the surface and underwater currents.

A few fossil fruits from the Upper Cretaceous and Eocene were described by Chandler (1954) from Egypt from *c.* 25—30° NL and they have again a Malayan-Tethyan tropical facies in which *Nypa burtinii* is represented, which she consequently assumes to have grown along the southern seaboard of the ancient Tethys Ocean. More exact affinity of a tropical flora on such small numbers as described (6 genera) is of course out of question. She reduced *Rubiaceocarpum* Kräusel to *Nypa*, a *Diospyros* of Heer to *?Euphorbiaceae*, and his *Palmacites* to *cf. Icacinaceae*, significant for the uncertainty of some records.

Even a subtropical to tropical world would only to a certain degree meet botanists' need of suitable land masses in the North Pacific (Beringia), but not so in the South Pacific, as even in a tropical world the geographical disjunction of *c.* 9,500 km between South Australia and South America would remain the same as it is today.

We might assume that in a warmer world the northern shores of Antarctica would have been suitable to carry a vegetation not unlike that of New Zealand today, but even in that case the closest distance between New Zealand and Antarctica was *c.* 3000 km.

This is about the same distance as between the east tip of Brazil and the westernmost cape of West Africa, which is *c.* 2,750 km, the subject of the problem of transatlantic disjunction as summarized by Engler (1905).

(ii) Polyphyletic origin of transoceanic disjunct taxa

The second alternative for an explanation could be that the facts are undeniable, but that the interpretation is fallacious because of polytopic or polyphyletic origin of tropical sections, genera, and tribes on both sides of the Pacific. In other words that the genus *Spathiphyllum*, Arac. (*map 5*), has originated independently on both sides of the Pacific from different, unrelated ancestors but because of the great similarity of the products of both parallel lines of descent, has been recognized by taxonomists as belonging to one genus. I cannot believe that this view would be shared by any specialist in *Araceae*, the more so because, as mentioned before, the Malaysian and Cocos I. species form together with the common tropical American *S. cannaefolium* a separate section and are so closely related that with a wide specific concept they could be envisaged as being one species. Moreover, the closest allied genus to *Spathiphyllum* is the New Guinean monotypic genus *Holochlamys* which occurs within the range of the Malaysian species of *Spathiphyllum*. Exactly comparable indubitable cases are found in the tropical transatlantic genera.

This doubt would be more likely or justified on the generic level when the alliance of two different genera is concerned. It could for example be assumed that *Corsia* and *Arachnites*, Cors., have originated independently and had no genealogical connection in the past, but would represent analogous or parallel development to such a degree as to force taxonomists to set them side by side in a separate family, which would thus essentially be an artificial classification, not one based on common descent.

A suggestion to this effect has been made by Fries (1959) who was so much intrigued by the transpacific tropical distribution of *Anaxagorea*, Annon., that he has taken to consider the possibility that the ancestry of the American species of *Anaxagorea* might have rooted in the worldwide distributed tropical genus *Xylopia*, but that the ancestry of the Asiatic species of *Anaxagorea* might have been in the Asiatic genus *Artabotrys*. Though I am less acquainted with *Annonaceae* than desirable, this assumption is in my opinion very unlikely, first because it would have been simpler to derive both groups of *Anaxagorea* species from the single pantropical genus *Xylopia* in two independent centres, Asian and American, second because the genus *Artabotrys* is very constant in its characters, and is always a hooked climber of specialized habit.

This reasoning presents, however, no solution to the problem, as it only shifts it to an earlier stage, *viz* to the distribution of the progenitors of such groups for the present argument suspected to be possibly polyphyletic, *in casu*, to *Xylopia*, for which the same problem remains: how did then *Xylopia* gain a pantropical distribution and cross both the Atlantic and Pacific Oceans?

The alternative that *Xylopia* originated from *absolutely unrelated ancestors* would be botanically untenable as the *Annonaceae* form undoubtedly a most natural coherent group in all kinds of respects, vegetative and generative.

Another argument against polyphyletic origin of the disjunct transpacific taxa is the fact that the disjunction is in many cases not always reaching from the continental shores of Indo-Australia to those of America, but that in numerous cases — the number differing in the five zones — the intercontinental disjunction is interrupted by assumedly relict stations. See for example *maps 4, 8, 11, 12—14,* and *18,* among which *Perrottetia* (*map 4*) is very illustrative and the data in chapters 4 and 5. If one assumes a diphyletic origin of *Perrottetia*, an extremely coherent genus in habit and flower structure, one is forced to seek an explanation for its migration to Hawaii from either Indo-Malaysia or from America. A more detailed account of the disjunction with intermediate island stations has been given in chapter 4.

It is true, that the chances of hypothetical polyphyletic origin increase with higher taxonomic level, and that taxonomists may sometimes be deceived in merging genera of different origin into one tribe. However, on the other hand it should be emphasized that phylogenetic divergence from a common stock ('Sippe') is not at all pleading against ancient land-bridges; because if such land-bridges have existed they must have been very old, probably Cretaceous or at least early Tertiary, and development of new species and genera has steadily gone on during that period. This again does not imply that *all* groups *must* have changed as there seems no reason to assume a uniformity in rate of change in unrelated groups, as is well known from palaeontology (see

Axelrod, 195, 50—51). *Spathiphyllum* must have reached under land-bridge conditions a similar distribution as the *Joannesieae,* Euph., but has not changed and has maintained a closer relationship to the species in its ancestral home than for example *Deutzianthus* and *Annesijoa* to the rest of the *Joannesieae,* or *Eriandra,* Polygal., to the rest of the *Moutabeae.*

These considerations on the problem of polyphyletic origin of the Angiosperms show that this is tied up with two other problems, *viz* the *age of the Angiosperms* and their *place of origin.*

That the taxonomic connections must be ancient is also sometimes remarked in passing, for example by Engler (1930) who among the *Cunoniaceae* supposed the pair of transpacific tropical genera *Geissois* (W. Pacific) and *Belangera* (Brazil) to represent the possibly most ancient genera in the family.

Another argument in favour of the very ancient nature of the transpacific tropical taxa is the fact that a few have otherwise only been recorded from Madagascar, *e.g. Weinmannia,* Cunon., *Omphalea,* Euph. (1 sp.), *Cynoctonum,* Logan. (*map 7*), *Helosioideae,* Balanoph. (3 genera in tropical America, 2 in tropical Asia, a sixth monotypic genus *Ditepalanthus* in Madagascar), and are *not entirely restricted* to the Pacific basin environment.

Leading botanists and palaeontologists, *e.g.* Bews (1927), Axelrod (1952, 1961) and Hamshaw Thomas (1961) agree with the old view of Hooker that the Angiosperms are of much older stock than often thought and that all major orders were already fully developed by the Middle Cretaceous; Axelrod even assumed their occurrence in the Jurassic (1952, 32), and probably even in Permo-Triassic (*l.c.* 36). Absence of fossils from the earliest stages he explained by their "tropical upland" origin, where their fossil remains have since vanished by erosion. He assumed (*l.c.* 48) that primitive Angiosperms originated in and later descended from these upland sites and succeeded, though only slowly, in displacing the gymnosperm flora which had dominated the lowland since the late Permian, "because of their more efficient means of reproduction and the advantage of bird and insect pollination". Gymnosperms of today, however, still occupy almost all sorts of biotopes throughout the world and their bulk (in vegetable matter) probably exceeds that of Angiosperms. Their seed formation and wind pollination is very effective.

The idea that the Angiosperms could "prepare" themselves for their glorious future in quiet seclusion on the tropical mountains but not in the lowlands because of the dominant gymnosperm flora, seems distinctly unwarranted, because the tropical mountains must also have been clothed with a gymnosperm flora; gymnospermous conifers still occur on tropical mountains, up to the timber line, often in great abundance.

Axelrod's points of circumstantial evidence, which he stressed again in 1960 (p. 233—235, 240), I cannot share for the reasons given above; they have also been disputed by Scott *c.s.* (1960, 288).

The concept of the tropical *upland* origin of the Angiosperms started obviously with Seward (1931) as a hypothesis to explain the sudden explosion of the phylum in the Cretaceous, and the absence of transitional proto-Angiosperms to Pteridosperms or any other fossil matrix in which they should root.

The evidence of the gap, however, is derived from the fossil record of non-tropical sites, such as Greenland, Oregon, South Argentina, *etc.* The fact that the gap is found there is in turn evidence that in pre-Cretaceous times the tropical Angiosperms had not yet spread from the tropics to higher latitudes.

Whereas all the authors agree on the tropical origin of the Angiosperms, it seems logical that *the fossil evidence of the ancestors should be sought in the Jurassic of the tropics!*

The very great age of Phanerogams is also accepted by Reid & Chandler (1933, 87) as they briefly remark that the history of the European and American floras is interwoven, "for the first links of which we must doubtless look far back into the Cretaceous Period, or perhaps even earlier. Already in the Cretaceous genera which have American as well as East Asian affinity were established in Europe, and many of them even continued into the later Tertiaries". They added: "Into the question of this connection we are not prepared to go. It lies in a past beyond the range of our studies. But there seems also to have been a late and more intimate connexion in the Pliocene, marked by the appearance of not only American genera but American species also. For example the genera *cq.* species *Decodon,* Lythr., *Proserpinaca,* Halor., *Liriodendron tulipifera,* Magn., *Nyssa silvatica,* Nyss., *Menispermum canadense,* Menisp., and *Dulichium spathaceum,* Cyp. Such occurrences seem to owe their introduction to a circumpolar flora. But it must be remembered that even a circumpolar flora may have some of its roots in the far past and depend, in part, for its origin on ancient migrations. The American Eocene floras are almost all based on fossil leaves and can therefore not be compared with the London Clay flora".

The obviously great age of the Angiosperms and their apparently more or less simultaneous appearance supports the hypothesis of Němejc (1956) of an early rapid splitting into many basic types, which concept of early Angiosperm evolution would lead to the view that, instead of a phyletic tree with roots in the Ranalian alliance, we should perhaps visualize the Angiosperm phylum as composed of many trunks rising out of an early proto-angiosperm plexus. This would be in agreement with the fact that although we distinguish more or less clearly defined families and orders there is on the whole a manifest reticulate relationship within the phylum.

To me it seems also inconceivable that the Angiosperm phylum is derived from one Angiosperm species or genus which has subsequently developed into the diversified array it now displays. The more I think about it, the more plausible it seems that the Angiosperms have evolved from an *already differentiated* older Gymnospermous stratum or phylum which in various foci or joints reached the *angiospermous condition.* This assumption would in many aspects yield a more satisfactory picture and more easily explain the present diversity. In a similar way we now regard the conditions of inferior versus superior ovary, or sympetaly versus choripetaly, as evolved independently in various not immediately related foci in an already differentiated stratum of Angiosperms. This infers that several independent genealogical lines run from *Choripetalae* to *Sympetalae* and that in many allied groups the ovary is either superior or inferior. If this trend of thought is applied to the development of the Angiosperms it involves the abandoning of the monopodial habit of the tree form generally used to depict the phylogeny of the Angiosperms. This should be replaced by a many-stemmed tree or stool, or even by a grove of trees rooting on the decayed older stratum, just as in archaeological sites civilizations are found in superposed sheets, each being built on top of a preceding one and partly constructed from its material.

To explain the rather sudden appearance of the Angiosperms Stebbins (1950, 508) is willing to accept hybridization possibility in its early history. This then must have been a period in which the genomes had not yet genetically fixed many "characters" which characterize the specialized groups of today. Beccari had obviously a similar idea in his mind, in speaking about the 'plasmatic epoch' (1904).

How this fixation of minor and finer hereditary characters can have evolved is not very clear. But it seems to me that something of the kind occurs in the monotypic Rhizophoraceous genus *Gynotroches* where Ding Hou (1958) found that the position of the ovules is surprisingly variable; the ovules can occur apically, axially, or basally attached. Whereas in most other genera placentation is very strict (fixed) there seems here a potentiality still 'free' to develop into more than one hereditary-fixed type. If a systematist would be faced with two different species with different placentation, the one basal, the other apical, it might well happen that he would make them the types of two higher taxa, sections or possibly even genera.

A similar very interesting case was communicated to me by Mr J. H. Kern from his study of the *Cyperaceae*. In this family the phyllotaxis of the glumes is very constant and generally of 'generic rank'; for example *Scirpus* and *Cyperus* are almost only distinguished by this character, spiral glumes in *Scirpus*, bifarious ones in *Cyperus*. However, Mr Kern has found that *Cyperus pulchellus* R. Br. and *Scirpus kyllingioides* Boeck. differ *only* in this character. Another exactly similar couple is that of *Cyperus pygmaeus* Rottb. and *Scirpus michelianus* L. Both "species" of both pairs are sometimes collected together, they grow in the same place and occur mixed on the same herbarium sheet, and there seems no doubt that each pair represents a single plant species in which the character of the phyllotaxis of the glumes is possibly random distributed or at most variable in a Mendelian sense, although it is absolutely fixed in the hundreds of other species of these very large genera.

Other instances of variable phyllotaxis are not rare, *e. g.* in *Lantana*, Verb., *Lysimachia*, Prim., *Faradaya*, Verb., *etc.* As soon as this character would get 'fixed' in such groups it would acquire a higher taxonomic status, as characters are attributed higher rank in proportion to their constancy.

In the ligneous flora of the tropics there are many instances in which plants have not a restricted habit, either tree or liana. These sprawling creatures have obviously not yet decided what to do and are free to develop into either trees or lianas which is still possible through their undefined habit.

It seems important to search for further examples of plants with such 'free' potentialities which, if we think along these lines, must have been common among proto-angiosperms. In proportion to the number of genes later 'acquired' or 'developed' fixing the specializations, the systematic characters must have gradually attained a narrowed, rigid definition, and potentialities decreased, to reappear again occasionally when the physiology of the organism is upset in teratologies.

Most recent authors agree that the Angiosperms originated in the tropics and have extended towards the temperate regions through producing specialized (morphologically exacting) groups from meso- towards microtherm ecologies, *e.g.* the *Capparidaceae-Cruciferae, Araliaceae-Umbelliferae, etc.*, and this seems a very reasonable assumption.

A strong botanical argument for the tropical origin of the Angiosperms is found in the remarkable two-hemisphere pairs of living genera and families, in which one partner of the pair is mainly developed on the northern hemisphere, the other on the southern hemisphere, pointing to a common origin in the tropical zone, where they mostly still grow side by side. Examples of such pairs are: *Fagus-Nothofagus*, Fag., *Staphyleaceae-Cunoniaceae*, *Magnolia-*

ceae-Winteraceae, Poterium-Acaena, Ros., *Ericaceae-Epacridaceae, Dillenia-Hibbertia,* Dill.

To a certain extent this is also found for tribes or subtribes within a number of other families, *e.g. Liliaceae* and *Cyperaceae,* with the related *Restionaceae* in the southern hemisphere. Florin (1962) stressed the early developed bi-hemisphere character of the conifer and taxad stocks which had already differentiated in the Mesozoic, and attained their greatest diversification at higher latitudes because of their subtropical to temperate thermo-ecology.

As far as I know no hypothesis has been advanced to solve the problem how this early *pantropical* distribution of the Angiosperms and their ancestors materialized.

The implications of polyphyletic origin of species, genera and families are botanically not acceptable, especially because this would then also be valid, not only for the taxa of Engler's transatlantic list, and my list of transpacific genera, but also ultimately have to be accepted for all pantropical genera and families which would lead to taxonomical absurdity.

(iii) Plant taxa as thermometers of the past

The problem of the amphi-transpacific disjunctions is closely connected with the assumption that plant genera and families are to a large extent representing thermometers for the past. This implies that plant-geographers and palaeontologists should be very careful in handling them as such. Only such groups can be used for this purpose which have a sufficient number of species, and cover a sufficient area of distribution to show the constancy of the ecological potentialities of their genome. I have at length dwelt on this subject in my studies on the Malaysian mountain flora (1934, 138—146) in which I incorporated only those genera of which the lowest localities of all species occur in the tropics at least above 1000 m altitude, showing the stability in their thermo-ecological behaviour. To any plant-geographer it would be ridiculous to question whether *Primula,* Prim., *Gentiana,* Gent., *Valeriana,* Val., *etc.* ever have evolved megatherm species. These genera were microtherm or semimicrotherm from origin onwards and this capacity was and is obviously deeply rooted in the hereditary qualities. On several occasions I could use this stable capacity to show that specimens had been erroneously localized and I could predict without previous taxonomic examination that a species was accommodated in the wrong genus (1934, 289—290)[1]).

Went (1960) wrote "that it is most likely that the reason that tropical plants, such as *Saintpaulia,* Gesn., and *Begonia,* Begon., cannot live at lower temperatures (around 10° C) is that their circadian rhytm is synchronized with the 24-hour external cycle at a high temperature, whereas temperate region plants ... have their clocks adjusted to 24 hours at a low temperature".

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[1]) The constancy of the thermo-ecology is so strict that the records of the three species of Phanerogams which have been found at too low an altitude in Malaysia (Van Steenis, 1935, 299) have all proved to be fallacious: *Eriophorum comosum,* Cyp., was doubtless erroneously localized and came from India, the Ambonese record of *Schisandra axillaris,* Schis., has been found by Dr. A. C. Smith to rest on wrong identification and concerns a *Kadsura,* Schis., a eurytherm genus, and the doubtful *Daphne,* Thym., from Mt Klamm was also wrongly identified and is a form of the eurytherm *Wikstroemia indica,* Thym., according to Ding Hou.

Furthermore, in his opinion (1957) "it seems that photoperiodic response is more easily changed in the course of evolution than the temperature response".

Conversely one must of course not identify the concepts 'tropical' and 'megatherm' for a genus now restricted to the tropical zone. Many tropical genera have produced montane or even subalpine species and have evidently the potentiality to breed microtherm taxa, although the mesotherm or microtherm taxa need not to have come into existence in the latitudinal subtropical or temperate zones.

Gleichenia, Gleich., is for example largely tropical, but ascends the tropical mountains to very high altitude, almost timber limit, at 4000 m; therefore it is not surprising to find species of this genus in southern temperate regions at low altitude. A similar thing can be said about tree ferns of the genus *Cyathea,* Cyath.

For palaeobotanical deductions such altitudinal and latitudinal ranges of recent plants are extremely important, nay essential, because palaeobotanists use these data to define the thermo-ecology of their fossil evidence. For example, Miss Chandler (1955), in a paper on the *Schizaeaceae* of the South of England in the Early Tertiary, stated (*l.c.* 291, 294) that *Anemia* and *Lygodium* "indicate a very warm and humid climate. They are perhaps survivors of an ancient widespread more or less uniform broad Mesozoic tropical belt of vegetation". She herself mentioned, however, that living *Anemias* occur from Florida and Texas to Uruguay beyond 30° NL and SL and that in Cuba, Mexico, Angola, and in the Nilghiris in the Deccan *Anemia* ascends to 1200—1500 m altitude, that is beyond the tropical zone into the tropical-montane zone. The complete living record of the genus indicates therefore a life space comprising the tropical *and subtropical* climates. Unless the very exact specificity of the fossil forms is known they can not be defined as simply 'tropical'. The same holds for the living species of the genus *Lygodium* of which the life space is even wider than that of *Anemia.* Its latitudinal northern border is in Florida, New Jersey, Massachusetts, and Japan (in China in Szechuan still at 500 m), its southern border is in South Africa and New Zealand. In the tropics it ascends (consequently) higher than *Anemia, viz* to 2500 m altitude, that is to the lower border of the subalpine zone. Miss Chandler defined the thermo-ecological amplitude of *Lygodium* as "tropical and subtropical" (*l.c.* 308) which I find an understatement of the generic life space which extends almost to the warm-temperate zone, that is an extension of at least 10 degrees of latitude.

On the other hand, species of *Pandanus,* Pand., also ascend tropical mountains to appreciable height, but hardly overstep even the border between the tropical and subtropical zones; potentially semi-microtherm species of *Pandanus* are feasible which could grow there as far as temperature is concerned.

The proper usage of the thermo-ecological concepts (*fig. 1*) seems to me of manifest importance for palaeoclimatical deductions from properly identified fossil floras. In an interesting succinct summary of the Baltic amber flora Mrs H. Czeczott (1961) showed that this is a mixed flora which she arranged into five groups, according to distribution, *viz* (i) tropical or subtropical, (ii) cosmopolitan, (iii) mostly restricted to temperate regions, (iv) discontinuous distribution, and (v) remaining families, with anomalous distribution. Of the total number of families they make up 23, 46, 12, 12, and 7 % respectively. In passing it may be remarked that percentages on the generic level would have been more important.

She assumed these distributional types to reflect also their thermo-ecological range. The first group consists of 10 families, making up 23 % of the total which she defined as: "tropical or subtropical families such as *Palmae, Olacaceae, Lauraceae, Dilleniaceae, Myrsinaceae, Apocynaceae, Theaceae, Commelinaceae, Araceae, Connaraceae*".

Save one, all these families extend in the living flora from the tropics to subtropical or warm-temperate stations as New Jersey, Virginia, Japan, Tasmania, New Zealand, *etc.*

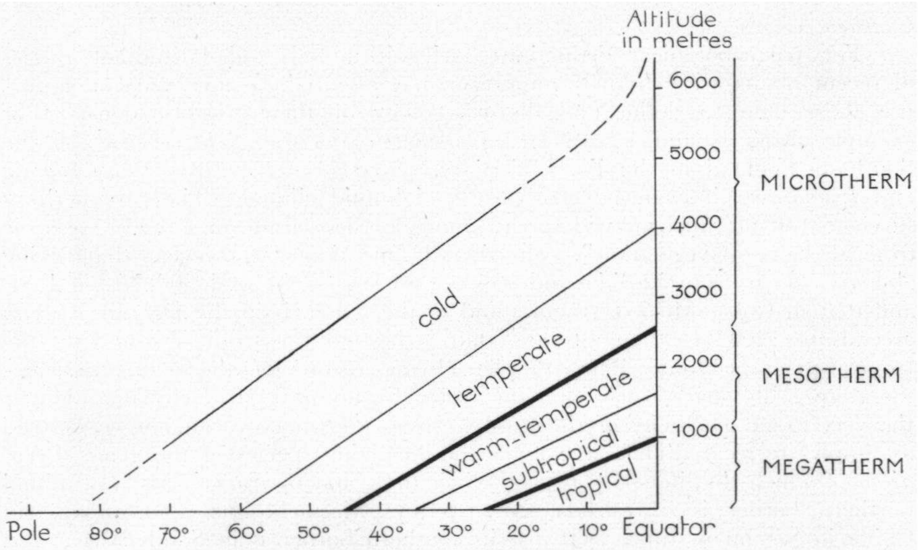

Fig. 1. Scheme of adopted thermo-ecological concepts: *microtherm plants* are characteristic of cold and temperate climatic conditions, *mesotherm plants* of warm-temperate and subtropical climatic conditions, *megatherm plants* are restricted to the tropical zone. The life-space of these categories is here diagrammatically correlated with latitude and tropical altitude. Mesotherm is in the equatorial zone equivalent to *tropical-montane,* temperate-microtherm to *tropical-subalpine,* cold-microtherm to *tropical-alpine.*

The one exception is the family *Connaraceae,* which is a truly megatherm family. The question arises whether the identification is correct. *Connaraceae* differ from *Leguminosae* mainly by the absence of stipules and collateral ovules, and by having mostly more than one pistil, but more pistils occur in some living (obviously ancient) genera of the *Mimosoideae* and sometimes as an abnormality in the subfamily *Caesalpinoideae.* In studying the figure of the flower of the fossil amber species *Connaracanthium roureoides* Conw. Dr. P. W. Leenhouts was struck by its clawed petals, a feature unknown to him in the *Connaraceae* which he revised for Malaysia (1958); in his opinion the fossil flower probably belongs to *Caesalpinoideae* in which clawed petals are characteristic.

Provided it would not allochthonously have been deposited after distant transport, the proper disposition of this flora, which is thermo-ecologically obviously a mixed assemblage, is probably mesotherm, that is warm-temperate to subtropical, but definitely not tropical. *Clethra,* on which attention is focussed in this paper, is subtropical; in the tropics it is colline to subalpine, largely confined to the mountains, (50—250—)500—3000 m. It is found northward in China and Japan to c. 42° NL; in China *extra-tropical* species are found largely between 600—1000 m, a few ascending to 2100 m; in West China *ser. Delavayanae* is even exclusively found between 2400—3800 m altitude (Hu, 1960).

A curious case is represented by the genus *Thismia,* Burm., which is truly tropical except one warm-temperate species in Tasmania and New Zealand and one species in the warm-temperate Chicago area in North America, which Schlechter and Jonker (1938) surprisingly recognize to represent together a separate section. One wonders whether the characters on which this section is based are not a thermo-ecological epharmosis [1]).

Berry (1930) argued that plants are not to be relied on as indexes of climate. He relied on information derived from cultivated plants which is of course inadmissable. And Seward (1926, 160) wrote "plants themselves have in all probability changed with the passage of time in their reaction to external factors", specially stressing (1930) that though admitting their climatic value "we must remember that the Cretaceous and Tertiary floras are all extinct and that the species are practically all different from any that are now living. We know at the present time what tremendous differences there often are in power of resistance to climatic conditions between species belonging to the same genus". This sounds perfectly true and induces caution, but I also fully agree with Hamshaw Thomas's remark hereon (*l.c.* 316) "that there seems no indication in the geological record of any gradual acclimatization in Eocene times in Europe as the Great Ice Age approached and the climates became colder, and presumably drier". One must of course be cautious and species of eurytherm genera are of hardly any value as a climatic index. And I agree with Reid & Chandler (1933, 69) that confusion is avoided in using the 'bulk of the Flora' as an index.

It is true that among the Tropical Type there are many groups which are decidedly small in number of species, but those which have an appreciable form development are truly megatherm, for example *Anaxagorea,* Annon., *Homalomena, Spathiphyllum* (*map 5*), *Schismatoglottis,* Arac., *Burmannia,* Burm., *Joannesieae,* Euph., *Guadua, Ichnanthus,* Gram., *Citronella,* Icac., *Cedreleae,* Meliac., *Heliconia,* Musac., *Taccaceae, etc.*

There are admittedly others which are often, or also, found in tropical hills of the montane zone, *e.g. Dendropanax,* Aral., *Microtropis, Perrottetia,* Celastr. (*map 4*), *Hedyosmum,* Chloranth., *Schoepfia,* Olacac., *Hydrangeeae,* Sax., *Turpinia,* Staph., *Eurya, Laplacea, Ternstroemia,* Theac., but not to the extent that they have produced really microtherm species. One might view them as transitions between the Subtropical Type and the Tropical Type.

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[1]) I cannot refrain from pointing to the remarkably similar distribution of the ancient relict family of frogs, *Leiopelmidae,* which is restricted to temperate North America and New Zealand (see Darlington, 1957, 164).

Even shifting them to the Subtropical Type would bring no solution to the major group of the truly megatherm tropical genera.

It is thermo-ecologically unimaginable that the megatherm pantropical families and genera stem from temperate ancestry. It is equally unimaginable that they have circumpassed the oceans via temperate climates by adapting themselves first to that climate, and when through the temperate zone developing again the same tropical forms, families, genera, and even (in a few cases) species. This would be opposed to the irreversibility principle under which specializations cannot return to their ancestral structure, and would not be acceptable from a genetical point of view. Also floristically this would be unacceptable because we would find up till the present day cold-adapted *Meliaceae, Annonaceae, Myristicaceae, Connaraceae* (*map 18*), *etc. etc.* in the temperate countries where these adaptations would have taken place. As a matter of fact we find none. The highest latitudes where we find representatives of megatherm families are countries favoured by an ameliorating effect of a warm current, for example in South Japan.

I conclude that there is no reason to assume significant changes during the geological past in the thermo-ecology of the majority of the tropical genera concerned.

Again, even if that would have been possible it would furnish no facility for crossing the Atlantic, the tropical and the Southern Pacific.

(iv) Relict hypothesis of formerly pantropical genera

This is the assumption that, similarly as in the northern hemisphere Temperate Type, in ancient epochs tropical genera extended from the beginning all over tropical America, Africa, and Asia, and thus could have arrived via Africa on both western and eastern borders of the Pacific without having the necessity of crossing the Pacific basin; in later geological epochs their area shrunk and they disappeared from Africa and West Asia (eventually because of assumed desiccation and retreat of tropical rain-forest conditions in that part of the globe) leaving intact both terminals of the once unbroken area, that is tropical America and Indo-Malaysia, where they survive as relicts.

In aid of this formidable hypothesis could be said that in fact a genus of which there are two such large areas, as for example *Ternstroemia,* Theac., possesses a single species in Africa. Further that of similar genera or other taxa sometimes a representative is found in Madagascar (see p. 283), but the number of such instances is very small.

If all these genera would be recorded in future from Africa they would become 'pantropical' in distribution. This would, however, give no clarification, as the problem is equally valid for both the amphi-oceanic genera and the pantropical genera: *how did they attain pantropical range?*

The question might be raised whether it can be expected that a number of the genera of transpacific tropical plants will be found in future in Africa. This possibility is difficult to fathom, but it seems not very likely, at least not for certain very showy representatives. And even though a few genera (*e.g. Ternstroemia*) might have to be removed from the amphi-list, it is significant that also several have recently been added, for which especially intensified work on the New Guinea flora is responsible (*Eriandra,* Polygal., *Batis,* Batid., *Oreocallis*, Prot.), but to which also extended exploration into tropical America (*Homalomena*, Arac.) has added.

On the whole the list is of long standing and no serious mutations have taken place in the past half century, notwithstanding intensified exploration and publication. There is no reason to expect it to change much in future.

We do not know what the *reliable* palaeontological record will reveal in future and for what genera the relict theory will occur to be valid.

Against the hypothesis is the argument, that if such distribution would have originally become tropical worldwide through Africa it would be clear that the species in the terminals, at both ends of the distributional area. would at least not be closely related, but in *Spathiphyllum* we find them precisely very closely allied.

It should further be added that even if this alternative is accepted, both migration ways, transatlantic and transpacific, may have existed side by side.

In his sharp requisitory Millot (1957) degraded the hypothesis of Gondwana Land, the former southern continent south of the Tethys Sea, originally only postulated by Suess (1885) to unite Africa, Madagascar, the Mascarenes, Ceylon, and India, later by him and others extended to immense size. Millot's alternative is to accept the steady state *cum grano salis,* whith which I agree, but to reject also the land-bridge theory and all East-West affinities by a simple preponderantly North-South migration; through this the southern floras and faunas become relicts of those which were of worldwide distribution in pre-glacial time. In passing I remark that this would imply either a tropical world or a thermo-ecological change of the tropical groups (compare sections i and iii). This alternative is, however, not acceptable, whether we accept the distribution from the Holarctis towards the south or conversely from the south towards the north, as advocated by Hemsley (1885) for Phanerogams and recently for ferns by Copeland (1939). The only pathway for the entire world flora, including all tropical plant families and all South Pacific groups, to reach all continents without help of land-bridges, would then have been Beringia and the Panama isthmus. As a matter of fact Axelrod (1952, 185—186) correctly attached great importance to its functioning under a favourable Cretaceous and Tertiary climate as the single pathway of migration between the floras of the New and Old World "giving access to all continents". Later (1960) he changed his ideas and at least accepted a trans-Atlantic land-bridge for the Mesozoic. Though Mayr (1952, 256) could not accept this land-bridge he had to admit: "How the pantropical fauna could have gotten from southeast Asia to Central America is still an unsolved problem".

It is precisely the amphi- and pantropical taxa which form the crucial problem. Beringia, situated between 60—70° NL has certainly served as an efficient migration route for and exchange of the frigid and temperate element as it was at least during part of the Pleistocene an ice-free terrestrial continuum *c.* 1000—1200 km wide. According to Hopkins (Haag, 1962) most of the bridge was above sealevel throughout the Tertiary and has doubtless served as a migration route for the northern mesophytic warm-temperate element. However, it is unimaginable that it has been a botanical 'Broadway' for the entire world flora, including the tropical and southern hemisphere floras. Neither can it account for the extremely clear East-West affinities found in the tropics, on both sides of the Atlantic, and especially on both sides of the Pacific.

It can also not account for the equally clear East-West affinities in the South Pacific. It is simply unacceptable that for example the genus *Nothofagus* has evolved either on the west side of the Pacific or on the east side and after having wandered all around the world to reach the other end, has become extinct everywhere except at these extremities, leaving no fossil record, although fossils (either Cretaceous or Tertiary) are found everywhere in the disjunct area it now inhabits! And all evidence, living and extinct, is against accepting an originally northern hemisphere origin and distribution of *Nothofagus*.

Diels (1942) has rightly concluded that on the whole the northern and southern hemisphere floras are pretty well distinct and well separated by the tropical flora.

Concluding it should be realized that the relict hypothesis cannot account for the origin of the tropical amphi-transatlantic and amphi-transpacific distributional types, for the pantropical type, and for the South Pacific type, under the present distribution of oceans and continental masses.

(v) Transoceanic dispersal under the steady state

No leading plant geographer has ever thought of the possibility that, even given enough time, long-distance dispersal could lead to transoceanic distribution, especially in the tropical zone, under approximately the distribution of land and sea as it is today. It is agreed that it may hold for certain very common littoral plants of the sandy beach and the mangrove, but not for rain-forest constituents. Even for littoral plants the correlation offers many problems and the littoral *Batis maritima* L., Bat., is a curious case. It occurs on both sides of the American continents, hence must have been there before the Panama isthmus came up, but it is extremely scarce in the Pacific where it occurs in the Galapagos Is. and Hawaii ¹). If *Batis* seeds were sea-borne from the nearest stations in Pacific Central America to the Galapagos Is., why did not *Rhizophora,* which is certainly not less old a genus, come along with the same currents or drift? And how is it that in New Guinea a second, very distinct argillicolous species of *Batis* occurs?

Even Guppy, who strongly advocated long-distance dispersal as a means to account for the flora of oceanic islands, turned to the supplementary hypothesis that the natural agencies, that were so wonderfully effective during bygone ages, have lost their efficiency; one is temped to question whether they ever existed.

In his famous lecture on 'Insular Floras' J. D. Hooker (1886) could not accept Darwin's view ²) that various agencies could carry most plants across wide expanses of sea, and expressed as his opinion that the peculiar endemics of insular floras, *e.g.* the Galapagos Is., are "relicts of a far more ancient vegetation than now prevails on the mother continent". He concluded that the peculiar upland species of the Macaronesian islands which have close relatives in the late Tertiary floras of Europe can only be explained with

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¹) By Hillebrand and Fosberg supposed to have been introduced into Hawaii. If this is true the generic distribution is still more curious.

²) In his autobiography Darwin stated that Hooker "was almost.... indignant because I had rejected with scorn the notion that a continent had formerly extended between Australia and S. America" (edition by Nora Barlow, 3rd impr., 1958, 106).

the help of "intermediate masses of land" which have since subsided, a view similar to that he had taken to account for the similarities of the subantarctic floras in the South Pacific, "a once more extensive flora which has broken up by geological and climatic causes". Recently Axelrod (1960, 277—293) has given a good renewed survey of the problem which has not changed since Hooker's time.

Miss Gibbs (1920) assumed New Guinea to be the focus of the Subantarctic element which would have been dispersed in the Tertiary by the poleward antitrade air currents from their birthplace in New Guinea to SE. Australia, Tasmania, New Zealand, and South America [1]). This would make land masses of no importance whatever in the biological history of the southern hemisphere.

It must be remarked, however, that Miss Gibbs possessed insufficient background knowledge of both plant geography and dispersal biology and Skottsberg (1936) naturally refused to accept this fantasy. Even for *Acaena* (with epizoic dispersal) he says (*l.c.* 307) "Not rapid transportation across oceans, but slow migration over land of an already differentiated genus, with isolation and dying-out processes, accounts for its kind of endemism".

A similar opinion as Skottsberg's was held by Merrill (1936) who wrote (*l.c.* 255) that the intimate relation between Malaysia and Polynesia cannot be explained by transoceanic dissemination but that "one is forced to postulate a different distribution of land areas at some time in the past... These land areas probably were of considerable size, not the narrow land-bridges which have been widely scattered over the Pacific basin by some theorists".

Especially Skottsberg (1925) has in a penetrating way discussed the impossibility of explaining the flora of Hawaii by transoceanic dispersal of diaspores and in my opinion his discussion is final. He showed this impossibility also for the origin of the Hawaiian mountain flora (1930, 1940).

He refrained, however, from postulating land-bridges in absence of geological evidence and in his final essay on the origin of the Juan Fernandez flora (1956) he indicated the possibility of former terrestrial links with Chile but in giving an ample digest of data for and against transoceanic dispersal found himself nevertheless in a biogeographer's dilemma, although maintaining that the effect of transoceanic migration has largely been overestimated (*l.c.* 331—351).

Good found himself in a similar dilemma by keeping silent about land-bridges but simultaneously rejecting long-distance dispersal.

One finds this dilemma in many biogeographical essays, and some face it in having a solution both ways. Godley (1961) for example accepted the geological record that New Zealand had, since the appearance of the flowering plants, probably only one slender connection with the outside world lasting from the Early Cretaceous towards the end of this epoch, which stretched towards the northwest to the region of New Guinea and East Australia (Lord Howe Rise and Kermadec Ridge) extending southward to the subantarctic islands and east to the Chatham Islands. This land-bridge was either continuous land or of archipelagic character. There was never land connection via the Tasman Sea to Tasmania or South Australia and there was none

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[1]) These air currents are found, however, only at very high altitude.

with the Antarctic continent. A number of plants Godley (*l.c.* 5) accepted to date back to this land-bridge, notably those of northern hemisphere origin, such as some *Ranunculi,* Ranunc., and those with tropical ancestry, such as *Rhopalostylis,* Palm., *Freycinetia,* Pand., *Corynocarpus,* Coryn., *Macropiper,* Pip., *Cordyline,* Lil., *Avicennia,* Verb., *Pittosporum,* Pitt., and the few epiphytic *Orchidaceae.* He then wrote (*l.c.* 5—6, italics mine): "*Because of the lack of land connection across the Tasman Sea* the typical Australian flora is not represented in any great measure. We lack such major genera as *Eucalyptus* and *Acacia* and have only a few members of.... the *Proteaceae.* Some of the genera which we have in common with Australia could have entered both countries by land, from the north.... When we share species with Australia (236 suggested by Dr Cockayne) then trans-Tasman dispersal by some means or other must have occurred". (*l.c.* 8): "Of the seventy-one species of New Zealand orchids, thirty-one species are also found in Australia, and these could have arrived by wind dispersal. If the plant is self-fertile only one successful establishment is required to start the species in its new home. The ferns which we also share with Australia could have arrived here, too, on the westerly winds. It may be just a matter of chance and time which has allowed some species to arrive here and not others". The latter view defeats of course the former one, and does not explain the present absence of *Eucalyptus,* Myrt., and *Acacia,* Leg.-Mim., in New Zealand, either by dispersal via the early northern bridge, or by chance dispersal via the Tasman Sea. More important is the question of the *Proteaceae* of which at present only *Persoonia* and *Knightia* are represented in New Zealand, both by one species; *Persoonia* otherwise with 60 species only in Australia, *Knightia* with only 1 species in New Caledonia. According to Mrs Lucy Cranwell (*in litt.*) "it is difficult to understand why most *Proteaceae* have died out in New Zealand, as they must have been abundant there with several genera and many species for a long time, according to the palaeontological record, both in the Cretaceous and Tertiary, according to Couper and Cookson. Introduced members of the family do amazingly well and are a nuisance in some places. As the genera seem so versatile it is especially difficult to understand their disappearance. Of these fossil genera there are no Cretaceous records from Australia. Proteaceous pollen is found in some abundance in Miocene and Upper Cretaceous Antarctic deposits. The late Dr. Cockayne used to feel very strongly that *the present is often a poor guide to the past*". From these statements it is clear that the past history of the *Proteaceae* is far more complicated than the present flora would show. In this connection it is entirely unjustified to explain the occurrence of the one *Persoonia* in New Zealand by chance dispersal; the area of *Knightia* likely points to the ancient northern pathway of the *Proteaceae, vice versa,* the occurrence of three other genera in Indo-Australia and Chile to very ancient distribution. And as far as the orchids are concerned, it is unclear why the epiphytic New Zealand orchids are assumed to have arrived via an ancient land-bridge and the others by change dispersal over the Tasman Sea. Although dispersal of orchids may seem easy by the large amount of dust seed, successful establishment may depend on presence of its mycorrhizal fungus and insects for pollination. That the three of them, fungus spores, seeds, and insects, will travel together over long distances by chance is utterly unlikely. This complication can only be overcome if foreign insects are capable of acting as pollination agent for the waif orchid and if the fungus would be ubiquist; for short-distance dispersal of orchids there would be no such complication.

As to *Eucalyptus, Acacia,* and similar genera, the explanation of their absence in New Zealand might be either their late Tertiary extinction in New Zealand (as the *Proteaceae*) which must then appear from the New Zealand palaeontological record, or that such groups were absent or not predominant in the Cretaceous flora of that part of Australia which was connected with New Zealand which might appear from the palaeontological record in Australia. Provisionally I vote for the latter explanation, because *Eucalyptus* is absent in New Caledonia and *Acacia* nearly so.

Though I am distinctly in favour of reticence instead of jumping to conclusions, I feel at the same time that progress in science is not only served by zealous assembling of data, their careful scrutiny, and detailed analysis, but also by a logical synthesis of such analytic considerations, even if such deductions cannot be fully correlated with present knowledge in other disciplines.

Du Rietz (1940, 240) in his study of bipolar plant distribution was also not in favour of long distance dispersal and thought that transtropical disjunctions are historically disrupted relict areas.

On the basis of his unique knowledge of recent and fossil Conifer floras Florin (1940, 86) commented as follows: "Some of the southern genera may even have originated in Antarctica. But as this continent was once apparently much larger than at present, it was of still greater importance as a bridge along which migration could take place. As I have already pointed out, several genera of conifers spread along such a trans-antarctic bridge from the Indo-Australian—New Zealand regions to southern South America in Mesozoic and Eocene times". More recent and detailed stratigraphic distribution data tend to confirm Florin's assessment of the role of Antarctica in providing a bridge between the Australasian and South American regions.

According to Cain (1944, 160—162) occasional and random long-distance dispersal is not in accordance with the many specific parallels under both continental and oceanic conditions that are shown by distribution patterns and areas. The frequent occurrence of endemics which can be understood by the extent and age of isolation is opposed to long distance dispersal. The phenomenon of local races is entirely opposed to the idea of long-distance dispersal, for such variation depends upon isolation which would not exist if such dispersal were generally effective. In many instances there is no correlation between dispersal mechanisms and distribution patterns. Furthermore, migration is usually not a random matter, but one of migratory tracts.

Florin (1962) agrees with Cain and Good and emphasized again that the transport of diaspores is only part of the story of effective dispersal. Apart from the hazard of the transport, the diaspore must remain viable, the new habitat must be suitable for germination and establishment of seedlings, the new environmental conditions must suit the species for its propagation in the future; in case of dioecious plants establishment must become a complicated affair, and additional hazards for propagation are added for all obligatory cross-pollinators which require specialized insects for transferring pollen. Florin agrees with Skottsberg that conifer seeds, whether winged or unwinged, have no chance of being carried very far.

In the opinion of Axelrod (1952) plant distribution at any particular time is largely a reflection of the climates available for occupancy, *i.e.* climate is the chief factor controlling plant migration. But "within any climatic region distance will finally impose a barrier to the migration of plants also. The water barrier that a continental flora can transgress within an epoch of time (say, 10—15 mln years) is not unlimited, while beyond 150—400 km the probability of colonization by a whole flora is low. It would appear that long-distance, over-water migration has not been generally effective in populating widely separated continents". In the same paper he also wrote (*l.c.* 185): "The suggestion that long-distance migration may have been more effective during the Lower Cretaceous than at any later time finds some support in certain inferences we can make from modern ecology and past floras. During that epoch the highly adapted Angiosperms were beginning to compete successfully in lowland regions with the older Mesozoic floras dominated by ferns, cycadophytes, and coniferophytes, and were gradually supplanting them. As the older types were being displaced, angiosperms may well have entered upon a stage of general widespread random migration which has never been equaled since that time. Sites suitable for occupancy by Angiosperms were now to be found everywhere for the older flora was on the wane. Ecological competition was at a minimum, for there were no closed communities to hinder establishment". Also for the Eocene he accepted (*l.c.* 178) that "tropical and subtropical species had a higher probability of long-distance migration than any modern equivalent on two counts: there were many more individuals supplying seeds to the various agents of transport, and areas suitable for colonization were greater in extent".

Both suggestions are unacceptable from the vegetation point of view and would defeat the actualist principle. There is no reason to assume open spaces in the Cretaceous left open by ferns and conifers who died of chagrin from being unable to continue competition with the Angiosperms. Ferns and conifers are generally aggressive in the vegetation today and there is no reason to assume they behaved differently in the past.

An example of plants which seem so well-adapted to easy distribution by wind but in spite of that assumed capacity keep to historically defined areas has recently been given by Woodson (1947, 1954) in his geographical survey of the large genus *Asclepias,* Asclep., in North America, of which the species possess comose seed. Woodson could demonstrate that the evolution of the genus can be correlated with the geological history of the North American continent. He insisted that "the size and shape of the area occupied by plants of our time are the product of *yesterday's and today's* facts, both genetic and environmental. If the study of evolution has taught us anything, it is that the past is the key to the present, and the present that to the past".

As a result of his cytogenetic work on the North amphi-Atlantic flora Löve (1958) has recently also expressed himself against transoceanic chance dispersal and in favour of the acceptance of former transoceanic land connections.

In a well-documented paper Couper (1960) has shown that the fossil and present distribution of *Podocarpaceae* and *Nothofagus* "appear to be most readily explained by assuming land connexions or at least closer proximity in the past, between the land areas of South America, Antarctica, and Australasia, although not necessarily all at one time".

As a corollary to his colossal taxonomic study of the genus *Ficus,* Mor., Corner (1961) surveyed the plant geography of that genus in the Pacific against the background of systematical affinities. The study of the figs of New Caledonia led him to state that: — "Such precise evidence, positive and negative, must deny any hypothesis of chance colonisation through sea-drift or animal-flight". The close affinity of the two sections of subg. *Pharmacosycea, viz* of sect. *Pharmacosycea* in tropical America and sect. *Oreosycea* in Malaysia and especially richly developed in Melanesia, and with one endemic species in Madagascar, shows two centres between which the differences are small and "which conceal the fact that some of the New Caledonian species could be classified with the American, if it were not for geographical inconvenience". Corner can see "no escape from the conclusion that there was land between the two regions before the existence of the New Hebrides, Fiji, Samoa, and the other islands of Melanesia and Polynesia. It was a tropical bridge which did not include New Zealand or Australia, and it disappeared before subg. *Ficus* had arrived from Asia or Malaysia. In vegetative habit the species of New Caledonia are more primitive than the American, having in some cases the pachycaul habit and, even, a trace of the pinnate leaf. Hence I conclude that the American species were derived from what is now the Melanesian centre, and that the New Guinean species separated to its west". In subg. *Urostigma* he found a similar transpacific alliance in that the American members of this subgenus are not related with the big African group, but with the West Pacific *Urostigmas.*

These conclusions, coupled with the fact that *Ficus* lives by the grace of its peculiar symbiosis with fig wasps and cannot travel alone by seed dispersal, represent extremely weighty evidence for the land-bridge theory.

In addition Corner found that other Moraceous groups show similar evidence of transpacific affinity, namely the relationship between the Malaysian-New Caledonian assemblage *Antarias-Antiaropsis-Sparattosyce* with the American *Olmedieae.*

Finally he concluded to the congenerity of *Maillardia* (Madagascar), *Paratrophis philippinensis* (Malaysia) and *Calpidochlamys* (New Guinea) with the tropical American genus *Trophis.*

In passing it may be remarked that the distribution of parasites, as the *Rafflesiaceae* and *Balanophoraceae,* in which also two organisms, host and parasite, are concerned represents similar evidence of particular importance.

In her report to the 10th Pacific Science Congress, on a coaly deposit in far-flung Rapa I. (S of the Marquesas and W of Pitcairn), lying between volcanic lavaflows, Mrs L. M. Cranwell (1961) concluded that though the exact age of the coal is not known, it must be considerable. In it she found pollens of many plants among which certain of today's endemics in Rapa, which prove they have had a long history there. "They are not chance migrants spread comparatively recently by birds, winds, or sea-currents. Indeed, in Polynesia the striking arborescent genera — lobeliads, amaranths, composites (with a *Fitchia* on Rapa today) — tend to huddle in disjunct island groups; they have the appearance of relict genera, and it is difficult to see how they could ever have been more closely knit without extensions of land within and even south of Polynesia".

The land-bridge theory has in recent time been disputed by Fosberg (1948) who assumed that the Hawaiian flora has always been insular 'oceanic' and is "exactly the type that might be expected from a random [1]) aggregation of chance waifs carried overseas by a combination of factors such as storms, currents, and birds. Of seed plants, an average of one successful arrival and establishment every 20.000 or 30.000 years would account for the flora. This is granting an estimate of 5 to 10 millions of years of above-water history for the entire Hawaiian chain". Apart from the fact that he did not provide a dispersal spectre, long-distance dispersal is only casually explained by storms, currents, and birds which would give random dispersal. It is most remarkable that such storms are, as far as we know, in the West Pacific always *towards the west* and cannot serve for dispersal towards the east to bring diaspores to Hawaii in a random way. The flora of Hawaii is also not random because of its preponderant Indo-Malaysian character on which Fosberg agrees, and because of its peculiar endemics. If random dispersal would have to account for the flora of oceanic islands their peculiar affinities and floristic regularities would be unexplainable, *e.g.* of Juan Fernandez, New Zealand, New Caledonia, *etc.* There are further no frugivorous oceanic birds migrating over many thousands of km and still carrying diaspores; the frugivorous ones are sedentary. Sea currents is another magic, but they can be helpful only for a few beach plants and obviously not even for the mangrove species which were absent in Hawaii before 1923 in which year they were planted by man. And nobody knows whether even long-distance dispersal of beach plants by sea currents really has ever been effective; we have no direct observations, and as they are impossible to make, we shall always have to depend on indirect, circumstantial evidence from diaspore spectra.

The chance of dispersal over long-distance is difficult to calculate. Simpson (in Mayr *et al.*, 1952) discussed the problem of the probabilities of dispersal in geologic time. Purely mechanically it would seem that it is inversely proportional to the third power, as volume is concerned. But how we might ascertain figures for the probability is obscure. Furthermore, it must be taken into consideration that the farther diaspores are transported the larger will be the chance that some factor interferes with their viability, probably in direct proportion to the time taken by the transport. Then we must pay attention to the places where the diaspore arrives which will be mostly unsuitable. If sea currents will deposit them after the hazards of the transport on shores they will be subject to the power of the surf. And even if big waves may bury them in the sand or debris behind the drift, such a place is generally unsuitable for germination and/or upgrowth of inland plants. In comparing islands of different size we cannot simply take their surface for the calculation how much larger the chance of establishment of chance waifs will be on the larger island, as we shall have also to measure the extent of suitable ecological niches in both islands.

Even provided the minute chance that diaspores of an inland plant have successfully negotiated the hazards of transport, and have arrived in spots fitting their ecological needs as to soil and climate, there are other biological

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[1]) It is not correct to use the term *random* here as winds, ocean currents, and migrating birds were and are not random, *i. e.* indiscriminately in all directions. The term *chance* should have been used in this context.

obstacles for successful propagation connected with pollination. Dioecious plants require several specimens together in order to maintain themselves. More important, all species requiring insect pollination will not be capable to maintain themselves unless there are in the new station insects available for this purpose. The chance that such insects are available will rapidly decrease with distance. One of the most important plant groups depending entirely on insects for fertilisation is the genus *Ficus* of which detail research by Dr. J. van der Vecht and Mr J. T. Wiebes for Mr Corner has shown that insect pollinators of *Ficus* are highly specific and that wasps and figs can disperse only together, that is very slowly and at short range; the old data provided by Cunningham pointing to the contrary are fallacious.

Further we have to consider that in general the arrival of one diaspore will not lead to establishment. Furthermore, the experience is that only part of the seed is viable and that in sowing seed in nature great quantities are needed to have success. In some way or other my own field experiments have entirely failed. I have sown thousands of seeds of *Primula prolifera* Wall., collected on Mt Pangrango, in various places of Mt Gedeh (they are twin peaks of one volcano in West Java) on the same day, without positive result. I did the same with about 100 nuts of *Stachys oblongifolia* Bth., collected on Mt Talun, which I have sown in five localities with patches of bare soil on Mt Papandajan, at the same altitude and to my eye of the same ecology (half-shade and somewhat damp soil), but have never found any specimen of this conspicuous species in these localities. Possibly I have no 'green fingers', but do the dispersal mechanisms of Nature have them? I have later done similar experiments in Holland with species which I liked to have in my neighbourhood, but the success was almost nil. The result is different if one establishes a species by *planting* a well-developed specimen of a perennial species (with root-system and an earth-clump) in a place where it did not occur before. Docters van Leeuwen did so with the said *Primula* on the Lebak-saät on the saddle Pangrango-Gedeh and with the Sumatran *Anemone sumatrana* De Vriese and some Sumatran species of *Impatiens* alongside a trail in the primary forest at Tjibodas. These foci maintained themselves, although hardly showing extension in ten years of observation. He planted also specimens of *Trientalis europaea* L. on his estate at Leersum, Holland, which plant spread enormously (by the very long thin underground runners of its rhizome); he found also a few seedlings.

From this experience I conclude that the amount of seed and seed reserve must reach a certain level before it can lead to new establishment. It appears that as soon as we try to figure out chances in more detail it will be impossible to make a rough guess. The assumption of 20—30 thousand years per species is therefore an entirely gratuitous supposition, it could be any figure between zero and an aeon.

Fosberg finally wrote: "If we resort to land bridges or continents to account for the presence of the Hawaiian flora, then we may well have to build them in all directions". This is, however, no characteristic peculiar to oceanic or island floras, but a characteristic of all floras. This can easily be explained if, for the moment, we single out, in our imagination, a random part of a continental flora of the size of Hawaii, Fiji, New Caledonia, or of any smaller size, and assume for the purpose it to be an island surrounded by a very wide expanse of sea with distant shores, and we further imagine that we would be ignorant of the surrounding flora subsided below that expanse of sea. If we would then analyze the floristic affinities of this imaginary island — let us say Holland, with the nearest land-masses in the Ural, N. Africa, Newfoundland, and Greenland — we would also find a situation in which we would be obliged to build bridges into various directions to the distant oceanic shores to account for the flora of our island, namely in those directions which were the lines of affinity in the original continental continuum!

This argumentation shows that the so-called *disharmonic representation of biota* in the Pacific islands, one of the main points of circumstantial evidence by the entomologists Zimmerman (1948) and Gressitt (1961) for a peoplement by random dispersal, is not a feature peculiar to oceanic islands. It will hold for any restricted continental area which has for some reason become widely detached from an original continuum.

Disharmonic floristic composition has two aspects, (i) an unequal representation of average composition of families and (ii) exceptional endemic development restricted to certain families or genera. The second aspect is certainly tied up with the site of origin of these groups, and not primarily with, for example, ecology. This can for instance be illustrated with the distribution of the family *Dipterocarpaceae* of which about 400 species form the most common feature of the Malaysian lowland rain-forest while a smaller set is found under more seasonal climatic conditions in tropical SE. Asia. Under both conditions they grow gregariously in enormous numbers of specimens. The family is ecologically extremely "successful" in all kinds of niches as to soil conditions, and is dominant, and "aggressive" under primary forest conditions. The fossil record shows that it occupied a similar position in the Tertiary of Malaysia. As to environmental conditions one cannot escape the idea that it would have been equally successful in the tropical lowlands of Africa or America if it had originated there. A similar observation can be made on *Eucalyptus* and *Acacia:* why did these genera become the largest ones in the Australian flora and not in the drought areas of the African and South American continents? Why did enormous genera as *Rhododendron, Primula,* and *Gentiana* develop to colossal size in number of species and specimens in the Sino-Himalayan area and not or less so in other mountainous area? Or the *Mesembryanthemums* in the drought areas of southern Africa and not in Australia?

A similar observation can be made on continental areas of restricted size where genera or families may show an extremely high 'species density', hence a completely disharmonic composition, as for instance California, SW. Australia, and the Cape Peninsula with its hundreds of *Ericas, Proteaceae, etc.* These restricted continental areas are directly comparable to the insular floras of Madagascar, Ceylon, New Caledonia, New Zealand, and Hawaii, in which also some families and genera show a similar, extraordinary local endemic development.

From this follows that disharmonic build-up of floras is not restricted to island floras but is found under both continental and insular conditions.

Any explanation of this phenomenon must start with the origin of these 'successful' groups and the genetic potentiality of the original local gene pool of such centres. It would be an oversimplification to assume that such a gene pool was originally carried by a single randomly arrived waif. Its roots must be sought far deeper in the history of the group.

In addition it is of course clear that such developments could only be successful if the site of development offered ecological variety. I mean with this that for example, if the Cape Peninsula had been situated under everwet conditions the same original gene-pool of *Erica* would presumably not have led to the present enormous development of this genus, and if Madagascar would have been a low saline desert flat the same starting gene-pool could never have led to the present remarkable flora. But, conversely, if there would have been no gene-pool with great potentialities in *Erica* in the Cape Peninsula, even the most diverse environmental conditions could not have 'stimulated' *Erica* to develop as it has done.

The chequered history of fractured areas will naturally render their floras and faunas to get more disharmonic in proportion to their age. Even relatively large islands which probably had not a very revolutionary history, as for example New Caledonia, have a disharmonic fauna, according to Gressitt (1961, 73). This is in part also due to the fact that in the large source areas evolution and speciation steadily proceeded.

Another argument for the perpetual insular nature of the Pacific islands Zimmerman and Gressitt derive from calculating the number of representatives of a certain group, starting from for example New Guinea which is assumed the main centre from where the group originated. They assume the distinct decrease in representatives in going eastward via New Caledonia, Fiji, Samoa, Austral Is., Society Is., Marquesas, Mangareva, and Henderson I. as a sign of former progressive migration, and this can of course be agreed with. They interpret this gradual decrease by decrease of chance with increasing distance. In passing it may be remarked that this conclusion is not fair, because the size of the islands they selected decreases also eastward in the same proportion; furthermore if the Hawaiian islands are added to the chain of islands the statement does not hold. Above all it should be emphasized that a decrease in number of species from a centre with distance is generally also found in continental areas where groups fade away gradually with increasing distance from a centre of development (source area). It is by no means restricted to islands, but is a general biogeographical phenomenon. The same argumentation could for the rest be employed if accessibility would gradually decrease in one direction. If for example the margin of a continental area was gradually fractured the most outlying foundered parts would be first isolated, then the next, *etc.* and with it accessibility would be impeded in the same direction. The number of representatives of a certain group would then also increase from the firstly isolated islands towards the continent.

It appears that all three arguments, fanwise affinity in many directions, disharmonic representation of taxa, and decrease in species density from source areas, are not characteristic of oceanic floras only but are equally present in continental continua.

In the symposium at the 10th Pacific Science Congress, Hawaii (1961) Fosberg still advocated his theory of chance dispersal to account for oceanic floras, and he summarized his points in favour of that idea in six theses. First, he maintains that the representation of the various plant groups that might be expected follows a random rather than a systematic pattern which

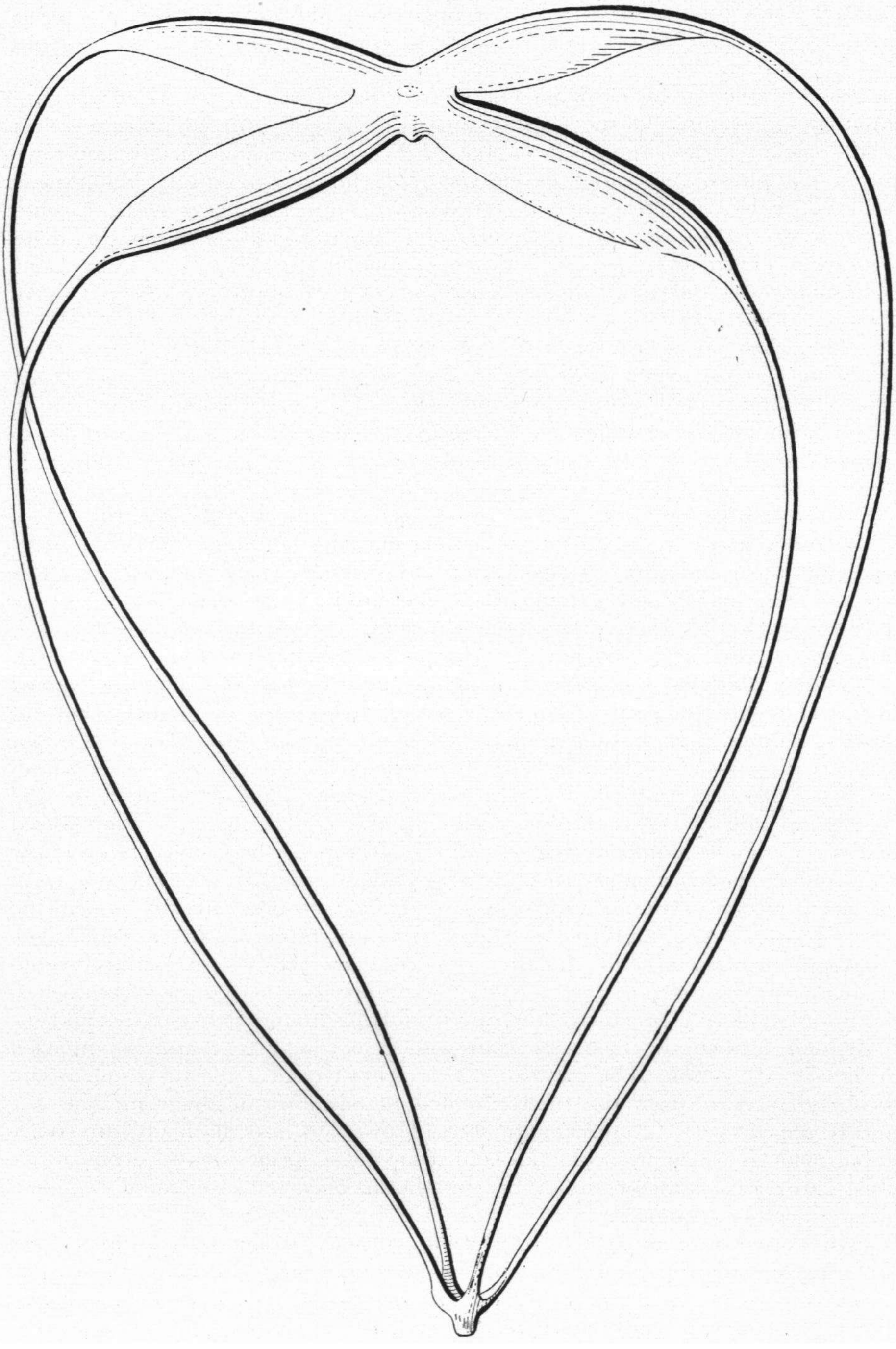

Fig. 2. Fruit of *Lepinia solomonensis* Hemsl., nat. size (after Hemsley, 1901).

should be the case under the land-bridge theory. Such peculiarities are found also in continental floras, however, and cannot similarly be explained, *e.g.* the absence of *Fagaceae* and *Juglandaceae* in the Deccan Peninsula, the distribution of *Platanus,* Plat., *etc. etc.*, The only plant name Fosberg mentioned in his paper is that of the genus *Lepinia,* a curious small rain-forest tree of the *Apocynaceae,* as far as I know only recorded from Tahiti, Ponape, and the Solomon Is., localities which form a triangle with sides which are *c.* 1650, 5500, and 6325 km long, about comparable with the triangle Amsterdam - Barcelona - Afghanistan. The four carpels form a unique kind of fruit (*fig. 2*). Why Fosberg precisely mentioned this very rare genus presumably as an example of long-distance dispersal is a mystery to me, because it is unacceptable that in a plant with such a remarkable fruit structure no short-distance dispersal would take place. There are only two possible explanations for the wide gaps separating the three known localities: either it has been overlooked in many islands, or it has a relict area. In the first case it cannot serve for illustrating long-distance dispersal, in the latter case it defeats long-distance dispersal and even short-distance dispersal. With the extremely chequered, ancient history of the islands in the Pacific this would not be surprising. Similarly disjunct areas are found in continental areas, but there they are equally considered to represent relict areas, not areas which have simply come into being by haphazard dispersal in the past. Disharmonic biota are not a feature peculiar to oceanic islands, they occur in continental areas as well. Conversely it is most significant that in the floristic affinities of the Pacific and its surrounding countries there are most marked regularities of sympatric or equiform distributional ranges. The Malaysian mountain flora exhibits a rigid scheme of tracks which is opposed to any idea of randomness. Second, Fosberg attributes great value to transport of diaspores by hurricanes and the tropical high altitude west-east directed 'jet streams' circling the globe not far north of the equator at *c.* 5500—16500 m on which Ratner (1955) reported. Admitting a theoretical mechanical possibility it seems highly improbable that the short-lived diaspores of tropical lowland rain-forest plants would reach the jet streams, and especially that they could stand such transport. Elevated to great height by hurricanes in a wet state they would already be frozen to 5—60° C below zero before being carried by the jet stream and though I cannot point to experimental data as proof I am convinced that no diaspores of tropical lowland plants could survive this *tour de force.* There is nothing in the dispersal spectra indicating that for example coarse, winged diaspores are more widely dispersed than others. A significant case is that acorns and chestnuts find, together with the winged dipterocarps, their easternmost station in the Louisiades. Third, Fosberg believes that open habitats (bare ground) in the Pacific Islands have been favourable for settling of new invaders. But it should be remembered that tropical rain-forest plants are forest dwellers; no dipterocarp would have a chance in such places. Fourth, Fosberg argues that there is no geological evidence for either former continents or land-bridges in the Central Pacific basin, but fifth, he weakens this argument by considering that former mid-ocean ridges and fracture systems have in the past provided numerous stepping stones to reduce the width of the water barrier. This approaches my idea of insular isthmuses, although we differ in degree, because my insular isthmuses require far more former land than Fosberg will find compulsory. If we observe the rather great differences in floristic composition of rather close and comparable islands of Pacific archipelagos, as *e.g.* within the islands forming the Hawaii, Galapagos, Fiji, Juan Fernandez, and Marianas groups, it is clear that the distances between the islands forming these groups which only run in some hundreds of km obviously present a formidable barrier, notwithstanding the assumed carrier potentiality of hurricanes and jet streams. As I have explained (see p. 310—311) Krakatao does not furnish much evidence of importance. Fosberg's sixth argument is that an enormous extent of time is available, possibly as long as from the Cretaceous. In this I fully agree, as I am convinced of the very slow dispersal in nature, in particular for tropical rain-forest plants. Besides, I have made clear that land-bridges and insular isthmuses must have had a chequered history, and consequently dispersal over them.

This brings me to the subject of mountain floras which are essentially island floras, as the contour lines are at almost all altitudes broken up and consequently the areas at any given contour (altitude) will appear as islands. The crucial question of long-distance dispersal can readily be studied here, and Stapf (1894) has given ample attention to it in his classic study of the flora of Mt Kinabalu which offers a unique opportunity through its isolated position. The nearest mountains of high altitude where Kinabalu species are found are in Java at 1600 km, Central Celebes at 1000 km, the Philippines at 1000 km, Tonkin at 1800 km, and North Sumatra at 2200 km distance.

Stapf introduced (*l.c.* 110) a statistical method of survey of dispersal means as can be derived from the morphology of the diaspores, which methodology I have named that of the 'dispersal spectrum'. Such spectra are of course rough, as they refer only to the mechanism of dispersal; they are rather flattering, because for example fleshy includes also berries which are not eaten by birds and it is not taken into account that spores and seeds sometimes cannot stand the cold or drought encountered in the higher levels during aerial transport. Stapf made dispersal spectra for different altitudinal levels and this analysis of the flora of Mt Kinabalu resulted in the following figures:

Dispersal method / Altitude	Fleshy in %	Winged & dust seed in %	Unknown in %
low to 900 m	46½	18½	32½
900—1800 m	45	29	26
1800—3100 m	50	32	18
3100—4000 m	59	30	11
bogs and rocks at 4000—4110 m	—	26	74

As there is an appreciable percentage at all levels in the third column of the unknowns — that is plants not provided with any special means of dispersal — which is surprisingly high at high altitudes, Stapf came to the conclusion (*l.c.* 113) that there is "no agency whatever operating on Mt Kinabalu to bring about in this way an exchange with those regions where these species or their nearest congeners are found".

I have similar spectra from other mountain floras with similar results showing that the situation on Mt Kinabalu is no exception.

The listed South Pacific disjunct plants from chapter 2 section 5 give the following dispersal spectrum: *fleshy fruits 19 = 30.1 %, epizoic dispersal 7 = 11.1 %, wind dispersal 5 = 8 %, unknown 31 = 50 %.* These figures show that it is absurd to attribute this assemblage to, for example, active dispersal by the gales of the westerlies. If that were so we would expect to find an abundance of Australian-centred affinities to have stray representatives in South America, but no species of American-centred genera to extend westwards. Besides, if wind would be the main agent to cover large distances in this area the wind-dispersed plants would range high in the dispersal spectrum, but it is remarkable that they range very low; the whole spectrum is present whether the genera are centred in Australasia or in South America. Furthermore, many plants with very different means of dispersal in this list are sympatric and grow together in one vegetation type. It is even remarkable that, although there are some genera with small seeds (*Jovellana, Gaimardia, etc.*) and a few with pappus there is none with dust seed and this group could precisely be expected to be very large if wind would be a decisive dispersal agent. Two of the three genera of *Compositae* have no or hardly any developed pappus!

From the morphology of the means of dispersal one would expect a strong selection of well-adapted diaspores in remote islands or on isolated mountain summits, but this interpretation of the morphology is defeated by the facts. In Hawaii one finds for example *Uncinia,* Cyp., and *Acaena,* Ros., with their conspicuously hooked fruits on the mountains where are also found *Nertera* (*map 14*), *Coprosma,* Rub., and *Astelia,* Lil., with drupes or berries, but also *Oreobolus, Gahnia, Machaerina,* and *Carex,* Cyp., sedges which have no special structures for epizoic or endozoic dispersal by birds. It is, however, most remarkable that representatives of these genera *grow together over an immense area,* from Patagonia to Borneo and that their areas are about equiform or even almost sympatric.

A similar situation can be observed among holarctic genera in Hawaii: *Sanicula,* Umb., epizoic, *Vaccinium,* Eric., and *Perrottetia,* Celastr., endozoic, *Aster,* Comp., anemochorous, *Silene,* Caryoph., *Peucedanum,* Umb., and *Vicia,* Leg.-Pap., without any special means of dispersal.

According to Skottsberg (1956, 338) it is surprising that Werth (1911), who wrote a detailed study of the Kerguelen flora, asserted that not one of the flowering plants possesses any special dispersal mechanism for either wind, water, or bird carriage.

It is significant that many large genera with a wide ecological tolerance and consequently a wide range, and which have minute seeds suitable for wind dispersal, are absent from the Pacific proper. An example is *Mitrasacme,* Logan., with more than 40 species, centering in Australia and Tasmania, but occurring through Malaysia to S. and E. Asia (from Ceylon to Japan and S. Korea); in the Pacific it is only found in the Carolines, New Caledonia, and New Zealand.

It is further remarkable that several families which possess diaspores easily dispersed by wind are so scarce in the Pacific Islands: *Bromeliaceae,* which are abundant in Central and South America are only represented outside the American continent by a few species in the Galapagos Is., Cocos I., Juan Fernandez, and one species in West Africa. *Bignoniaceae* are almost absent in the Pacific Islands except in Melanesia. *Orchidaceae* are still rather abundant inside the Andesite Line, in Fiji, and just outside it, in Samoa, but there are only 5 native orchids in the Hawaiian Is. One might assume that the Hawaiian Is. offer no suitable localities but the reverse is true, as proved by the dozens of species which are spreading by natural short-distance dispersal from the orchid nurseries; we found them in the rain-forest, but also in clefts of barren lavas and on lavastreams with pioneer seres.

In this connection it is significant that large phyla with spore dispersal, ferns, mosses, and hepatics, show plant-geographical areas and affinities which are exactly comparable to those of the Angiosperms, although the number of ubiquist genera is proportionally larger. The latter phenomenon is, however, not very surprising because the genera of these groups are possibly also older.

Good (153) observed that we have no proof that species equipped with special dispersal mechanisms are more widely distributed than others. It is of course theoretically possible that small seeds without special means of dispersal could be transported by adhering through mud to feet or feathers of migratory birds, and Taylor (1954) in his study on Macquarie I. suggested this possibility, but much more data are wanted to assume that this can lead to bridge large gaps and to establishment.

Such form of transport was formerly also assumed for the local occurrence of *Eriocaulon* in Ireland, but the Löves (1956, 1958) have been able to show that this assumption is untenable on cytotaxonomic grounds.

Camp (1952) studied the distribution patterns of various families from a phyletic point of view, amongst others the pantropical water-plant family *Pontederiaceae* of which the genera show an east-west trend from the Malaysian *Monochoria* through Africa to tropical America with its highly divergent genera *Hydrothrix* and *Pontederia.* He could find no arguments for long-distance chance dispersal in this family.

There is of course one mode of dispersal in which diaspore spectra will be of no use and that dispersal mode has been called 'rafting'; large floating trees, drift wood, floating islands, or debris masses tangled together bringing about transport across the seas. Zoologists in particular sometimes adhere great importance to such drifting masses. The evidence for them is very meagre, and for their functioning it is nil. As has been alluded to on p. 275. Moseley observed that within a few tens of km from the estuaries leaves, fruits, and bark become detached in sea-water and soon after the bleached skeleton timber is drifting apart from the fruits, assuming that both possess the capacity of buoyancy. Agassiz (1892) found that currents off Panama, sometimes moving 120 km a day, carried immense quantities of drift toward Cocos I. and the Galapagos Is., and said some unflattering things about persons who built bridges to these islands. As far as I know nobody has ever actually seen this debris arriving on the shores of Galapagos, with living animals, let alone these animals (♀ and ♂) going ashore, propagate, and establish themselves. The observation of drifting debris itself is of course interesting, but there is nothing new about it and Agassiz's criticism would only have carried weight if he had actually observed the arrival of living continental material on the coastal rocks of the Galapagos and verified its establishment, instead of making a rash deduction. Surely the enormous number of endemic species cannot have arrived in this way.

Floating islands are of course known to occur in freshwater lakes; they can occur through land-slides or wind, and mostly consist of detached portions of marginal swinging bogs. These are, however, confined to shallow inland lakes of restricted size and carry only animals and plants which are found already around the lake. When such lakes have an outlet such rafts are rapidly disintegrated by river transport as commonly observed in Malaysia; they have no significance for sea transport.

The only case I ever heard of a large seaworthy raft is the state-horse alluded to by Matthew (1915, 206—209, see also 203—204) and Darlington (1957, 15). This is said to have been described by a certain Mr Powers in an article titled "Floating Islands" (in Popular Science Monthly 79, 1911, 303—307). It was cited to be "a raft 100 ft square with trees 30 ft high, evidently tied together by the roots of living plants, observed in the Atlantic off the coast of North America, in 1892, said to be known to have drifted at least 1000 miles". I have not seen this publication and I cannot tell what and where the course then must have been during the 1000 miles, along the coast, in the sea, or on a river, and who is responsible for observing it during this voyage; it seems very strange to describe such a unique phenomenon only in a popular magazine nearly twenty years after it happened.

Whatever its merit, I neither believe that it entitles Darlington to the sweeping statement (*l. c.* 16) that for long-distance dispersal exceptionally large debris rafts "might carry almost any land animals almost any distance where ocean currents, winds and climates are favorable", nor that "adequate rafts exist" for transatlantic transport of "hystricomorph rodents and possibly one or two other mammals" (*l. c.* 592, obviously copied from Matthew, 1915, 229—231). Even if such rafts would exist, the chances for a successful *trans-oceanic* voyage of several thousands of kilometres of such Arks of Noah, with living vertebrates (♀ and ♂), to a suitable anchorage for unloading, seem extremely doubtful; in my opinion they are zero.

My negativism is borne from the fact that Darlington himself (*l. c.* 593) concluded from the lack of native placental mammals in Australia, "except bats and a few rather recent rodents, that the continent was separated from all other continents by water throughout the Tertiary". The question arises why hazardous long-range oceanic rafting dispersal can be assumed covering thousands of kilometres, but none or almost none has taken place in the tropical Malaysian Archipelago connecting Asia and Australia, where floods are common, debris plenty, and distances short (in the range of tens to a few hundreds of kilometres and even shorter during the Pleistocene Ice Age). Under these archipelagic conditions such rafts should anyhow have yielded infinitely more effect for steadily progressing dispersal towards Australia by *short-distance rafting*, because he admits (*l. c.* 484—485) that the probability of successful stranding on beaches with living cargo (animal species of course at least in duplo, ♀ and ♂) progresses geometrically with shorter distance. However, very important botanical and zoogeographical demarcations run straight across Malaysia.

His own enthusiasm to apply the success of dispersal with rafts is surprisingly small for in explaining Tertiary vertebrate distribution he keeps strictly to the terrestrial Beringia and Panama pathways; under that viewpoint it is also not understandable why Madagascar, which was according to him insular since the Palaeozoic, has not more profited from rafting during that immense lapse of time.

All that I can say about it is that, similarly to the monster in Loch Ness, successful transoceanic dispersal by rafting cannot be ruled out on theoretical grounds.

In my study of the origin of the Malaysian mountain flora (1934, 401—416) I naturally paid a great deal of attention to the effect of dispersal but have not found sufficient evidence for a clear correlation with distributional patterns.

And I have applied Stapf's dispersal spectrum analysis to species belonging to one 'track', that is areas which are at least sympatric along the track. It appeared that also in such a track plants with dust seed, spores, berries, mechanisms for epizoic dispersal, *etc.* occur in various percentages among the constituents, with always a rather large percentage of 'unknowns'.

If wind dispersal would be important to cover large distances, or even average gaps, one would expect a large percentage of wind-dispersed Australian plants in the Lesser Sunda Is., which are for many months subject to steady and strong south-eastern dry winds. But it is remarkable that the mountain flora of these islands is a typically Javanese one, *i. e.* of Himalayan affinity, without a marked increase of Australian representatives in proceeding eastward (*l. c.* 404—405).

As to endozoic dispersal it is true that several birds in the Javanese mountains mainly feed on fruit, but according to Prof. Stresemann and other ornithologists such birds are principally sedentary which is *inter alia* derived from the fact that one finds a marked degree of raciation among them, each race being restricted to a separate mountain or massive. Migratory birds are practically all predators and those which feed on seed or fruit cannot cover distances larger than roughly a few tens of kilometres before their stomach is empty.

Another consideration pleading against the effectiveness of long-distance dispersal is the observation that wide distribution has materialized irrespective of whether the genera or species possess bisexual flowers (or are monoecious) or are dioecious. Dioecious plants cannot be expected to spread as fast as monoecious ones, except if their fruits are many-seeded and spread as a whole to guarantee that ♂ and ♀ plants will be present in the offspring colony within pollination reach. At short distances there will be no great difficulty for dioecious plants but for long distances the chance that two seeds, one producing a ♂ plant and the other evolving into a ♀ plant will arrive independently close to one another within the plant's life span is reckoned to be infinitely small, in practice to be *nil.* Still, widely distributed genera of dioecious plants, as for example *Coprosma,* Rub., with only 2 pyrenes in the drupe, have been very successful. Furthermore, dioecism is certainly not a modern feature in the plant kingdom, it is mostly considered to be ancient.

Raciation is further very common in mountain plants, both in temperate and tropical floras, and each mountain has its own race or ecotype, which is genetically defined. This is not only true for species without special means of dispersal but also for plants which are entirely dependent on endozoic dispersal, for example *Loranthaceae.* For example two neighbouring mountains in East Java, Mts Tengger and Ardjuno, are inhabited by two different races of the Loranthaceous *Macrosolen pseudoperfoliatus* Miq., with no intermediates whatsoever. If dispersal would be a random affair in nature, geographical raciation of plants and animals, resulting in these locally homogeneous races on each mountain cannot be properly understood.

This leads us to consider endemism of a higher sort which is a striking feature of the Pacific islands, even in the high islands of the Hawaiian chain which are separated by distances not exceeding 50—150 km and which hence fall rather short of our concept of short-distance dispersal. One of the marvellous endemic mountain genera is that of the famous silverswords, forming the genus *Argyroxiphium,* Comp. Most species inhabit the volcanic ash-cones at high altitude, where they grow sparsely on almost bare soil where there is no question that one species would be capable to crowd out others through competition. This condition has always been represented in these entirely volcanic islands. The achenes are rather large and lack plumed pappus. One would assume that all the species would be present in all the islands bearing high volcanoes, but this is not so. Although the ecological niche for all the species seems the same, one might assume some peculiar environmental factor might prevent settling of dispersed achenes. Transplanting experiments performed by Mr L. W. Bryan, Kailua, Hawaii, carried out in nature, however, have been successful, as he kindly reported to me. In 1946 he secured seed of *A. (§ Wilkesia) gymnoxiphium* (A. Gray) Keck, endemic in the island of Kauai and raised plants in a nursery. Five of these were planted out at 2000 ft elevation in the Kau Distr., Hawaii. They have grown well, produced seed, and have become established. In 1936 he had already introduced the silversword from the island of Maui, *A. macrocephalum* A. Gray to Mauna Kea volcano in Hawaii, at 8000 ft elevation. There were 10 plants which all grew well, flowered and seeded in 10—12 years, and have continued to reproduce naturally ever since. At that time this species was assumed to be a species distinct from *A. sandwichense* DC. which was thought to be native of Hawaii only, but which has been found to be conspecific by Keck (1936) who revised the genus. It does seem strange that other species of the same genus, *A. virescens* Hillebrand, *A. caligini* Forbes, and *A. grayanum* (Hillebr.) Degener, all three endemic on the island of Maui, have never been able to reach the island of Hawaii, although the distance between the two islands is only *c.* 40 km at the closest point. One could argue that the silversword species are too young to have been able to disperse to all islands, but this seems unwarranted as the affinities of the genus seem distant; according to Keck it is closest to other Pacific Composites, notably *Dubautia* (incl. *Raillardia*) of the *Helianthoideae-Galinsoginae.*

Furthermore, Mr Bryan experimented with the characteristic *Hillebrandia sandwicensis* Oliv., the only native *Begoniacea* of the Hawaiian Is. which occurs in all islands save Hawaii. In 1938 he secured a few plants from Molokai I. and planted them out in the land of Olaa (Kilauea section), Puna Distr., at 3800 ft elevation. They have grown well and established themselves naturally.

These experiments prove that not the ecology is deficient, but evidently the accessibility. Hundreds of similar examples can be given; those given here are very clear because of the fact that the distances are known, the diaspore sources are restricted, and competition or lack of ecological niche is ruled out.

A far more formidable body of evidence pointing in the same direction is found where major plant-geographical divisions find their delimitation in a sometimes remarkably narrow boundary, for example Torres Straits separating the Indo-Malaysian and Australian floras. In this comparison we should not reckon a few hundreds of lowland savannah plants which are common to North Australia and the southern coastal seasonal lowland of New Guinea. They came to New Guinea during the Glacial Epoch when these savannah areas were a terrestrial and ecological continuum, as Torres Straits and the Arafura Sea were land due to the lowering of the sealevel. However, the true indigenous forest floras of the interior of New Guinea and North Queensland show a remarkably large difference, although there is plenty of rain-forest in North Queensland, and there must have been much more during the pluvial Tertiary. The distance between the rain-forest areas of Papua and North Queensland is in the order of 500—750 km. Here again the discrepancy is not correlated with the morphology of the diaspores; *Medinilla, Vaccinium, Dimorphanthera, etc.* with berried fruit abound in New Guinea, but are absent in Queensland or have one or two stray representatives. *Rhododendron, Nepenthes,* and many genera of *Orchidaceae,* which are all dispersed by wind behave in an exactly similar way, and are either absent in Queensland or are only represented by a single species.

In passing it may be remarked that in the Tertiary the distance between the New Guinean and Queensland rain-forest has probably been larger because the sediments now crowning the Snow Range are Young Tertiary. Originally they must have been deposited by large rivers flowing southward from another, older, large North New Guinean mountain range, probably parallel with the present one, of considerable altitude providing the sediments for the filling of this trough. During the decay of the old range and the building up of the present range, rain-forest and mountain plants were exchanged between them. The remains of the old range, for instance Mt Cyclops, became finally too low to carry a true microtherm mountain flora.

Sometimes botanists are impressed by the great rapidity of the spreading of weeds and aliens in man-inhabited country and assume this would to some degree be a reflection of what happens in nature. The revegetation of Krakatao has also been a favourite of believers in rapid dispersal, who did not realize that this cannot provide a clue to long-distance dispersal, for three reasons. Firstly because there is no agreement about the sterilization of the island. Secondly, even if we admit — and I am prepared to do so — that at least part of the new flora of this island is derived from post-1883 immigrants, the case is exceptional because of the bare soil offered by the ash slopes. Thirdly, because of the fact that the island is on all sides surrounded by vegetation at short distance, two near islands (Lang I. and Verlaten I.) which were not entirely devastated, whereas the main island of S. Sumatra and W. Java are at *c.* 40 km distance, with Sebesi I. halfway. These distances are of an order which can be admitted to fall within the normal reach of dispersal in nature.

Still others point to the few widely distributed or even pantropical species of the sandy beach and have trust in sea-borne dispersal for long distance, or find that, given sufficient time, an accumulated effect of currents, winds, and birds must be sufficient. But none of these factors, hence also not their combination, is valid for dispersal of inland plants of the tropical rain-forest. In this respect attention should be focussed especially on the fact that the seed of the majority of rain-forest plants does not have a resting period and generally *very soon* looses its power of germination, and can neither stand desiccation nor immersion in sea-water.

On the whole the rapidity of active extension of area by means of dispersal in nature has been greatly overrated, even under terrestrial conditions. There is, for example, a great inertia in post-glacial distribution on the northern hemisphere to 'recover' from the glacial destruction.

Even Ridley (1930, xviii—xix), who had an unsurpassed knowledge of dispersal and its effectiveness, in comparing certain plant associations on the mountains of Malaya and Sumatra, at a distance of 400 km, found it "clear that at one period there must have been a land connection between Berastagi in Sumatra and Telom in Selangor at the height of 4000 to 4500 feet, otherwise it would be impossible for these plants to have got to the two places". A similar conclusion he reached from a comparison of the high mountain floras of the Mts Tahan in Malaya and Kinabalu in North Borneo, 1600 km apart.

Axelrod (1952, 187) estimated that "within an epoch of time probabilities seem in general to have been sufficiently high so that continental floras have transgressed water barriers up to 300—400 km in width. At greater distances lower probabilities have resulted in random dispersal of migrants, a dispersal which accounts for waif floras lacking floristic balance". It is my conviction that barriers 100—200 km wide approach the practical ceiling of the 'march of floras' by progressive dispersal.

Skottsberg (1956, 379) pointed to the difference between the floras of Masatierra and Masafuera which are of equal age and origin but only 150 km apart, and the great difference between the flora of this group and the mainland of Chile at 575 km distance.

Though it should be admitted that active trans-oceanic dispersal in nature can in exceptional cases be accepted for a few tens of km and, given sufficient time and ecological opportunity, can lead to establishment, it will be almost impossible to cover a few hundreds of km in that way, and in practice absolutely impossible if the range comes into the order of thousands of km. These considerations give also an idea about the critical distances for effective dispersal in a vegetation in nature.

Finally I want to draw attention to the ancient, relict nature of the indigenous flora of the high islands of the Pacific in which many, though not all, genera occur often clearly disjunct, that is, are absent from interjacent islands. Such plant-geographical disjunctions are of course also found in terrestrial or partly terrestrial continua. In the latter case, however, no initiate will ascribe such disjunctions to chance dispersal in the past, *e. g.*

for *Taiwania, Picea* § *Omorika, Cedrus,* Conif., *Platanus,* Plat., *Juglans,* Jugl., *Ostrya,* Betul., *Osyris, Comandra,* Sant., *Zelkowa,* Ulm., *Cotinus, Pistacia,* Anac., *Aesculus,* Hippocast., *Paliurus,* Rhamn., *Wulfenia,* Scroph., *Ramonda,* Gesn., *Forsythia,* Oleac., *Rhododendron ponticum* L., Eric., *etc.,* Axelrod (1952, 185—186) who tried to fathom the reach of the probability of dispersal correctly concluded that "the likelyhood of reassembling" the representatives of the Asa Gray disjunction for northern mesotherm plants (list 1 on p. 244—247) "by long-distance migration amounts to zero" and can only be explained by a favourable climate in the Cretaceous and Tertiary in a terrestrial Beringia enabling these now disjunct mesotherm plants to migrate from East Asia to North America *vice versa* by short-distance dispersal through a terrestrial continuum.

Some plant geographers might explain these disjunctions by the action of the Pleistocene Ice Age on the northern hemisphere and might cherish the idea that such disjunctions would not arise in tropical countries which have not suffered from major climatic changes. This is, however, not true, as most marked disjunctions occur in the tropical Old World flora; Madagascar-African-Indian-Malaysian disjunctions in the genera *Angraecum,* Orch., *Baphia, Copaifera,* Legum., *Schrebera,* Oleac., *Petersianthus,* Lecyth., *Tetraria,* Cyp., *Taeniophyllum,* Orch., *Nepenthes,* Nep., are a few examples out of many.

If we accept that the Pacific high islands harbour vestiges of exactly similar disjunct relict distributions, there is no sound reason to explain these disjunctions by long-distance dispersal. This measuring by two standards is entirely due to prejudice, *viz* that there has never been continuous land in the Pacific and consequently no former botanical continuum. Such prejudices should of course be banned from scientific plantgeographical reasoning. The present plant world of both the continental and the oceanic islands shows in certain areas and in certain families and genera signs of rather young and progressive development. However, *the world's flora is predominantly a conservative relict flora with a long history behind it, it was of very slow growth and disinclined to change, tenaciously clinging to what was achieved.*

Concluding, the negative and positive circumstantial evidence against long-distance transoceanic dispersal can be summarized in the following points:

(a) *The great regularities in distribution patterns of island and mountain plants* plead against long-distance chance or random dispersal.

(b) *Absence of correlation between plant-geographical affinities and distance* (New Caledonia and New Zealand versus Australia; Lesser Sunda Is. and Kinabalu against Australia and New Guinea; Galapagos and Juan Fernandez against America; Hawaii preponderantly Indo-Malaysian).

(c) *Island floras are not more disharmonic or random in composition than similar portions of continents* within their surrounding flora. Mountain floras behave in an exactly similar way as insular floras, and show great regularities all over the world.

(d) *Raciation of mountain plants* can only be explained by slow dispersal, most of it being obviously relict endemism through isolation, and is contradictory to the idea of long-distance dispersal.

(e) *Specific, and especially generic endemism* cannot be reconciled with the idea of long-distance dispersal.

(f) The rather *sharp plant-geographical boundaries* marking the delineation of major floristic provinces of the plant world which do not coincide with distinct changes in environmental factors or other barriers point to slow dispersal and defeat the idea of long-distance dispersal.

(g) *Dispersal spectra of tracks or of single mountains* give no evidence that certain dispersal mechanisms or natural vectors provide better opportunities for long-distance dispersal, even if such assumed vectors are present in nature (wind for Lesser Sunda Is. and South Pacific floras).

(h) *Sympatric plants or genera which have almost equiform distributional areas* and have a similar ecology often possess very different means of dispersal; some have no special means. Therefore, there seems in nature not much correlation between the morphology of dispersal means and their effectiveness as expressed in size or shape of range.

(i) *Plant families with diaspores clearly adapted to wind dispersal* (plumed seeds or fruit, dust seed, and spores) *and water plants* do in many cases not bear evidence of having gained their area by long-distance dispersal and sometimes show a remarkable tenacity in clinging to present continental areas or continental islands and an 'aversion' to disperse to oceanic islands; in both area and phyletic trends they agree with other families lacking supposedly easy means of dispersal.

(j) There is also *no discrimination between monoecious and dioecious plants,* although the latter would seem infinitely less welll adapted to long-distance dispersal than the former. Species of both categories may show equiformal or sympatric areas.

(k) The assumption of long-distance dispersal was presumably raised as an *ad hoc* explanation of disjunct areas or localities. It is, however, remarkable that (*i*) although all mechanisms assumed suitable for long-distance dispersal must be equally effective for short-distance dispersal and chance dispersal must decrease rapidly with distance no isolated intermediate stations expected from probability are found, and (*ii*) that there is no significant correlation between means of dispersal and occurrence of disjunct areas; see the example of *Lepinia* (see p. 303).

(l) Dispersal in nature goes very slowly and gradually and in short steps by a closed frontier, as exemplified by the explanation of the *mass elevation effect* shown by mountain plants (Van Steenis, 1961b).

(m) *Sea-borne dispersal of a few pantropical or widely distributed species of the sandy beach is sometimes essentially not comparable to dispersal biology of inland rain-forest plants. Anthropogenous dispersal* is neither a model nor in any way a standard for plant dispersal in nature. *Krakatao* and other revegetations of newly born bare soil have given only a vague insight into the procedure nature follows in the way of short-distance dispersal, but we cannot infer data from it for long-distance dispersal.

(n) There are *no direct observations* providing the slightest proof for long-distance dispersal; the absence of high percentages of wind-dispersed plants under conditions where they could precisely be expected (see point e) is significant.

(o) It is absolutely *impossible that any agent can be held responsible for active long-distance dispersal* under the present distribution of land and sea for the tropical amphi-transpacific and amphi-transatlantic rain-forest plants. Consequently there is also no such dispersal possibility for the very numerous pantropical genera, leaving the few beach plants for safety's sake out of consideration.

(p) *The disjunctions of the ancient relict distribution in the Pacific are exactly similar to those found in warm-temperate, subtropical, and tropical countries* under conditions of terrestrial continua and which defeat any explanation by long-distance dispersal. There is therefore no reason to explain the Pacific disjunction by this *deus ex machina.*

(vi) Continental drift as opposed to the steady state principle in plant geography

The idea of continental drift, a secular process assumed to have taken place in the past as propagated by Wegener, has met with strong criticism from plant geographers. Notably Diels (1928, 1934, 1936) has, on the basis of an enormous wide experience, shown that plant geography is against it, at least in its implication of divorcing the Malaysian, Papuasian, Australian and South American floras. Hooker in his analysis of the Australian flora (1859, civ) has shown that over the very ancient southern Fago-Proteaceous flora a somewhat younger but undoubtedly early Tertiary other flora has extended among which *Leguminosae* and *Myrtaceae* were significant, the root of which is found in the Indo-Malaysian flora but which has specialized into an enormous autochthonous aggregate of the present "Australian flora". In addition I have shown that the basic flora of New Guinea is beyond doubt Malaysian to which is admixed the border of the ancient Fago-Proteaceous southern element (1950, 1953). Further the Araucarian-Fagaceous subantarctic element joins Australia to New Zealand and South America very naturally in the geographic position they occupy today. Indo-Malaysia, Australia, New Zealand, and South America thus form a very ancient and unbreakable plant-geographical whole. This would be incomprehensible in the light of the Wegenerian decay of Pangaea and the drift of Australia to the north with its rather recent joining the Indo-Malaysian block.

None of the contributors to the symposium on the problem of land connections across the South Atlantic (Mayr, ed., 1952) accepted continental drift.

According to Reid & Chandler (1933, 69) the London Clay Flora cannot be reconciled with Wegener's drift hypothesis which they reject, as according to this hypothesis the Atlantic Rift began in the south, working northwards, the separation being not completed until the end of the Tertiary, up to which time the British Isles remained in contact with Newfoundland; but the London Clay flora has almost no American plants.

Furthermore, the drift hypothesis is of no use for explaining the tropical affinities, because, although it might be useful to explain the occurrence of pantropical and of tropical amphi-Atlantic taxa, it can neither be reconciled with the existence of a distinct tropical amphi-Pacific group, nor with the fact that this group is numerically not inferior to that in the Atlantic. See also p. 266, 324.

The only conclusion to which we can come on plant-geographical grounds, and these grounds rest on an immense body of *facts* which we have in our herbaria, is that a reasonable explanation of these facts can only be arrived at with the theory of the steady state of the crust of the globe.

Under "*steady state*", a term first introduced, I believe, in modern astronomy, as opposed to the explosion theory[1]), I understand that on the whole the situation of the continents, the polar axis, and the major climatic zones have not changed drastically from the situation in the late Palaeozoic, or at least the early Mesozoic era. The core of it is essentially the same concept as the "hypothesis of permanence" introduced by Dana (1863), who also admitted Australasia as a "fragment of the Triassic World", and applied until the present day by most geologists. Following Vening Meinesz's theory on convection currents in cells in the mantle of the earth (1956) and his work on contraction of the upper crust during orogenesis (1957) it is quite certain that the old sial shields are moulded continuously and replacements take place on an appreciable scale, but not of continental size, that is, they remain within the bounds of the steady state.

Continental drift is admitted by Umbgrove (1947, 230—239) only if this process would have occurred during the Pre-Cambrian. He wisely agreed "that biological and palaeontological data may be able to furnish more or less convincing evidence in favour of trans-oceanic land-bridges, but not — generally speaking — of the nature of such land-connections." I can fully agree with this idea.

Under the steady state principle there is, however, the "rejuvenation" of the relief, as Umbgrove calls it, and he admits "that the idea of permanence is of course untenable in its extreme sense, and that the aspect of the continents and oceans has not escaped frequent alterations. We need only think in this connection of the East Indian basins, Melanesia, and Appalachia."

But just as Schuchert (1916, 1932) and Willis (1932) proclaimed themselves advocates of the theory of permanence, in spite of borderlands and isthmian links which they themselves reconstructed, so, too, we can speak *cum grano salis* of permanence regarding the oceans as long as we refrain from reconstructing hoge submerged sialic continents. Willis constructed a Brazil-Guinea Ridge (reproduced by Umbgrove, *l. c.* 238, fig. 149) crossing the Mid-Atlantic Rise which is a thin sialic layer in the Atlantic at least since Cambrian time. Umbgrove (*l. c.* 239) remarked that although "the existence of land connections during certain given periods cannot be proved geologically, and trans-oceanic land-bridges must necessarily retain a hypothetical character, they need yet not be discarded *a priori* as mere products of imagination."

Umbgrove (1947, 227—229, fig. 142) called attention to the occurrence of many linear ridges and troughs, occasionally intersecting, found in the tropical South Pacific which are believed to have been caused by the rising of magma along faults and fissures in the ocean floor. These lineaments have relatively straight courses, are extremely long, and are supposed to be due to transcurrent faults. They bear many volcanic (simatic) peaks crowned by atolls.

Furthermore Umbgrove (1947, 228—229) admitted that in the borderlands of the continents sialic blocks of restricted size have foundered in

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[1]) A noteworthy parallelism with the disagreement between Lamarck who pleaded for the steady state principle in biological evolution and opposed the theory of catastrophes by Cuvier.

some parts of the Pacific, the borderlands being of unknown extent. Such sialic blocks have later sunk to considerable depth. Such a land mass of unknown dimension has undoubtedly sunk into the Pacific off the coast of South America. The assumption that the eastern margin of Melanesia is a fault zone, on top of which formed the series of islands extending from New Zealand to Samoa, would logically imply that a block must have foundered east of this area.

Though curiously he did not enter upon the crucial subantarctic area in the South Pacific it seems to me that under these geological provisions there are possibilities to explain plant-geographical distribution under the steady state.

The theory of continental drift seems gradually to have come into its final phase of interpretation, thanks to the theory of convection currents by Vening Meinesz (1939, 1944, 1952, 1956) whereby it is argued that it is well conceivable that the shape and geographical situation of the continents has in rough outline been settled once and for all in pre-Cambrian time, and this has been fully agreed by Umbgrove (1943, 124) who also provided geological arguments against any later drift (1951) which in my layman's opinion seem to be final[1]). Although hereby the Wegener idea and the principle of permanency are both acceptable in modified form, continental drift is dated back to such early stages in the development of the earth, pre-Cambrian or earlier, that it can have no place in biogeographical considerations. Vening Meinesz admitted smaller, local multicell convection currents in the outer zone of the mantle of the earth in later periods, which gave rise to local deformations of the crust.

In other words, the guiding line in explaining plant distribution must be the principle of the steady state, with the allowance of the rejuvenation of the earth crust, *on the continents and below the oceans*, *i. e.* subsidence and upheaval orogenesis, folding, synclines and anticlines, throughs, erosion and sedimentation, faulting, and marginal fracturing, and the occasional change of the world temperature not leading, however, to a "uniform" climate but capable to telescope the perpetual climatic zonation. It is agreeable to know that the palaeobotanist Axelrod (1960) has accepted this very basis for his discussion (*l. c.* 280—281).

(vii) Polar shift

The geophysical aspect of polar shift falls absolutely beyond my judgement. My impression is that astronomers and geophysicists generally have never been very enthusiastic about the idea. Umbgrove (1947, 302—308) declines the idea of wandering poles. He could even not adhere to Vening Meinesz's (1943) hypothesis of a large shift of the poles in the early pre-Cambrian. It is of course a many-sided subject, as it may involve a shift of the crust only, or a shift of the earth's axis; a shift of the rotation axis is of course

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[1]) Palaeomagnetists have recently revived the idea of continental drift, see p. 320. I should not conceal that at present Prof. Vening Meinesz, who favoured me by reading the chapters 7, 8, and 11, is less positive than formerly about continental stability. He suggested (*in litt.*) that it is rather probable that mantle convection currents caused some continental deformation and continental drift.

out of question. Arguments for it are, amongst others, derived from ancient plant fossils. This is, however, a markedly dangerous source, in many points. In the first place the identity of the fossil record contains so many errors and uncertainties. If one observes the rapid palaeontological identification of leaf imprints with some dried ones picked by the palaeontologists from a herbarium, we, tropical botanists, are sometimes stupefied by this boldness, because of the fact that if we are confronted with sterile living material complete on the twig, with glands, indument, *etc.* present, we are not seldom at a loss to identify it. Moreover, it is extremely difficult to handle even trustworthy fossils if it comes to use them for ecological, hence palaeoclimatological and geographical purposes, as the thermometers of the past; the older they are the less facts we have at hand for judging their ecological, and especially for making a guess of their thermo-ecological characteristics. The average leaf size of a fossil flora is sometimes used to get an idea about the climatic conditions under which this flora once lived. But in this respect there are curious discrepancies in the living floras known to the taxonomist. If one computed for example such an average for the fossils of a Bornean heath forest the most likely conclusion would be a flora of a microtherm or of a dry climate. It is averagely a typically micro-sclerophyllous leaf type which is preponderant on the podsol sands under equatorial everwet heavy rainfall conditions; and an ecologist who would not know its origin would judge such an assemblage to have come from mountain summits and ridges or assume it to belong to some subtropical drought flora. Furthermore, in evaluating reliable fossil evidence, palaeontologists are sometimes curiously ignorant of the ecological tolerance of living plants, although taxonomists have mostly given at least a rough outline of the ecological amplitude of each genus and species. I have already alluded to this very essential point under section iii. At the Botanical Congress at Paris in 1954 I happened to attend a lecture by a palaeobotanist who "to his great astonishment" had found living palms and bamboos at 2000 m in the southern ranges of the Himalaya together with tree ferns and conifers, facts which he could easily have learned before from the 'Flora of British India'. Edwards (1955), in speaking about *Dipteris,* Polypod., *Matonia,* Maton., and *Gleichenia,* Gleich., says that they are only found in places "fully exposed to the sun" and that *Gleichenias* have "somewhat xerophytic fronds". The natural habitat of the first two is, however, light forest, they can tolerate open places; *Gleichenia* is a genus of which at least all Malaysian species are strictly bound to an everwet climate shunning all seasonal drought. "Xerophytic" is in this respect a dreadful term as it is strictly referring to "plants living under dry climatic conditions"; frequently it is confused or identified with "xeromorphic" which is also an ambiguous term, as it is also mostly linked with the idea of drought; as a matter of fact very many characteristic tropical rain-forest trees, thriving under an evenly distributed rainfall of 3000—5000 mm/year, have surprisingly brittle and hard, coriaceous leaves. There are curious facts in important groups, for example that one normal-leaved *Podocarpus* species (*P. polystachyus,* Conif.) is confined to the equatorial beach forest and that several others grow in the tropical lowland, that oaks and chestnuts grow already on low coastal, tropical hills and that acorns are a common feature of the drift on Malaysian shores and are obviously fossilized in estuaries together with remains of other tropical shore plants. On the other hand fossilized material from high altitude may contain representatives of families which are generally considered as typically tropical; for example the genus *Alpinia,* Zing., is found up to 3600 m altitude, *Pittosporum pullifolium,* Pittosp., ranges in New Guinea from the lowland up to 3800 m; of the genus *Schefflera,* Aral., large-leaved species grow near the timber line in Papua, where their leaf size seems out of place, and so forth. Indeed, many are the pitfalls for the phytopalaeontologist, whose tedious task cannot be envied by the systematist of living plants. I have already alluded to this point in discussing the essential issue of autochthonous versus allochthonous origin of fossils in section i of this chapter and the conclusions of palaeobotanists in defining thermo-ecology of fossils in section iii. Tropical botanists, who base plant-geographical conclusions on many thousands of species belonging to *c.* 1500—2000 genera are sometimes genuinely astonished at the far-going conclusions of palaeobotanists who design deductions from less than ten fossil species without knowing whether these species are indeed indicator species. And though in recent revisional work living plants appear to have been misplaced as to family the synonymy lists in palaeobotany show a much more marked instability.

This criticism is, besides intending to show the unreliability of many fossil plant records as additional evidence in indicating palaeoclimates for proving former polar shifts, meant as an encouragement for phytopalaeontologists to seek very close co-operation with and advice from plant-taxonomists and plant-geographers.

The term 'tropical' for fossils belonging to a genus which is now predominantly tropical may be misleading as indicating a former tropical climate. Outliers of tropical genera have often ecologically no tropical demands. And if in a fossil 'community' of *Alnus, Betula,* Betul., *etc.* there is also a *Menispermacea* one can by no means conclude to a tropical climate. The Gesneraceous relicts *Ramonda* and *Haberlea,* now found in the Mediterranean are certainly of tropical affinity, but are outliers now growing under a warm-temperate climatic condition.

Conversely the temperate element is found in the tropics but cannot be characterized as 'tropical', it is largely '*montane-tropical*', that is, it remains temperate as to climatic requirements.

There are instances, however, that holarctic genera have produced 'climatic-tropical' outliers; for example *Ajuga bracteosa* Wall., Lab., grows in the tropical lowland and hills. The conclusion of the fossil record would be that *Ajuga* indicates a temperate climate.

Such outliers should not deceive palaeontologists, they exist among the living flora, and they will have existed among the fossil floras. Naturally these outliers are proportionally few in number, and if the majority of a fossil plant 'community' points to a temperate flora one or two species of an otherwise tropical genus must be neglected for concluding on the nature of the climate under which the community has once grown, as properly explained by Reid & Chandler (1933, 69).

In envisaging which portion of a flora will enter the fossil state, it is clear that the presentation of the fossil record will always give a fragmentary and besides selective picture of the total flora of an ancient epoch, as for example dryland, upland, and herbaceous plants, small-seeded, and fleshy-fruited genera and species must always be much less well represented than woody plants, those inhabiting marshy areas and riverine lowlands, and genera and species with hard or fibrous shells, and those having large fruits. In the present flora plants from such specialized habitats only make up a small portion of the total flora. Reconstruction of fossil biota from palynological data must give also, but other, inadequacies in representation, and caution is needed and recommended. Insufficient recognition of this matter may have misled Hansen (1956) to reach the fantastic conclusion that life forms may represent age indicators for the fossil record.

Botanists should provide of course adequate identification and it must be admitted that they fail sometimes to do so. And this can lead to unexpected and far-going phantasies. A curious example of this kind started with a paper by F. B. H. Brown on the dogwoods (*Cornaceae*) of the Marquesas (*sic*) and neighbouring islands (1928) from where he described a new genus *Lautea* (from Rapa!), allied to *Corokia*, which he appended with speculations on its northern affinity in East Asia and North America, linking it with Cretaceous fossils ascribed to *Cornaceae* in North America. He connected it with primitive *Celastrus*, Celastr., and *Ilex*, Aquif., which he speculated to belong to one ancestral stock. The inadequate map he published was copied by Longwell (1944) in favour of continental drift, and then re-copied in a work on the world's geology by Umbgrove (1947, 233). It is tragic that in the latter work, for which its author has tried so much to base speculation on hard facts, this sole plant-geographic map is erroneous, or to say the least, is of very dubious value. It has namely appeared that *Lautea* is synonymous with *Corokia* and that it is no dogwood at all, but that it belongs to the *Saxifragaceae-Escallonioideae,* a group which is typical of Malaysia-Australia - New Zealand - SW. Pacific; thus plant-geographically it is entirely "in place".

From their study of the London Clay Flora Reid & Chandler (1933, 58) concluded to a stable North Pole.

Basing himself on the distribution of living and fossil palms Kaul (1944) concluded "that the distribution of palms in the Cretaceous and Tertiary clearly indicates that throughout this time and later the tropical zones and the equator must have remained unchanged. The changes in the climate of Europe must be due to other causes purely local in character and not a world-wide one as shifting of poles, since the extra-European areas of the world do not show any change in the character of vegetation since the Tertiary".

This is also in accordance with the conclusion of Chaney (1940) who tried to reconstruct the climatic zones of the Eocene (isotherms) from forests of the past: "it seems entirely reasonable to assume that a similar distribution of vegetation and temperature during the Eocene resulted from the same controlling factors, and to conclude that land and sea relations, as well as planetary circulation, were essentially like those of today." Like Berry, he also concluded that "all palaeobotanic data plead against the idea of a shifting of continents and poles since the Eocene. North America and Eurasia have stood in their present positions since the dawn of the Cenozoic."

Edwards (1955) in discussing polar shift proposed by magnetologists wrote at the end of his paper on the geographical distribution of past floras that if wandering of poles over great distances "should prove true, then all I have said here is no more than a tale told by a palaeobotanist, signifying nothing."

He was alluding to a new branch of research of geophysicists who study the "fossil" magnetic record of ancient lavas and who have come to be in favour of substantial shifts of the magnetic North Pole, in the Mesozoic up to 45° NL (Opdijke & Runcorn, 1959). Under this theory it is assumed that the magnetic axis of the Earth is at least approximately correlated with the geographical axis and that this correlation also existed in the past, allowing for a deviation of not more than *c.* 20—30° latitude. Another axioma is that the remanent magnetism in basalts and red earths has remained unchanged through the ages. If applied to palaeogeography its implications are very wide-going, even in the Tertiary. Besides shifts of the crust in relation to the rotation axis it has led to a renewed consideration of continental drift of no mean magnitude. A curious, unexplained, fact is of course that the magnetic axis of the dipole magnetic field of the globe does not coincide with the geographical axis but is excentric for *c.* 17° latitude (Gordienko, 1961, 98) and does not run through the centre of the earth. Properly it is not known what causes the magnetism of the earth: is it terrene or cosmic? Research with this methodology, which yields figures in palaeolatitude, not longitude, has started only in recent years and many more facts must be known, especially from the southern hemisphere, to gain confidence that there was indeed in the past a persisting, approximate correlation between the two axes which is axiomatic for palaeographical deductions. Provisionally the course of the shift of the magnetic North Pole cannot be reconciled with what is known from palaeontological data at least for the Cenozoic. Besides, an uncertainty of 20—30° latitude, which has an enormous significance in plant geography, is too coarse for phytogeographical purpose.

If polar shift is accepted over many tens of latitudinal degrees it is clear that all vegetation zones, including the equatorial forest belt, must have shifted with it. This implies that it must have left a fossil record far outside the present tropics. But also the boreal zones have then shifted and left their record far outside the present boreal zones. This would create a tremendously complicated situation in the fossil record, the implications of which I cannot very well fathom. The assumption of former significant polar shifts would entirely disturb the present not unsatisfactory understanding of the gross pattern of affinities and floristic and palaeontological relationships between the floras of different parts of the globe, gradually developed under the steady state principle. Whether it will be possible to reach an equally satisfactory understanding of the gross features of plant geography with large polar shift seems doubtful to me.

It seems still more doubtful how the fossil record which is now climatically in accordance with the theory of the steady state can be reconciled with revolutionary surface shifts.

Durham (1952, 1959) who critically examined the palaeontological data, both floral and faunal, concluded that no polar wandering was possible because the faunal and floral evidence placed the North Pole onwards of the Cretaceous in about the same position as it is now.

As far as critically known the bi-hemisphere symmetry of the living flora corresponds well with the fossil record of both the phanerogams and the conifers and taxads (Florin, 1962).

The major physiographic changes onwards of the Early Tertiary seem to have been the Alpine orogenesis, the crumbling of the Tethys Sea, the origin of the Panama isthmus, the disappearance of the Cretaceous sea in Australia (Crocker & Wood, 1947), the gradual desiccation of the African and Australian continents towards the close of the Tertiary period, and finally the implications connected with the Glacial Epoch: the crushing of the warm-temperate flora on the northern hemisphere and its disappearance along the borders of the Antarctic continent.

As I have formerly discussed (Van Steenis, 1935, 393—401) the influence of the Ice Age consisted in the tropics only of the consequences of the universal lowering of the sea-level which has in Malaysia obviously led to an increase of the drought area (Van Steenis, 1961a). Otherwise a lowering of the temperature of *c.* 2° C will have had practically no vegetational consequence in the tropics, and caused only a slight telescoping of the altitudinal ranges. At high latitudes, however, a lowering of the average temperature of 2—3° C must have had an enormous telescoping influence and would have wrought havoc in the temperate and warm-temperate leafy forests on the northern hemisphere.

How far-going the influence of the Glacial Epoch has been in the southern regions is not very clear. North New Zealand is situated at *c.* 35—45° SL and has of course not so much suffered from glacial influence as similar latitudes in the northern hemisphere, where continental conditions added to the effect of glacial influence. It is further a fact that there are trustworthy fossils (leaves and pollen) from the Cretaceous through the Tertiary till the present of *Nothofagus,* Fagac., in New Zealand. Now *Nothofagus* is a unique climate indicator, as all living species of the genus respond to two rather restricted conditions, *viz* an everwet, cool climate with constantly high relative air humidity[1]). Wherever New Zealand has been with an assumed polar shift it must have been situated under such climatic conditions. Under the steady state principle there is nothing against survival of *Nothofagus* in New Zealand during the Glacial Epoch, although the timber line will have come down over a large altitude as glaciation of the mountains must have increased considerably.

In the Malaysian tropics we have a similar climatic indicator of which entirely reliable fossils are known onwards of the Miocene through the Pliocene, *viz* the *Dipterocarpaceae,* which represent a large typically tropical lowland family dominating the Malaysian forest on the Sunda shelf at least onwards of the Miocene, with apparently the same genera as are thriving there today.

Finally, as we have observed, there is a remarkable latitudinal two-hemisphere symmetry in the floristic affinities of the Pacific on both sides of the Tropical Zone, temperate and subtropical in the North and in the South. This coincides with land between Japan and Alaska in the North and also land in the South (New Zealand and surrounding islands) although much more scattered and scant than on the northern hemisphere. The strong

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[1]) This is equally valid for he northern genus *Fagus,* Fag.

bonds between S. America-New Zealand and SE. Australia and Tasmania suggest that there must have been more land formerly, as this southern bond is botanically about equal in strength to that between E. Asia and N. America.

Whether this remarkable symmetry could have developed under conditions of polar shift seems doubtful to me.

Anyhow I fail to see that polar shift would have brought America closer to Africa, Indo-Malaysia closer to tropical America, or New Zealand closer to Tierra del Fuego.

Concluding I see no reason to abandon the conservative idea of an explanation of the gross features of plant geography under the principle of the steady state, that is without polar shift and drifting continents, but under which principle cosmic changes of temperature and sea-level, and rather large geological revolutions ('rejuvenation of the crust') causing passing changes in the distribution of land and sea are of course admitted.

If polar shifts of large magnitude have only taken place in the very early stages of the globe as suggested by Vening Meinesz (1943) there are of course no objections, but in that case they are irrelevant to our problem.

The general conclusion is that none of the seven possible explanations provides us with a satisfactory clue to the solution of the problem of trans-oceanic distribution.

7. BOTANICAL THEORIES ON TROPICAL TRANSOCEANIC LAND-BRIDGES

There is certainly no unanimity of opinion among botanists about the explanation of tropical trans-oceanic plant distribution. Some are or were adepts of one of the explanations discussed in the foregoing chapter. Several others are not in favour of any of these explanations and declare themselves in a plant geographer's dilemma; their negativism leads them to refrain from a definite opinion for the synthesis. They have of course thought of the possibility of past land-bridges, but in their opinion a plant geographer should not venture on geomorphological speculation of the past in absence of a reliable basis of geomorphologic evidence.

They share this view with many zoogeographers, for example Wallace (1880, 236, 497) and Matthew (1915, 202). Darlington Jr even went so far as to state: "The history of the world's surface is known primarily from geology. Zoogeography is, in this connection, of a secondary nature" (1957, 578). But it is not clear with *what* geology then zoogeography must be correlated, because geologists and geophysicists differ, or have differed, in opinion about most primary principles regarding the crust, for example continental drift *versus* permanence, polar shift *versus* steady state, shrinking earth *versus* expanding earth, origin of the Pacific by the birth of the moon (to which he declares himself an adept, *l.c.* 609, 614) *versus* its origin by convection cells, *etc.* Why these authors attribute only a subsidiary function to biogeography, past and present, is not clear, as historical geology is almost entirely based on fossil evidence, that is, zoogeography. This point of view or reasoning would necessitate to reshape zoogeography with each new theory of geology. In my opinion it is a discipline in its own right, as well as phytogeography.

As follows from chapters 2, 4, and 5 the body of factual botanical evidence which needs an explanation one way or another is formidable. As a matter of fact under the point of view given here it concerns the development of the entire Angiosperm distribution in its early phases. Pantropical and amphi-oceanic distribution did in the past not receive the attention it deserves; in my opinion it is the core of plant-geography.

It is this body of facts which must now be subjected to the test of the hypothesis of past land-bridges, as the other explanations have failed to furnish a satisfactory clue.

I do not agree with biologists and geologists who maintain that biogeographical evidence can not provide a factual basis for palaeogeographical speculation. Critical biogeographical data represent, I believe, independent evidence and this branch of the natural sciences is a discipline in its own right. After all historical geology is for its major part dependent on fossil evidence, fossils are used for synchronizing fossiliferous rocks and for defining past climates. Why then can the *present* flora and fauna, together with the fossils, not serve as evidence for palaeogeographical conditions?

Because in the last century and the early decades of this century geomorphological evidence of land in the oceans was absent or meagre, land-bridges were a subject of wide-going speculation. Although this absence of a palaeogeographical basis is in itself no objection against such speculation, geomorphological knowledge has fortunately progressed and at present some light has come into this obscure matter, especially through the intensified efforts of American scientists in the Pacific. Although the present palaeogeographical knowledge is admittedly not forcing to accept Mesozoic land-bridges, the new factual material unearthed from the depths of the oceans is most encouraging for biogeographers.

Already in the last century various botanists touched on transoceanic plant distribution in various parts of the world, but none of them has, as far as I know, exposed this problem for tropical plants in a more exhaustive, detailed way with an orderly array of facts than Engler (1905). And though the tropical amphi-transpacific distribution seems to me of larger magnitude and to have more implications than that of the transatlantic one, it is certainly an excellent model deserving high merit.

Although Engler's theory of a former tropical transatlantic bridge has tacitly been accepted, and as far as I know with no serious objections against it, it is curious to find that so little work has subsequently been done on this subject. It is true that later authors added to its record, for example Pax (1924) and Lanjouw (1931) in their studies on the *Euphorbiaceae,* and Lanjouw (1935) in his discrimination of two allied Moraceous genera, but as far as I know no serious attempt has been made to elaborate the scope of Engler's concept.

Engler postulated an ancient land-bridge as compulsory for the understanding of tropical amphi-transatlantic plant distribution. He was reluctantly prepared to accept the land-bridge in an insular form, or as an insular isthmus (*l.c.* 229), and this should at least be adorned with large islands to explain the transatlantic occurrence of certain plants bound to a dry or arid climate. There can be even no objection to this condition, as the trade winds in striking land cause rain-shadow effects, as they do at present in the tropical Pacific. In Hawaii arid and everwet climates are found in each larger island and the vegetation under either climate possesses peculiar endemic species. Engler would prefer, however, land-bridge conditions *with continuous land which,* of course, *needs not to have its full width, height, and length at one time.*

The body of facts he had assembled he grouped into several categories among which the tropical rain-forest components are for the present essay of course the most interesting. I have carefully scanned his records and have selected the cases along the same lines I have followed for the Pacific and found that he had about 81 cases.

In considering these cases I was struck by the fact that the 'character' of the list is identical with that of the Pacific: sometimes there are allied species of one section representing a case, sometimes there are two closely allied genera, sometimes it is a tribe, in a few cases a small family which shows the amphi-transatlantic disjunction. Frequently the New and Old World parts are unequally divided and 'gravity' may be situated on either side of the Atlantic. Engler also found that in a few cases these ancient distributions had a stray outlier in East Africa or Madagascar, or Ethiopia.

For tropical amphi-transpacific distribution Hallier (1912) has made a guess, but the unsatisfactory form in which it was offered to the botanical public must have had a negative effect [1]). Hallier postulated a transpacific land connection from Japan, stretching via Hawaii eastward to South California, and southward to Columbia, Ecuador and North Peru. Another land-bridge he postulated in the South Pacific, the so-called Juan Fernandez bridge.

The slight floristic connection between Hawaii and Juan Fernandez fits Skottsberg's conclusion (1925) that "for nearly all species, no direct relation is obvious and I feel no temptation to build a bridge from Hawaii to Juan Fernandez, or to imagine that these island groups are fragments of one old continent", although "it is satifactory that several notable plants belong to the same circle of affinity", and (*l.c.* 35) " cannot see how we can do without a connection between Hawaii and Micronesia". Skottsberg was, however, against the postulate of a transpacific bridge.

Hallier's Juan Fernandez bridge corresponds of course largely with that intended by Hooker and others after him and defended as subantarctic continental masses by Skottsberg (1925)[2]) and by the present author (1953), for the reason that South Pacific subantarctic plant distribution can only be understood properly in accepting an earlier very much larger land area in the South Pacific between 40° and 60° SL. Because of the much more plausible

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[1]) The fact that his arguments are partly ethnographical and linguistic and that he believed the land connection to be very recent shows that he was completely unaware of the issue at stake.

[2]) Skottsberg (1925, 33) refrained from linking Juan Fernandez directly to the west but preferred to regard the Antarctic continent as a former centre and to lead the waves of distribution over New Zealand—Polynesia on one side and over subantarctic America on the other. He keeps silent about the question how the plants of these waves travelled.

way in which this hypothetic land-bridge or landmass of an extended Antarctica was introduced, and the very striking examples and showy distribution maps of amphi-South-Pacific temperate plants published (see Hutchinson, 1926), this postulate was more favourably received, and I believe that botanical insiders will unanimously share the assumption of this land-bridge, extension of the Antarctic continental mass, or whatever name is given to the concept.

This in itself is a sign that botanists are in principle open to land-bridge concepts of considerable reach, because though it is true that the suspected area is surrounded by continental landmasses or their remains (Fiji, SE. Australia, Tasmania, New Zealand, Antarctis, and South America) except in its north, the distance to cover is a vast one, *c.* 7200 km as the crow flies between New Zealand and South America between 40° and 50° SL.

A land-bridge extension between Southeast Australia and Tasmania to New Zealand is further obvious to most Australian and New Zealand botanists, who are fully aware of the intimate botanical bond between their countries now separated by an expanse of almost open sea for at least *c.* 2000 and 1400 km respectively.

For similar reasons there is unanimous agreement upon a Beringian land-bridge which under more favourable climatic conditions has served as the link between the mesotherm E. Asian—E. American groups.

There is therefore in the temperate northern and southern parts of the Pacific I believe almost unanimous agreement among botanists upon the acceptance of the land-bridge theory, as the present amount of land in the southern areas is insufficient to understand plant dispersal and distribution in an intelligent way even under a warmer climate. In itself it is significant that in these two instances plant-geographers agree in principle on the necessity of assuming former land-bridges.

There is of course also no doubt about the distributional significance of the present isthmian land-bridge connection between the two Americas in Central America.

No more can there be any doubt about the actual functioning of the insular isthmus represented by the Malaysian islands as a link between the Asian and Australian floras.

This leads me to consider the transtropical situation, for which the assumption of a land connection seems at first sight less obvious, although the map shows that the Pacific Ocean is in its western part strewn with islands and islets, most of them small, isolated and oceanic. Small as these emerged parts may seem, they represent the summits of gigantic structures, as each of them rests on a lofty submarine mountain at least 5000 m high. Judging from the large diameters of certain atolls there must be basalt massives with enormous plateaus hundreds of miles across. The mighty submarine range from Japan via the Marianas to Palau, which is double in its central part, compares favourably with the Himalayas in length and height above the surrounding earth surface. The same can be said of Central Pacific lineages, for example the Hawaiian ridge.

My interest in the degree of extension of the Indo-Malaysian flora into the Pacific has led Mr. Van Balgooy (1960) to analyse the Pacific flora on the basis of generic distribution and, as I foresaw, he has found that the Indo-Malaysian influence extends very far into the East Pacific. The making of some maps for 'Pacific Plant Areas' by Dr. Leenhouts for some Loganiaceous genera and by Mr. Nooteboom for the Simaroubaceous genus *Picrasma* again stressed the remarkable transpacific relationships, not considered by Van Balgooy. Impressions of these I had already gained earlier in describing with Dr. Van Royen a peculiar Polygalaceous Papuan genus *Eriandra,* of the *trib. Moutabeae,* which consisted of three genera in tropical America (1952), and in taking notice of the fact that the closest relative of the pararubber tree is the Papuan genus *Annesijoa,* and further remembering that the family *Corsiaceae* consists of two genera, one in Papua and one in Chile.

By the strength of these cases and the preparation of new maps of tropical transpacific genera I have tried to go deeper into this problem. For this purpose I have assembled a body of factual material which I have offered in list iii, see p. 250—253.

I have the conviction that the number, though not very large, and the character, and weight of the cases is impressive and that it is impossible to wave them away. I believe that further study will reveal a larger number of cases on the suprageneric level than presented here; it is a time-consuming work to unearth them. Moreover, it must be pointed out that part of lists ii and iv must be added to list iii if we want to compare it with Engler's list which is not segregated into purely tropical and subtropical taxa.

The tropical list contains genera which have a varying number of species on both sides of the Pacific, frequently very unevenly distributed, the major portion either Indo-Malaysian or American. Very often it happens that such species constitute separate sections. Not rarely a similar relationship is on the level of pairs of related genera, or suprageneric, on the level of tribes or even families. The character of this list is therefore basically comparable to that of Engler's for the Atlantic and to the lists of the other types of transpacific distribution. This can of course not be ascribed to mere coincidence.

From the considerations given above I derive two important things, first that plant-geographers are, in principle, not against former land-bridges, second, that if these are accepted for the North, and especially for the South Pacific where there is so little land at present, there is no sound reason not to accept them in the tropical zone, as the list of tropical disjunctions is in no way inferior to the others and fits in with that of the transatlantic distribution given by Engler.

8. GEOMORPHOLOGICAL EVIDENCE OF PAST MESOZOIC LAND-BRIDGES

In the preceding chapter and elsewhere I have alluded to the fact that historical phytogeography is tied up with three major land-bridges which are still existing, *viz* the Panama isthmus, Beringia, and the Malaysian Archipelago. As will appear from chapter 13 the same situation is found in zoogeography; zoogeography is unthinkable without them, and agreement about their function is unanimous.

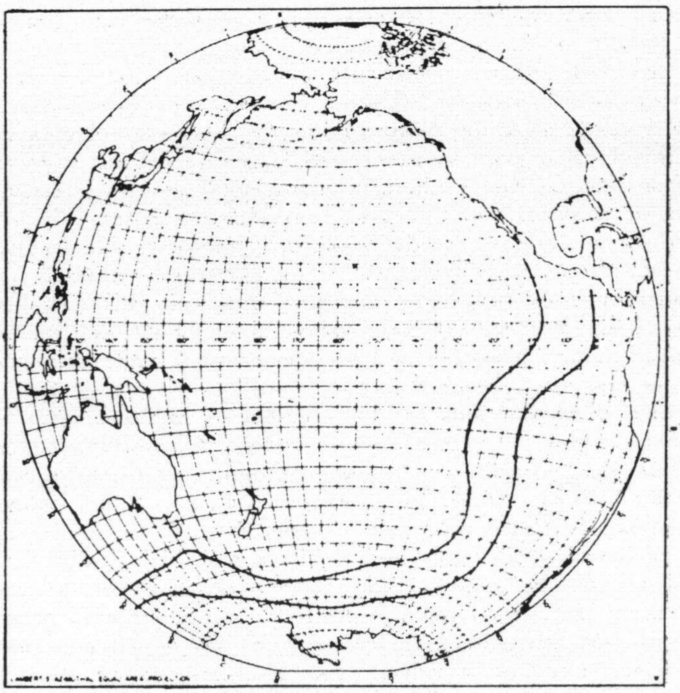
From the body of botanical evidence it has appeared that for a proper understanding of the tropical and South Pacific floras these three bridges, which have presumably existed through the Kainozoic period, are insufficient for a reasonable understanding and reconstruction of the early genesis of the distribution pattern of the Spermatophytes.

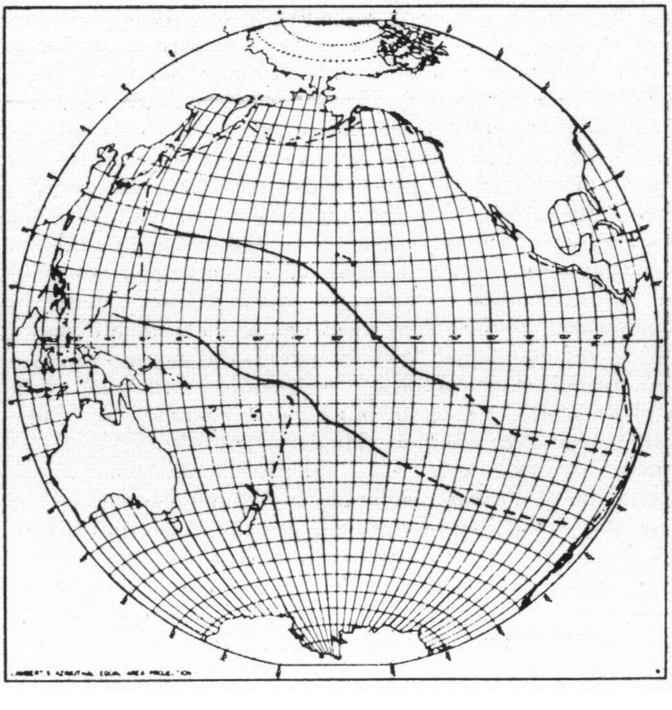
In the preceding chapter it has been pointed out what are the needs of phytogeography for the Mesozoic. Until a few decades ago not much palaeogeographical backing could be derived from the undersea relief of the ocean bottoms. Though their permanence is still largely accepted, it is no longer a matter of speculation that similarly as continental crusts the ocean bottoms have undergone a steady 'rejuvenation', and that on a large scale, at least in certain of their sections. In the geological time-scale these rejuvenations have been termed 'ephemeral' but their actual duration in millions of years is of such magnitude to the biologist that they illuminate his speculation with a shy ray of light. We shall, I hope, know more about this matter in the next decades, although assuredly much evidence must have disappeared forever in the far and dim geological past.

There have been and still are palaeontologists and geologists in favour of former land-bridges. Schuchert, once an adept of Suess's Gondwana Land in its most extended form as a southern continent (1916), later shifted this concept to that of "Gondwana land bridges" (1932). Bailey Willis (1944) sought at one time to trace transatlantic connections as mountain ranges and the concept of isthmian links appeared to him sound, biologically, dynamically, and climatologically. He wrote "that it does not, however, fit the Pacific conditions, except perhaps to link the Antarctic continent with Australia and South America. The connections in Oceania are too broad and too complex to be explained by mountain ridges. The alternative assumption of uplift, followed by subsidence of the ocean bed, is more reasonable. Such conditions are widespread throughout the western Pacific and to them I would attribute former expanse of land which once bore the now dispersed floras and also its disappearance beneath the waters. The average depth of the Pacific is not excessive with known uplifts and subsidences in continental areas". For plant distribution it is of course irrelevant whether the land-bridges originated by orogenesis, volcanism, uplift, or fragmentation of continents.

Land-bridges of the size as those under consideration are of course no mean structures of the crust of the earth and I can agree with M. Millot (1957) that biogeographers should be very careful with postulates to their effect. He may be correct in stating that biologists have sometimes too freely played with them in adding a motto to his paper, derived from a letter by Darwin, stating: "They make continents as easily as a cook makes pancakes". In passing it may be remarked that Darwin himself did not refrain from playing sometimes with equally fanciful ideas, for example with that of the worldwide cooling of the earth, which he immediately withdrew after the criticism by Hooker (1859, xviii—xix, and see Huxley, 1918).

In regional plant-geography the botanist should, however, endeavour to think in terms of geological magnitude and time. He should fully realize that the crust of the earth shows indeed colossal ranges on anticlines, orogenesis and faulting. Examples are the Andes, the Rockies, the Himalayas, and gigantic oceanic anticlines crowned by island garlands such as are found in the Kuriles, the Aleutians, the Ryukyus, the east Himalayan spurs descending through SE. Asia over Burma, the Andamans and Nicobars to Sumatra and continuing via Sumatra and Java into the Lesser Sunda Islands and


LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION


LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION

Moluccas, further the Madagascar-Seychelles bank and the garlands in the Caribbean. Finally there are those anticlines which are still — or again — submersed beneath the level of the sea, as for example the immense mid-Atlantic ridge, and the large Lomonosov ridge dividing the Arctic Ocean (Gordienko, 1961). Recently evidence has been gathered of a gigantic submarine ridge, the 'East Pacific Rise' (*map 19*), discovered by expeditions of the Scripps Institution of Oceanography during the International Geophysical year, running from New Zealand onwards to Mexico over 14,500 km. It is further assumed that Hawaii would make part of a still older system of ridges, the Mid-Pacific Ridge (*map 20*), all of which tend or tended, to throw up land as volcanic islands (Anonymous, 1960; Hess, 1960). To the botanist the low coral reefs and atolls of the Pacific are insignificant specks only offering a poor uninteresting littoral flora, but they are really the tops of gigantic mountains 4000—5000 m high and those of the larger atolls represent the emergent summits of large submarine highlands. Probably they were "high islands" in the past.

And as it seems that Darwin's hypothesis of the sinking tendency of the semi-submarine Pacific mountains, now capped by atolls, is fully confirmed by recent investigations, it is clear that the amount of land above the Pacific Ocean was very much larger in the past. Unfortunately we will never know what size and height they attained and what flora they had, as erosion must have removed the little fossil evidence they might have possessed during the process of their peneplanation.

Numerous of these volcanoes have obviously subsided at such a rate (at least temporarily) that coral growth could not keep pace (or, as has been suggested, subsided under such cool conditions that coral growth was impossible). These so-called 'guyots' are flat-topped but must have been former islands, later peneplained. Hamilton (1956) found shallow-water fossils of Mid-Cretaceous age on Mid-Pacific guyots. Ladd (1960) reported Eocene sediments above basalt from the bottom of the Eniwetok bore hole.

Ranges built on anticlines are of course nowhere even in altitude and, if they emerge from the sea bottom, are probably sometimes elevated and broken up into islands. It is for example not at all certain that the Lesser Sunda Islands have ever formed one continuous land mass. Such anticlines consist mostly of parallel ranges in which the orogenesis and folding takes place, and in which frequently magmatic forces build up volcanic mountains of considerable size. It is clear that anticlinal deformations of the crust must have taken place through the past epochs from time immemorial.

Conversely, there are the effects of faulting, the sinking of continental (sial) land masses, which is observed all along the coast of the West Pacific. This has probably happened mostly along the margins of the continents and fragments of them are still found as islands separated by deeps, for example Japan, Formosa, the Philippine Islands, the Moluccas, the Solomons, New Hebrides, New Caledonia, Fiji, and New Zealand. The geological processes

Map 19 (above). Outline of the present East Pacific Rise which possibly represents a very young oceanic ridge so young that it has not yet developed a median rift zone and pre-Rise sediments still cap most of its crest (after Hess, 1960).

Map 20 (below). The former location of a Mid Pacific Ridge (after Hess, 1960).

needed for the decay of such continental masses are beyond the normal terms of human understanding of magnitude and time, but not beyond those of the geologist's who thinks in terms of the uplift of the Rockies, the Andes, and the conversion of the huge Tethys Sea into mountainous country from Europe to the farthest end of Indo-Malaysia in a not particularly distant geological past.

The opinion of several geologists is not inconsistent with the idea of isthmian links between the continents. Schuchert (1932, 878) suggested a transatlantic bridge which was in existence from the Pre-Cambrium to the end of the Cretaceous to be submerged gradually from the Eocene to the close of the Miocene, disintegrating during the latter period into a gradually dwindling archipelago of islands. According to Kaster (1952, 145) "The Atlantic Basin was apparently initiated in Latest Triassic time; no Jurassic sediments are known yet on either side of the whole Atlantic outside the Tethyan-Caribbean belt; by Cretaceous time the Atlantic Ocean and Basin were in existence and its waters were transgressing the opposing continents". This does not exclude of course that in the Cretaceous land-bridges were still present, be it in decayed insular condition. Dunbar (1952, 154) pointed to a map published by Gutenberg and Richter in 1949 which shows a nearly unbroken ridge crossing the Atlantic basin between southern Brazil and South Africa, now deeply submerged. Bucher (1952, 95) showed that "The South Atlantic ocean floor shows large and conspicuous transverse welts that connect the longitudinal Mid-Atlantic Ridge with Africa and South America, such as the Rio Grande swell which separates the south Brazil basin from the Argentine basin, and the Guinea, Walfish, and Cape swells which enclose the Angola and Cape basins".

In passing it must be remarked that though I found Engler's work nowhere cited in geologists' publications, it would precisely fit their needs. Willis (1932) shared his views, pointing out that such isthmian links still exist in the Americas. Schuchert (1916) also postulated land in the Cretaceous and Eocene in the West and Central Pacific, but without a connection with South America; he concluded to subsidence in the Pacific basin. Chubb (1934) considered the Pacific and concluded that its southern hemisphere portion contains three large areas of ancient subsidence, (a) Melanesia, a gradually folded and fractured subcontinent submerged in Mesozoic and Tertiary time, (b) the atoll zone, and (c) the Albatross Bank, which areas together would replace the land which we need for tropical and subtropical transpacific plant distribution. And though this comes close to a South Pacific continuation of Suess's Gondwana land, the concept could easily be transformed into one of isthmian links which I would prefer. Axelrod (1952) pointed to the Macquarie Swell and the New Zealand Plateau which link Australia and New Zealand with Antarctica. In the east this is easily united with Patagonia, either directly or else by island arcs through the Falklands, South Georgia, and the South Sandwich Is. to Palmer Peninsula. Umbgrove (1937) stood not unsympathetic against the idea of former land in the South Pacific basin; he found no objection to rejuvenation of the submarine relief (1951), pointing to the Mid-Atlantic Rise and the Carlsberg System. He was inclined to the view that no essential objection can prevent geologists from accepting the idea of isthman links as postulated by Schuchert and Willis.

The location of the East Pacific Rise (*map 19*) has in no mean way contributed to a revival of the idea of trans-oceanic isthmian or insular links. In the summary by Menard (1960) this rise is described in more detail; it is a vast low bulge of the sea-floor comparable in size to North and South America. The average relief is 2—4 km, exclusive of the additional local relief of features such as volcanoes. The Rise is 2000—4000 km wide and it extends from New Zealand to Mexico over a distance of 13000 km. It is the scene of shallow earthquakes and it is sliced by a number of transverse fracture zones; intensity of heat flow is correlated with topography, especially with the crest of the Rise. It is suggested to represent a mid-oceanic ridge *statu nascendi.*

Hess (1959) recently paid special attention to the mid-oceanic ridges and emphasized their ephemeral nature (100—300 million years, the duration of the convecting cell); he assumed the former presence of a transoceanic 'Mid-Pacific Ridge' (*map 20*), largely disappeared since Middle Cretaceous time, of which the traces would be represented by the belt of atolls and guyots which have since subsided 1—2 km. The width of this belt is about 3000 km and its length *c.* 14000 km. In 1960 Hess elaborated this Mid-Pacific Ridge further (Hess, 1960, 10, 19, fig. 4) and located it tentatively in a WNW—ESE direction from the Micronesian arcs towards Central Chile.

In passing it may be remarked that this coincides in a remarkable way with the connection casually indicated by Hallier f. for his transpacific bridge. Hess explained this and other transoceanic ridges by basing himself on Vening Meinesz's multicell convection currents in the mantle of the globe through which many previously unrelated facts fall into a regular pattern suggesting that a close approach to theory is thus being obtained. These ridges would represent the rising limbs of the cells while the descending limbs would be represented by the circumpacific belt of deformation and volcanism. The East Pacific Rise is regarded by Hess as a new ridge *statu nascendi.*

Leaving the details and new questions¹) aside, it is for our purpose clear that again some geologists are thinking in terms of former large-sized isthmian or insular-isthmian transoceanic connections, which are particularly interesting in that they would in major degree be satisfactory for an explanation of ancient Phanerogamic plant distribution through the tropics; they are Mesozoic and of long duration.

In 1952 the palaeobotanist Axelrod, though admitting there were three basic continental floras, a tropical and subtropical one in lower and middle latitudes and two temperate floras which have been maintained down to the present day (*l.c.* 186—187) and accepting permanence of continents and a favourable Tertiary-Cretaceous climate thought at that time that "access to all continents was made possible by migration across Beringia and across Antarctica.... by archipelagos of only slightly larger extent than those at present". It is interesting that in a recent stimulating contribution (Axelrod, 1960), which came to my knowledge after I had framed the rough draft of this essay, he now clearly emphasizes the necessity of assuming the Mesozoic transoceanic land-bridges I have outlined here, for Holarctica (*l.c.* 263—273),

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¹) For example such marginal belts are not found along the Atlantic borders although the Mid-Atlantic Ridge must in his views be considered homologous with that in the Pacific.

trans-Atlantic (*l.c.* 253—256), for Gondwanaland (*l.c.* 250), and for the South Pacific (*l.c.* 271—273). He keeps silent, however, on tropical trans-pacific connections which I have shown to be as important as the tropical-Atlantic connection.

Although I have in this chapter naturally assembled all data and opinions in favour of former land where there is at present sea, I am fully aware that the factual geological data, as far as known at present, are insufficient to explain present and past plant distribution. Speaking about the crucial area in the tropical and South Pacific, Umbgrove said to me in 1934: "how are we, geologists, supposed to know about the past what is now hidden by the sheet of ocean water?" It is a pity that he cannot enjoy the amount of new data wrested from these depths.

In the next chapter I will make some notes on the nature and functioning of land-bridges as biological pathways.

9. NATURE AND FUNCTIONING OF LAND-BRIDGES AS BIOLOGICAL PATHWAYS

On the background of the succinct geological record given in the preceding chapter, and thinking in geological terms of age and size, the plant-geographer should consider the degree of functioning and limitations of land-bridges for plant distribution, either as continuous land-masses or as insular isthmuses.

Though terrestrial isthmian connections are of course more welcome for plant dispersal, hence distribution — in which I definitely agree with Engler — if compared with insular isthmuses, the importance of the latter must not be underrated for plant distribution. In my work on the origin of the Malaysian mountain flora I have been confronted with such 'insular connections', as similar conditions prevail for the pathway of mountain plants along the Himalayan Ranges, the Andes, *etc.*, which are in no way different from the distribution over island garlands. Studies on the Aleutians have been made by Hultén (1937, b), on the Ryukyus by Horikawa (1960), *etc.* One prominent point emanated from such studies, *viz* that species derived from a source on one end of the island arc mostly fade gradually away one by one, which shows, in my opinion, that the arcs have indeed functioned, and that in both directions. Similar pictures are found in the Rockies, Andes, *etc.* The functioning of an insular land-bridge on a small scale was studied at my instigation by C. Kalkman (1955) in the Lesser Sunda Islands, which form an eastward continuation of Java and are situated on the same anticline but are separated by deep straits. The major result of that work was that it clearly demonstrated a gradual decrease of Javanese plants towards the East and of eastern species towards the West. The largest, *cq.* highest islands, that is those possessing the largest number of biotopes, are richest in endemic species within the series. The Australian continent is not more than *c.* 300 km from the most eastern island but the Australian element is only sparsely represented. As the Northern Territory, the Lesser Sunda Islands and East Java are all tropical seasonal, it is not the climate but rather the distance which is decisive for active dispersal, and a gap of open sea of 300 km is apparently significant as a barrier.

For the mountain flora also land connections will always be comparable with insular isthmuses, as for the mountain plants it is irrelevant whether the intervening lower level is occupied by land or sea; that view is valid for all altitudinal levels, montane, subalpine, and alpine. It hardly ever occurs that in lofty ranges all levels are continuous land, especially not because mountain building is, from its beginning, always exposed to the effects of erosion.

Naturally continuous levels are more easy pathways for plant dispersal than those broken up. In the latter, insular, situation dispersal, hence distribution, will go infinitely slower and will be more selective, and more subject to chance and to other limiting factors than when plants can march over continuous isthmian land masses on the level that suits the ecology of the species, either for permanent or temporary establishment, as I have explained these terms for mountain floras (1961, b).

As we cannot assume that even for tropical lowland plants land-bridges have always been wide continuous pathways of land we must be aware that many bridges have been 'insular isthmuses' and that these have functioned less effectively than the continuous land masses.

A second point we have to consider is that such bridges have certainly not all existed simultaneously and not always extended over their whole length at one time. Many anticlines show dips; in Sumatra for example the proper anticline dips gradually towards the south, going from over 3500 m height in the north to below sea-level in Sunda Straits.

A third point to consider is that the time during which the bridges, or their terrestrial parts, were suitable for plant dispersal must have varied from place to place.

Therefore, if it were thus that we could assume that enormous insular isthmuses had been complete through long geological periods, they would not have been very much inferior for plant distribution as compared with continuous landmasses, but it is liable to doubt whether this was frequently realized in the history of the earth. Most probably each bridge has had a chequered history peculiar to itself, with respect to duration, width, elevation, and age. Some will have gradually decayed entirely, or almost so, through the sinking tendency of the once uplifted anticline, and species and genera already distributed over part of the bridge will have been wiped out completely. Others will have maintained by chance some foci of land which remained intact where the land mass was higher or larger; in these foci already transported plants are found as relicts and may have changed during their isolation.

This reasoning does not rest on phantasy; in mapping localities of mountain plants we can observe distributional patterns of plants which have evidently 'followed' mountain ranges, in Malaysia, in the Andes, *etc.* where at higher levels plant distribution is exactly comparable to that along insular isthmuses (see Willis, 1932).

The more chequered the history, the more ancient the bridge, the less we can expect survivors to be numerous, conversely, the more land is left, and the higher it is, the more links and survivors can be expected. And that is exactly the situation found in such islands as New Caledonia, New Zealand, and Juan Fernandez.

Dispersal over oceanic land-bridges is not precisely comparable to that over about equally large stretches of continental land, as both insular land-bridges and sizeable terrestrial isthmuses (let us say 500—1000 km wide) will generally have one longitudinal ridge or range from which short transverse rivers flow down on both sides. It will rather seldom occur, as in Alaska, that there are two ranges between which a river flows lengthwise over the land-bridge. Besides, it is reasonable to suppose that most transoceanic land-bridges must have been caused by upheaval connected with abundant volcanic phenomena. Such conditions will not or hardly slow down dispersal in plants, but they will do so probably for certain animals, freshwater fishes in particular.

I found it necessary to dwell in a general way on the existence of land-bridges, terrestrial and insular, and their functioning, in order to bring them from the hidden corner of imagination into the limelight of reality. We need to be confronted with them before entering on a discussion on the pro and con of the main topic of this essay, tropical transpacific connections in the past by means of land-bridges, isthmian or insular.

In the next chapter I will give the arguments in favour of the land-bridge concept.

10. ARGUMENTS IN FAVOUR OF TRANSPACIFIC DISTRIBUTION VIA FORMER LAND MASSES OR LAND-BRIDGES, ISTHMIAN OR INSULAR

I have arranged the theses and statements of this chapter, which rest partly on the foregoing considerations, under three headings: (i) axiomas, (ii) negative evidence, and (iii) positive evidence in favour of the land-bridge theory.

(i) Axiomas

(a) *Steady state principle.* — For reasons, explained in chapter 6, I have accepted the principle of the "steady state", *i.e.* that in overall aspect the situation of the continents, the axis of the crust, and the climatic zonation have not changed drastically at least from the Mesozoic era onwards; orogenesis, faulting, crumbling of continents, regressions, transgressions, *etc.* are of course fully admitted, as controlled by the law of isostasy. Fluctuations in temperature are admitted but at least from the Mesozoic onwards the development of the tropical flora has not been interrupted, and has been situated in the same equatorial region where it is found at present. Climatic zonation is bound to cosmic factors (rotation of the globe on an oblique axis) and has therefore necessarily persisted throughout the earth's history, with the polar circles and the tropics of Cancer and Capricorn as fixed boundaries. The idea of a once *uniformly* warm earth is therefore as unacceptable as that of a once uniformly worldwide temperate climate, ushered rashly by Darwin in order to explain the tropical mountain flora but soon suppressed. The secular, universal cooling since the early Tertiary, and culminating in the Pleistocene Ice Age caused a telescoping of the zones, probably slightly narrowing the tropical zone, more narrowing the subtropical to warm-temperate zones, but widening the temperate and polar zones. See p. 271—281 and 321.

Continental drift and polar shift are rejected at least for later stages in the development of the earth; Palaeozoic and older shifts are irrelevant to our problem. See p. 314—322.

(b) *Plant taxa as thermometers of the past.* — Stenotherm plant genera and families have not changed their thermo-ecological potentiality through the ages. Large plant groups now restricted to the tropics and not showing the potentiality of producing microtherm species either altitudinally in the tropics or latitudinally on the northern or southern hemisphere, have evolved as megathermous stocks and have retained this restricted ecological amplitude. Conversely large groups were from the beginning microtherm; in entering the tropics they had to escend the mountains. See p. 285—290.

(ii) Negative evidence

(a) *Transoceanic dispersal,* leading to transoceanic distribution is unacceptable for constituents of the tropical rain-forest, both physically and ecologically. Guppy's idea that dispersal methods of plants were more effective in ancient time is without the slighest evidence and is untenable under the principle of uniformitarianism. See p. 292—314.

(b) *Polyphyletic origin of now transoceanic taxa,* amphi-transpacific and amphi-transatlantic, is for the great majority of disjunct tropical groups not acceptable. And even if the possibility might be admitted, it will not lead to an acceptable explanation as it means pushing the problem back towards a more remote past, *viz* the problem of the transoceanic or pantropical distribution of their progenitors. See p. 281—286.

(c) *The relict hypothesis, i.e.* that groups may be at present tropical amphi-atlantic or amphi-pacific but were formerly pantropical is feasible for a certain amount of cases but has in all probability not been universal for the disjunct groups.

Even admitting the possibility for all groups it will not give an explanation for transoceanic distributions, neither across the Atlantic nor across the Pacific, as it raises the problem how the groups became pantropical, for which anyhow transatlantic distribution must be assumed. See p. 290—292.

(iii) Positive evidence

(a) *Number of amphi-transpacific disjunct genera and higher taxa.* — From the lists in chapter 2 the following figures have emerged:

Amphi-transpacific	Number of cases	Number of supra-specific affinities
(ii) *North subtropical-warm-temperate*	115	17 = 15 %
(iii) *Tropical transpacific*	80	39 = 49 %
(iv) *South subtropical and warm-temperate*	23	6 = 24 %
(v) *South temperate*	62	4 = 6½ %
Tropical amphi-transatlantic (from Engler)	81	

Although it is true that the transtropical group is numerically smaller than the north subtropical-warm-temperate type, its number is surprisingly large. There must be still more cases, specially on the supra-generic level, which I have not yet unearthed. In 'weight' it exceeds the north subtropical-warm-temperate group as it contains more groups of a higher taxonomical level (couples of genera, tribes and even families) than the other types, indicating that the tropical connection must have been ancient and have allowed for later phylogenetical development. Only a single species [*Cynoctonum mitreola* (L.) Britt., Logan.] is common to the tropics of Indo-Malaysia and tropical America; a very close situation is that in the genus *Spathiphyllum,* Arac., (*map 5*), a case which is outstanding in taxonomic clarity. The number is still more significant if one ponders on the details of the chequered history as such badly functioning insular isthmuses must have had, and in that light it appears remarkable that any plant group has succeeded to proceed, admittedly slowly and step-wise, across this immense distance. In that light the list as presented here is what could be expected from a laborious extending of plant distribution.

It is highly significant that the number of amphi-Pacific distributions are of the same order in the three main zones, northern, tropical, and southern, although at present only the northern Beringian area shows enough land for an approximate explanation.

(b) *Engler's figure for tropical amphi-transatlantic distribution.* — Engler (1905) has given a detailed survey of the facts assembled of transatlantic distribution. I have carefully scanned this list and have come to about 80 cases, a figure which, although slightly larger than the tentative one for the Pacific, appears perfectly well in order.

The geographical situation in the Atlantic is not so much different from that in the Pacific, with some island groups (Cape Verdes, Ascension and St. Helena) and a minimum distance of *c.* 3000 km between the mainlands.

In character the list shows a marked similarity with that of the Pacific; gravity centres are either American or African; taxa differ in status, in many cases genera divided between the two continents, but sometimes allied genera, tribes, or families are concerned. The number of species occurring on both sides of the Atlantic is larger than in the Pacific where there is only one. In a few cases genera are wider spread and have a stray representative in India (for example *Rhipsalis,* Cact.).

I conclude that the similarity is significant; the fact that the number of amphi-transatlantic tropical cases is larger may be accounted for by the fact that Engler did not segregate the affinities into tropical and subtropical.

If pantropical or circumtropical distribution had been brought about only by the trans*atlantic* bridge the number of cases of *amphi-transatlantic* distribution should have been very much larger. Even admitting that the number of pantropicals has been higher in the past but has decreased through the desiccation from which Africa has suffered, the cases of amphi-transpacific distribution remain so significant by the very close affinity between many West and East Pacific members that they cannot be explained by assuming them to represent the terminals of former trans-African ranges.

(c) *Balanced situation.* — The amphi-Pacific floristic relationships form in many respects a well-balanced whole in which the transpacific relationships are clear and understandable, in all zones, temperate, subtropical and tropical on both hemispheres. They smoothly intergrade and although the number of cases is higher at higher latitudes, they are all of the same order.

The small numerical preponderance of disjunctions of the type north of the equator over those south of the equator, in proportion of 115 to 80 + 23 = 103, is in accordance with the larger land surface on the northern hemisphere and the larger gap between the southern land masses; it is precisely what could be expected.

(d) *Symmetry pattern.* — There is therefore a marked symmetry in the floristic composition in all zones, from the tropics towards the northern and towards the southern hemispheres. See also *map 9.* Discrepancies on the northern hemisphere (high latitudes for subtropical plants in Japan, absence of many of such taxa in West and Central North America) can easily be explained by the mild climatic situation of Japan and by the shift caused by the Glacial Epoch; this is sustained by the palaeontological record.

(e) *Symmetry in migration tracks of microtherm genera.* — The balanced position is strengthened by the descending of both North temperate and subtropical genera and those of the South penetrating into the tropics by ascending the mountains. In this way these elements are also found in a markedly symmetric bi-hemisphere position; South Pacific genera (*e.g. Dacrydium,* Conif., *Lobelia* § *Pratia,* Camp., *Nertera,* Rub. *map 14, etc.*) stretch over very large uninterrupted distributional areas even over the tropics to SE. continental Asia (see *maps 9, 11—15*). North Temperate genera extend along the same way southward towards Borneo, Java, and New Guinea (*Trisetum spicatum* (L.) Richt., Gram., *Primula,* Prim., *Distylium,* Hamam., *Potentilla,* Ros. *etc.*) (*map 2*), but they extend beyond New Guinea to similar high southern latitudes if compared with the high northern latitude reached by the southern genera. A similar picture is obtained in the Americas with areas extending southwards from the north and areas extending northwards from the south, although the latter seem seldom to have gone further north than to Mexico.

(f) *Fossil record in place.* — The reliable fossil Pliocene and Miocene record shows that in the Malaysian tropics the *Dipterocarpaceae,* identical with or closely allied to the living genera and species, are found precisely in the place where the family reigns today, showing that the Malaysian tropical flora has perpetuated dominance at least since the middle Tertiary. The fossil record of *Nothofagus,* as established in New Zealand, Australia, and New Guinea shows also that it is exactly in place and has in New Zealand perpetuated even since the Upper Cretaceous.

(g) *Atlantic and Pacific disjunction of the megatherm families. Maps 16—18.* — In chapter 5 (see p. 267) a very brief account has been given of the fact that a large number of pantropical families are strictly megatherm, or almost so, and that many other families with a wider thermo-ecological tolerance contain many hundreds of genera which are strictly megatherm and pantropical in range. It has been argued that they cannot have circumpassed the Atlantic and Pacific oceans through temperate or warm-temperate climates (see p. 272, 290). It has also been found impossible to assume a three-phyletic origin of all these families and genera (see p. 282). As among these pantropical groups almost all basic types of the Phanerogams are represented, they must be very ancient, and they, or their ancestral stock, must have been already developed when the transoceanic distribution took place.

It would seem that the (now pantropical) proto-groups must have migrated first and that the amphi-types were the last to make use of the transoceanic bridge(s) before the latter disintegrated.

One might assume that one bridge would then be sufficient, for example that over the Atlantic. But this is most unlikely because of the fact that the amphi-types of the Pacific are so striking, and of the same weight as those of the Atlantic.

(h) *Gravity centres.* — In the case of *Spathiphyllum,* Arac. (*map 5*), the gravity centre is decidedly in the American tropics, notwithstanding the occurrence of the monotypic allied genus *Holochlamys* in New Guinea. The reverse may also be true when the preponderance of morphological development and speciation lies in the Old World Tropics, *e.g.* in *Schismatoglottis,* Arac., of which *c.* 80 species are confined to Malaysia with a few in the Indo-Chinese Peninsula and only 2 in tropical America (forming a separate section). A similar case is *Homalomena,* Arac., with *c.* 60 species in Malaysia, 5—10 in tropical continental Asia and a few forming a separate section in tropical America. An American preponderance is also found in the *Moutabeae,* Polygal., *Joannesieae,* Euph., *Trigoniaceae, Guadua,* Bamb., *Ichnanthus,* Gram., *Xylosma,* Flac., *Hedyosmum,* Chloranth., and *Heliconia,* Mus., and will be significant for the probable origin of these groups. In small groups there is sometimes hardly a gravity centre, *e.g.* in *Cynoctonum* (*map 7*), *Gelsemium,* Logan. (*map 6*), *Corsiaceae,* and *Oreocallis,* Prot.

(i) *Living evidence of tropical and subtropical land-bridge relicts.* — In chapter 4 it has been shown that in all climatic zones there is a certain number of the amphi-transpacific genera represented in the Pacific Islands. The more land there is, especially the more high islands there are, the larger is the number of such representatives; this land is, therefore, mostly found in the islands west of the Andesite line. Buit the relict stations are also found in Polynesia and even further southeast. Some genera are represented only by one species, others have more species. In the *Saxifragaceae-Hydrangeeae* there is even an endemic genus in Hawaii. *Perrottetia,* Celastr. (*map 4*), shows only one intermediate station, but *Nicotiana,* Sol. (*map 8*), has a number of such stepping-stones. On the whole, however, these relicts form only a fraction of the original assemblage which has obviously been heavily splintered, retaining isolated refuge stations here and there, as for example what Diels and Skottsberg have called the 'Old-Oceanic' element.

The main point, of *essential importance,* is *that in all the zones plants which we might fairly expect to find in view of a former land connection* *are really present.* In the North the little land there is (Bonins) has such plants, in the tropics the percentage is fairly low, but significant, in the South Pacific it is abundant.

Some are of course clearly direct relicts of the original assemblage but others have apparently undergone evolutionary change and became very different from the original stock, as possibly the lobelioid *Campanulaceae* in Hawaii and many endemic genera of other families. There may also be secondary invaders which have dispersed over parts of the bridge after it had decayed, mostly from the West. This makes the situation extremely complicated because of our ignorance why certain groups are vigorous and evoluate and others are less virile and get extinct. It will cost a thorough study of particular groups to unearth some illustrative detail, but we can hardly expect to get much detailed insight into the vicissitudes of terrestrial and environmental conditions and of the history of the plant groups and correlate these into a satisfactory overall synthesis.

A similar situation is found with the *pantropical genera;* they also are represented in relict stations on the oceanic islands, evidently in greater number than the amphi-oceanic genera.

That the number of the land-bridge relicts of the ancient flora is proportionally low is doubtless tied up with the fact that evidently almost nothing of the original tropical bridge has persisted, even the high islands being largely later formations on which some of the plants found a secondary refuge. The situation is still more complicated because relict species will in the course of time have encountered opportunity for resuming active dispersal, either by short-distance island-hopping, or over new or changed terrestrial continua. It is not at all certain for example that the three oceanic stations of *Spathiphyllum,* Arac. (*map 5*), *viz* in Palau (Micronesia), Bougainville (Solomons), and Cocos I. are original ones; they may have originated secondarily from the Malaysian and American mainlands respectively.

From this would follow that several plant taxa must be much older than the bedrock formation on which they grow now. My pessimism towards gaining more detail knowledge is borne from the inadequacy of the factual record and the immense time involved. We will never be capable to reconstruct the complete story of the steadily changing situation during bygone ages and must be satisfied with a hypothetical broad outline.

(j) *Living evidence of temperate South-Pacific land-bridge relicts.* — In chapter 4 it has been shown that of the amphi-transpacific cases of list v all except two are found in New Zealand (sometimes with endemic speciation) and adjacent islands (Norfolk, Lord Howe, Chatham, Campbell, Kermadec Is.), and mostly also in Tasmania. See *maps 10—15.* I am prepared to accept New Zealand and Tasmania, both as to land and flora, as relict parts of the original South Pacific land-bridge of which the main course must of course have been situated at higher latitude.

(k) *Proportion of land surface and relict centres.* — In the over-all picture it appears that the more land there is, the more species are represented in any of the five transpacific zones here distinguished. This would appear natural in West Pacific islands situated within the "Andesite line", a geological boundary accepted as the former (now fractured) continental frontier of Australia, Malaysia, and Asia. These islands would represent smaller and larger sial blocks left in the marginal area of subsidence and faulting (New Zealand, Fiji, New Caledonia, New Hebrides, Solomons, New Britain, Formosa, Ryukyus, *etc.*). Such islands would have a much richer stock, part of the original flora or its later products and not derived from subsidiary dispersal. But the same holds also more or less for old truly oceanic basalt (sima) islands, some of which may have made part of the early land-bridge.

(l) *Preponderance of Indo-Malaysian flora in western half of Pacific.* — From this it is conceivable that whereas the amount of land in the western half of the Pacific is far greater than in the eastern half, Merrill (1936, 247) said that "the flora of Polynesia, whether we consider that on the high or the low islands, is Malaysian in origin, with certain characteristic Australian elements which also occur in Malaysia and particularly in Hawaii, with a small admixture of American forms". Hooker (1859, lxxxvi and xvi, footnote) already pointed to the Malaysian-Australian nature of the Polynesian flora. Van Balgooy (1960), who could fully confirm this thesis, has found the preponderance of the Indo-Malaysian element in the Pacific not counterbalanced by a proportional increase of the American element in proceeding eastwards. Obviously the western end of the insular land-bridge functioned much better in that it lasted longer or consisted, and still consists, of more land. Van Balgooy (1960) has demonstrated the striking fact that the Central Pacific flora is largely derived from Malaysia which moreover extends its influence on the southern hemisphere to the Tropic of Capricorn, where one would expect to find Australian influence. This can partly be ascribed to the fact that of course Malaysia is partly situated on the southern hemisphere to *c.* 10° S, but mainly, I think, to the fact that the amount of rain-forest in Queensland is in size not comparable with that of Malaysia. And it is especially rain-forest plants which would climatically have fitted isthmian foci, for which monsoon plants and arid country plants from Australia would have been unfit ecologically.

On the other hand it must not be forgotten that the high islands and mountainous isthmuses must have been subject to the trade winds and therefore must have had dry leesides, similar to those which are now found in several of the Polynesian islands. They should have offered the drought niche required by the Australian drought element.

(m) *Land-ridges in the East Pacific.* — The extent of land in the eastern half of the Pacific is negligeable at present, but it is extremely doubtful whether it has been so all through the past. Most of it has long been accepted to be flat-bottomed ocean deep, and observing the tiny specks of coral islands and atolls we little realize what gigantic structures underlie these specks, specially those bearing the large atolls of hundreds of miles diameter. It has appeared that there must be a multiple of volcanic mountains which are submerged and whose summits, either conical or flat (guyots), are situated between 500 and 2000 m below the level of the sea. From the survey by Menard (1960) on the research of the East Pacific Rise (*map 19*) it clearly appears that the structure of the Pacific Ocean bottom is far more complicated than assumed before and that there are anticlines bearing arcs of submerged volcanoes over immense distances; the East Pacific Rise is said to run from New Zealand to Mexico. According to that report the Hawaiian group was also born on such a submarine ridge, the Mid-Pacific Ridge (*map 20*), but that ridge was obviously far more ancient and has almost entirely disappeared by immersion (following isostatic readjustment through crustal convection currents in the mantle?); it can of course not have disappeared by erosion, a process which is almost unknown undersea. These findings, which are just the beginning of deeper knowledge of the Pacific Ocean bottom, are promising evidence for the ancient crumbled isthmian or insular land-bridges the plant geographer has designed in order to explain past and present plant distribution. See chapter 8.

(iv) Conclusion [1])

In conclusion I believe to have shown that by accepting two axiomas and ruling out certain possibilities by negative evidence, there is an abundant positive evidence in favour of accepting the land-bridge theory.

In accepting this I have tried to fathom the minimum requirements plant geography needs in that respect in order to have a rough idea of the genesis of the angiospermous distribution.

In addition I had to try to give some idea about the age, size, and duration of these former land masses, insular or isthmian and the result of this exploration is embodied in the next chapter and illustrated tentatively by *maps 21—24.*

11. POSSIBLE AGE OF THE LAND-BRIDGES

The approach to the problem of the age of the land-bridges, and their duration, can of course only be very tentative. The answer to it depends also

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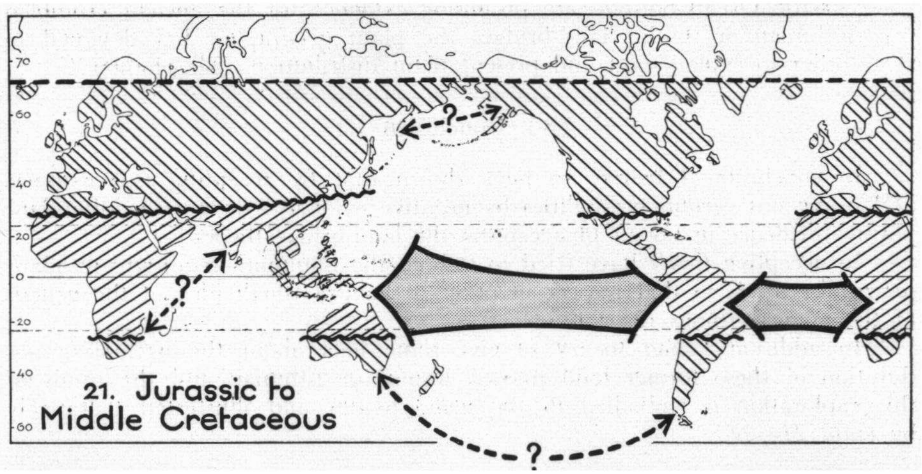
[1]) Professor Florin (1962) has just finished a large study on conifer and taxad distribution in time and space, in which he has critically sifted factual material and in a masterly way synthesized his immense knowledge of this group, fossil and living. I enjoyed the singular privilege of studying his MS which, though based on entirely different material, shows an imposing degree of similarity with the views attained in this essay. Basing himself on the principles of the steady state and limitations of dispersal, Florin has assumed that vertical crustal movements have repeatedly and often considerably changed the surface features of the earth in many regions. Virtually he is an adept of the land-bridge theory by accepting in addition to the Beringian and Panama bridges, three Mesozoic land-bridges also designed in the present work, viz the North Atlantic, Lemurian, and South Pacific Antarctic bridges. From the fact that conifer and taxad genera are and were thermo-ecologically largely subtropical to temperate he has no need of tropical land-bridges, except the Lemurian. A remarkable fact appears to be the early bi-hemisphere symmetry in the development of the conifer and taxad genera maintained till the present day, a further argument in favour of the steady state. Florin attaches great importance to the long role of the Tethys Sea which should receive in future full attention in angiosperm plant geography.

on the question about the age of the phylum Angiosperms and the time needed for their development and expansion over the globe. This must have taken a very long time. The definite progress made in phytopalaeontology indicates that their ancestral stock is far more ancient than formerly understood; in the Middle Cretaceous they were in full development and their origin is by several other authors tentatively dated back to the Jurassic (Edwards, 1955), and their first beginnings even to the Permo-Triassic.

Among the amphi-transpacific affinities shown in chapter 2 the disjunction is either between a number of species on one side of the Pacific and the rest of the species on the other side, or the affinity concerns different sections or genera on both sides. It is significant that the latter, supraspecific affinities attain their highest percentages in the tropical and south subtropical zones, as appears from the following figures: north warm-temperate-subtropical 12 %, tropical 43 %, south subtropical 25 %, south temperate 3.2 %.



Map 21. Mesozoic. Tentative situation of land-bridges when the early Angiosperms attained their pantropical distribution. Broken lines and question marks indicate that there may or may not have been narrow insular land-bridges in Beringia, Antarctica, and the Madagascar-Ceylon area.

In this and following three maps the approximate latitudinal extension of the tropical and subtropical to warm-temperate climatic zones has been indicated by different hatching. No attempt has been made to approximate the palaeogeographical delineation of the continents in each epoch.

It seems to me that these figures are a reflection of the different age and duration of the land-bridges in the different zones, that of the tropical zone being the oldest disintegrating earlier than the others. The south temperate zone shows a remarkably low percentage. This may be connected with the much poorer flora of the south as compared with that of the north, since for other reasons the South Pacific bridge cannot have been geologically very young.

Though primarily intending only to cover the problem of land-bridges in the Pacific basin, it was found that the situation there cannot be divorced from similar problems in the Indian and Atlantic Oceans. In my opinion the tropical transatlantic land-bridge advocated by Engler must be of about the same age as that in the Pacific.

The Central American land-bridge is of course not under dispute and the Panama isthmus has served, with intervals, to join the Americas; Caribbean connections may also have existed, but this matter lies outside the scope of this work.

There has probably also been a North Atlantic land connection at some time (Engler, 1879), but I am not sufficiently in command of the phytogeographical relationships of the boreal Atlantic to judge its necessity and minimum dating. Florin (1962) finds it compulsory for the explanation of conifer and taxad distribution.

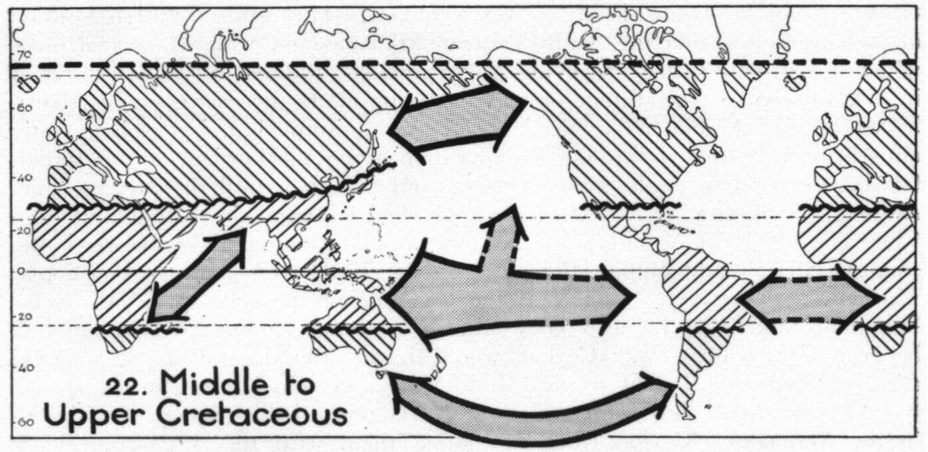
Furthermore there must have been an isthmian connection between Madagascar and Ceylon over the Seychelles-Comores bank ("Lemuria"), as the other solution for this affinity is very unlikely. This other solution consists of the assumption that the South Tethyan Madagascar-Ceylon-Malaya affinity, which is a striking fact in the living Angiosperms — though still to be examined in detail — was in the distant past also thriving along the east coast of Africa, in Aethiopia, Arabia felix, Persia, and Afghanistan, but has subsequently entirely been destroyed through a desiccation along the borders of the Indian Ocean which set in in the Early Tertiary and persisted until the present time. Although it is true that a *Dipterocarpoxylon* is found in Somaliland (see Chiarugi, 1933) it would seem strange that no living links between the tropical African and Indian floras are found in the wet parts of Aethiopia. This alternative is very unlikely as the dry zone of the subtropics has always been there and is, as far as I know, due to a cosmic cause. An isthmian link between Madagascar and Ceylon would have offered, conversely, a good climate for distribution of tropical Indo-Malaysian rain-forest plants.

Engler (1882) has hinted already at the remarkable botanical affinities in the Madagascar-Ceylon tract correlating them with the submarine ridge-system in the Indian Ocean. Florin (1962) finds an ancient Lemurian land connection or bridge essential for a proper understanding of the distribution of conifers and taxads south of the Tethys Sea.

I have added these two land-bridges to complete the picture of the major changes in land surface which plant geography needs in order to give a rough outline of the genesis of the Angiospermous flora of the earth. I have summarized my ideas in the four *maps 21—24.*

(i) **Bering Bridge.** — It seems certain that most of the Bering Bridge was land during the Upper Cretaceous and Tertiary (Haag, 1962); during the Pleistocene the bank became shallow sea. The isthmus is situated between 60 and 70° NL. During the Late Tertiary the climate was too cold for the survival of the warm-temperate disjunct E. Asian-N. American element, which must then have gained its range in the warmer Early Tertiary (Reid, 1915), or in the Upper Cretaceous. Most of the time the cold polar surface current now running through Bering Strait was probably absent and the ameliorating effect of the Kuro Shio current will have exerted more influence than in the Pleistocene. As the Beringian isthmus was obviously some 1000—1200 km wide, its southern area will have been suitable for warm-temperate genera and its northern border and mountains for temperate and boreal plants. It is not impossible that certain subtropical genera could migrate stepwise along its southern shores. The Kuriles have probably also served as an insular land-bridge, but possibly never formed a continuous land.

(ii) **Marianas Bridge.** — There must also have been land-bridge connections for Micronesia, but this land-bridge ended blind south of the Bonins, as the flora of these latter islands is very distinctly Holarctic being almost entirely Japanese. The Micronesian flora is entirely Malaysian and whereas it shows distinct affinity with East Malaysia, especially the Philippines, it can be envisaged as an East Malaysian peninsular bridge or extension in north-eastward direction. There is no special reason why it should be early; species from the Carolines and Marianas might well have originated over relatively narrow, and possibly insular isthmuses. The necessary land-bridge is tentatively dated in the Tertiary and its course must have been eastward of the Philippines and northward of the Moluccas and New Guinea. It had probably connections with the western extremity of the tropical transpacific bridge which was then in its latest phase.

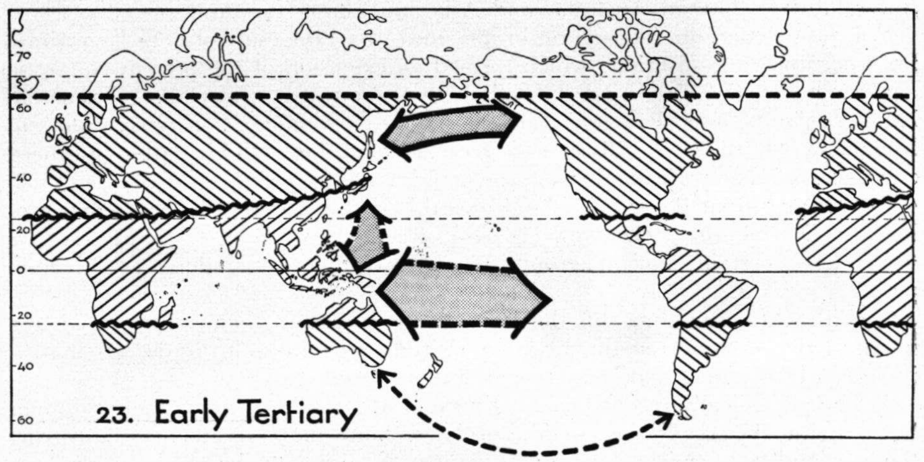


Map 22. Middle to Upper Cretaceous. The trans-Pacific bridge broke down in the East Pacific, and became an insular isthmus in the Central Pacific with a similar extension towards the Hawaiian area; the trans-Atlantic bridge crumbled to an insular isthmian condition; the Beringian, Subantarctic and Madagascar-Ceylon bridges were in full swing.

(iii) **Tropical Transpacific Bridge.** — First it should be said that, because the pantropical families which constitute the major display of morphological development of the Angiospermous plant world and include both 'primitive' and 'modern' groups, one cannot escape the idea that at the time of the functioning of the transatlantic and transpacific land-bridges the Angiosperms must have already reached a high state of development and differentation. This was obviously the case in the Cretaceous and might have been so even in the Jurassic; the more becomes known about fossils, the earlier all groups seem to have their root.

The tropical transpacific bridge must, it seems, have been very ancient and effective — by size and duration — in having given opportunity for dispersal to the still pantropical Angiospermous families or their progenitors. This phase fell probably in the Jurassic or early Cretaceous. The bridge has probably been largely at or south of the equator where there are distinct isolated vestiges of crumbled continental masses.

The tropical transpacific bridge cannot have been a narrow isthmus, because it is most unlikely that the huge mass of almost all Angiosperm families in their early stage could spread effectively under the hampered conditions of a narrow isthmian link. It has probably approached the nature of an insular isthmus similar to the Malaysian arc connecting at present the Asiatic and Australian continents.



Map 23. Early-Tertiary. The trans-Atlantic bridge has disappeared; the trans-Pacific bridge has crumbled to insular-isthmian condition still connected with the West Pacific continents; the latter have an insular isthmus towards Micronesia; the Subantarctic bridge is reduced to a narrow isthmus of islands; Beringia is still a well-functioning bridge; the Madagascar-Ceylon bridge has disappeared.

Because of the fact that the Old World flora in its Indo-Malaysian facies is reaching so far into the Pacific it would seem likely that the connection in the *East* Pacific broke down first and early, and gradually decayed towards the West, enabling Indo-Malaysian advanced types to remain dispersing eastwards into the West and Central Pacific for a considerable period.

Taking into consideration that the Andes must represent a formidable geographical and ecological barrier to the distribution of tropical lowland rain-forest plants it is clear that the pantropical distribution must have been settled long before the origin of the Andes. This is in agreement with the dating of the North-South Andean distribution of temperate genera which must have taken place in the Tertiary, as suggested on p. 261.

Along the southern side of the transpacific land mass part of the subtropical element may have come along simultaneously, but in much smaller quantity than the tropical.

At some time, but rather early, the tropical bridge had a northern blind extension of isthmian link towards Hawaii, which is justified by the distinctly ancient features of the Hawaiian flora. This was, probably, of relatively short duration.

(iv) **Subantarctic Bridge.** — The Subantarctic bridge must have been a rather wide one, and in the Cretaceous and Early Tertiary it must have harboured a flora running from warm-temperate to cold, ecologically more or less comparable with that of the combined Types II and I of the higher northern latitudes in the Pacific. It is not impossible that the northern shores of this bridge could even serve for a transpacific exchange of a substantial part of the now southern Pacific subtropical element. The microtherm element spread northward in all available directions ascending the mountains towards lower latitude both in Australia and Asia, and along the Andes.

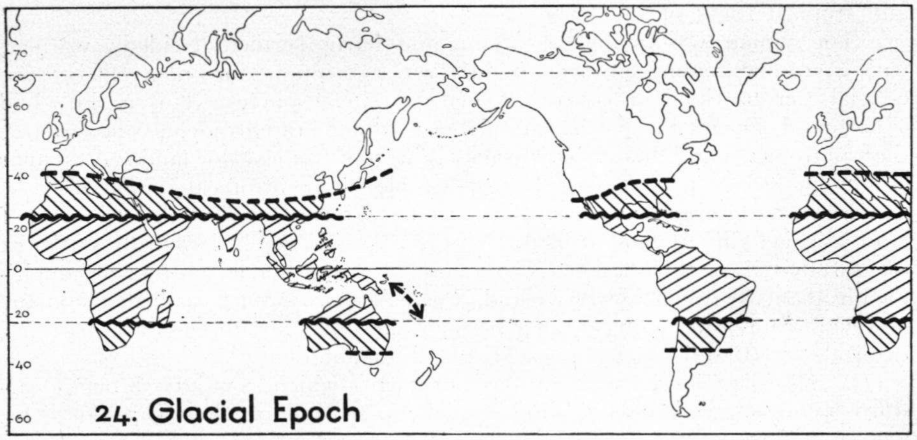
I prefer to join Skottsberg in his idea that this subantarctic temperate flora occupied a land-bridge which formed an extension of the present Antarctic continent between 50° and 60° SL, connecting SE. Australia, Tasmania, New Zealand, and Patagonia; in the west extending northward also to Melanesia (Lord Howe Rise and Kermadec Ridge). This latter northern extension of New Zealand was the only land connection Wallace (1880, 465—468) postulated for this island and this is still a current idea among zoologists (Darlington, 1957) and is also accepted by Godley (1961, 1) for vertebrates, certain ancient groups of earthworms and spiders, and certain plants.

With the crumbling of the transpacific southern hemisphere land the subantarctic element remained where latitude permitted it to do so, that is in isolated positions, and montane at lower latitudes.

The geologically recent Glacial Epoch in the southern hemisphere wrought havoc with the vegetation of the isolated land mass fragments, destroying the lowland subtropical and warm-temperate flora to be replaced by the microtherms which descended from the mountains from where they were driven by the southern glaciation. There is reason to assume that the telescoping effect of the Glacial Epoch at southern high latitudes was similar to that at high northern latitudes. However, in the north far more land was available for migration southward, whereas insular conditions prevailed in the subantarctic, save in South America and in Tasmania-Australia where the vegetation had opportunity to escape northward, both for microtherms and mesotherms, ascending with lower latitudes.

If we may again accept the fossil record to be trusted, and if Cretaceous and Tertiary fossils of *Nothofagus*, Fag., *Cunoniaceae, Araucaria*, Conif. *etc.* were derived from trees growing in the same place and altitude where the fossils were found, the margin of the Antarctic continent between 60°—70° SL could have had a temperate forest at the same latitude as Alaska in the Tertiary. This temperate flora which must have been subsimilar to that now found in Tasmania, Victoria, and New Zealand, was montane at lower latitude (for example in New Zealand) and subalpine in the subtropics. But the northern extensions or borderland of the Antarctic continent had already crumbled away at that time and during the Glacial Epoch the telescoping of the climatic zones took hence place in the isolated islands and land blocks separately without escape migration possibility! I would tentatively conclude that the land mass connections along the northern border of Antarctica must also at least date from the Lower Cretaceous and crumbled up onwards of the Upper Cretaceous, as was already suggested by Hooker, Hutton, Engler, Von Ihering (1893), and others.

It is true that the percentage of the south temperate supraspecific affinities tabulated in chapter 3 is only 6.5 % which is much less than in the holarctic warm-temperate where it is 15 %. This difference might lead to the conclusion that the South Pacific land-bridge offered great difficulty for migration, either because it was narrow or much broken up, or of short duration, or that the bridge was effective only in a more recent epoch. But the situation should be given justice by considering, first, that the fossil record points to its Cretaceous age, second, that the amount of land surface and richness of the South Pacific flora is, and probably was, much less than in the holarctic North Pacific, and third, that therefore migration possibility and refuges for a formerly South Pacific flora during the Pleistocene Glacial Epoch were much less than in the north.



Map 24. Glacial Epoch. Of all the bridges only a slight indication of a narrow insular isthmus is still present in Melanesia; climatic zones have been severely telescoped.

The great age of the South Pacific affinity is also found for *Araucaria* sect. *Bunya,* Conif., which was according to Calder (1953) already found in the Middle Jurassic in Patagonia with the closest allied member still living in Queensland, *A. bidwillii.*

A similar distribution of fossil conifers of the genus *Athrotaxis* is found fossil in the Cretaceous and Tertiary in Patagonia, New Zealand, Tasmania, and eastern Australia.

12. GENERAL CONCLUSIONS

Amphi-transpacific distribution can be observed in the warm-temperate, subtropical, and tropical zones, in both the southern and northern hemispheres. Lists have been given of these amphi-Pacific categories. *See maps 1—8, 10—14.*

A comparison has been made of the tropical amphi-transpacific distribution pattern (*maps 4—6*) with that found by Engler for amphi-transatlantic tropical affinities; they are of essentially the same character and numerical order. These two patterns represent specialized cases of the pantropical type of distribution which is found in far more genera, tribes, subfamilies, and families. See *maps 7, 16—18.*

This pantropical type of distribution is interrupted by two oceanic disjunctions, and offers therefore one of the most intriguing plant-geographic problems, especially because island relict stations occur in these oceans.

The major aim of this essay has been to ascertain how these transoceanic affinities can be explained.

It must be concluded that plant distribution, past and present, cannot be understood and satisfactorily explained without accepting major physiographic changes in the distribution of land and sea, both in the temperate and tropical zones of the globe.

The climate was in the Cretaceous and Early Tertiary decidedly warmer, with a gradual cooling onwards of the Tertiary, culminating in the Pleistocene Glacial Epoch which of course affected both hemispheres. This cooling had a profound (telescoping) effect at higher latitudes, rapidly decreasing towards the subtropics and almost indiscernable in the tropical lowland. A similar but much feebler telescoping effect is feasible on the tropical mountains.

Even admitting a warmer Cretaceous-Tertiary climate, the amount of land as it is found at present in the Northern Pacific would be hardly sufficient for substantial interchange of warm-temperate and some subtropical amphi-Pacific plants between East Asia and North America. Such a warmer climate, however, cannot account at all for the other disjunct distribution patterns, tropical transatlantic and transpacific, and subantarctic.

A discussion is given of various arguments which could be brought forward against accepting land-bridges in the past, and of alternative solutions, notably a former tropical world, polyphyletic origin of now disjunct taxa, unreliability of plants as thermometers of the past, the relict hypothesis, active transoceanic dispersal, continental drift, and polar shift. These arguments have been found either futile for an explanation, even if one accepts them, or fallacious.

Accepting two axiomas, *viz* the steady state principle and a cautious use of plant taxa as thermometers of the past, negative and positive evidence is brought forward leading to the conclusion that the reliable palaeontological record and the living plant world in and around the Pacific forces us to accept land-bridges in the past as the only reasonable way to explain the present plant distribution, land-bridges which have either existed as extensions of present continents and were of subcontinental size, or have been large isthmian or insular arcs.

The ample considerations given on the subject of dispersal have shown that sympatric areas are not dependent on uniform means of dispersal and that assemblages of such sympatric plants have gained their distribution slowly and together. It has been concluded that the reach of successful dispersal (accessibility) of inland plants has often been greatly exaggerated, that it decreases geometrically with distance, and that only in exceptional cases distances up to *c.* 500 km can be covered. The probability of long-distance dispersal is assumed to be zero, consequently disjunctions of a 1000 and more km are always relict areas.

It is emphasized that the present plant world and its major geographical features are the result of an extremely long and slow growth which has in general a relict character. 'Progressive change' leading to extending or retreating areas was and is largely limited to countries and sites where major revolutionary changes of the environment, orographic, geographic, or climatic, take place, for example through orogenesis, regressions and transgressions, desiccation, glacial epochs, *etc.* The majority of the families, genera, and species show disjunctions in the area they occupy today and this relict character is not only found in the continental areas but also in the island floras. It is not only shown by autonomous organisms but also by those which live parasitic or symbiontic. It is not restricted to temperate floras but is also found in the subtropics and tropics where such changes were, however, not climatic. The occurrence of disjunctions cannot be correlated with dispersal mechanisms. In short, the amount of circumstantial evidence points indubitably to the fallacy of the diffusionist point of view to explain the disjunctions by progressive long-distance dispersal.

Whereas the pantropical set of genera and higher affinities of the Angiosperms was evidently already fully developed in the Middle Cretaceous, their dispersal must have taken place before that time.

As furthermore this distribution could only be gained by short-distance dispersal (up to *c.* 40—50 km, with a probability of dwindling at *c.* 200—250 km) it is evident that the primary pantropical distribution cannot have been achieved along narrow arcs of spaced and small islands. There must have been broad terrestrial connections or wide and sizeable archipelagos of nearly continental surface — almost comparable to the Malaysian archipelago connecting the Asian and Australian continents — to account for the origin of pantropical distribution. It is found that the hypothesis of such land-bridges is not inconsistent with the opinion of several prominent geologists.

Great attention is given to the occurrence of mid-oceanic ridges and rises which seem to be a regular phenomenon of all oceans. They have provided land but it is difficult to estimate how much land, its chronology, and its duration. The tentative conclusion of some geophysicists is that they were ephemeral in the geological time scale, but amply sufficient for permitting biological distribution. The Mid-Pacific Ridge is probably the most interesting approach towards problematic transoceanic land-bridges.

It must be admitted, however, that as yet geophysics have not provided sufficient support for the land-bridge theory. If they had, the present essay would of course have been superfluous.

At which period in the geological past transatlantic and transpacific distribution has taken place is difficult to ascertain and will also have been different for the different zones.

In the North the Beringian connection and Aleutian Arc provided in the Late Cretaceous or Early Tertiary more and continuous land by a bridge of at least 1100 km width under a considerably milder climate than that of today.

In its now temperate to polar counterpart, in the South Pacific, there would be required, besides a milder climate, a very much larger land surface with land masses or insular arcs connecting Tasmania and New Zealand along an Antarctic borderland with Patagonia, or, conversely, there must have been a substantial extension of Antarctica or a borderland of subcontinental size. Fossils of *Araucaria* and *Nothofagus* in the Tertiary in Seymour I. and in the Tertiary and Upper Cretaceous of New Zealand indicate that the land or land-bridge and the suitable climate must have existed at that ancient time.

For the interjacent North and South subtropical types and the tropical type itself, an equally ancient isthmian or insular connection must be postulated. Future geomorphological research of the bottom of the Pacific basin may, possibly, reveal more indications still left of such connections which have probably been situated mostly on or south of the equator, except in the area of Micronesia where they have obviously also been north of it.

If the land connections in the Beringian and New Zealand areas were wide enough, it is not impossible that both temperate and certain subtropical plants could have migrated together which would slightly simplify matters.

For the tropical transoceanic affinities, however, the latitude would be too high. There is no other possibility than postulating for them separate tropical land connections, in the Atlantic, and in the Pacific. Whether these bridges have consisted of sima or sial rock does, for plants, not matter at all.

Engler already pointed to the fact that in the transatlantic connections many groups of Angiosperms participate which represent taxonomically 'modern' or 'specialized' groups. The same holds for the transpacific set in which all kinds of groups participate, from the *Winteraceae, Annonaceae, Myristicaceae,* and *Fagaceae* onwards to the *Campanulaceae, Scrophulariaceae,* and *Compositae, Corsiaceae, Burmanniaceae, Araceae, etc.*

From this it can be derived that the whole of the Angiosperms must have already been developed when these ancient distributions took place, both for the transatlantic and transpacific tropical and for the southern connections.

From this again one would gain the impression that it is not obvious that the evolutionary sequence as based on typological-morphological considerations can directly be correlated with the age of the different groups, in other words that there might not be such great differences in age between, say *Magnoliaceae* and *Scrophulariaceae* or *Liliaceae* and *Araceae,* as is inferred on typological-morphological grounds. From their geographical area it appears that genera as *Geum, Euphrasia, Primula, Spathiphyllum, Ficus, etc.* are really of great age, however 'modern' or specialized their aspect may be on the grounds of comparative morphology. It would seem that they are *all* very ancient and the impression is that many 'structural plans' of the Angiosperm orders were in principle already present in the differentiated stratum from which they developed towards the angiospermous condition. The array of orders may have taken place during a relatively short geological period.

I feel strengthened in this tentative conclusion by my analysis of the genus *Nothofagus,* Fag., the species of which can, on typological characters, nicely be arranged in morphological series, but to which I commented that the relative age of the scheme of morphological interrelations should not *per se* be regarded as a measure for the antiquity of the stages or species concerned.

It seems likely that the pantropical angiosperm families or their immediate forerunners had ample opportunity to gain their pantropical position and that at that time the transtropical bridges must have been in full swing.

Most amphi-groups were evidently among the latest to cross the oceans, either Atlantic or Pacific, either W—E or E—W. Those which possess on the other side only one species must then probably be reckoned among the latest migrators of which only one pioneer species succeeded before the crumbling of the bridge started.

This would exactly fit in with the situation which could be expected if distribution would have taken place along a land-bridge with shortcomings. Such a land-bridge can be imagined to have been one broken up into ridges and islands and that more than once through the ages, never to form one continuous broad strip of land. Such conditions, deficient for abundant plant dispersal, would permit single species to slip through and this would lead to a limited supply of genic material on the other side of the land-bridge. This limited supply would then in all probability not lead to a conspicuous secondary centre of development, as the condition for the differentiation of such a centre should be a sufficient potential gene reservoir which, through isolation, crossing, mutation, selection, and whatever other agent, may be responsible for such a development.

In chapter 11 it has been tried to summarize in a very global way the minimum amount of major land-bridges, their age, and duration, which would be required in historical plant-geography towards an approximately satisfactory explanation of the major frame work of present plant distribution of the world's flora. This discussion is illustrated by the schematic *maps 21—24.*

13. ZOOGEOGRAPHICAL CORRELATION

I have purposely refrained from weaving data derived from zoogeography in my essay and originally I had no intention to touch on it, although it is of course clear that the plant and animal kingdoms have developed simultaneously, and that their histories are partly parallel or interwoven: animals rely in last instance on plants for food (and often shelter), conversely the higher plants depend to a certain degree on animals for dispersal and pollination; besides they share some methods of dispersal.

This decision was primarily due in realizing my insufficient insight in the immense amount of zoological facts of both the present and past faunas, their ecological and geographical implications, and the interpretations based thereon. Such trespassing on another field of science may easily lead to erroneous deductions and obscure the reasoning of the restricted issue one wants to pursue.

Furthermore, there is a distinct difference between phyto- and zoogeography by the fact that most animals possess *active motility* and therefore show types of accessibility unknown in the plant kingdom. The groups of higher rank have also often a much wider thermo-ecological amplitude, and a much more varied pattern of propagation and dispersal behaviour. The variety in form and life cycles is also much less uniform than in the plant kingdom. Finally, zoologists attach basic importance to competition for selection, succession, and evolution, a line of thought less popular with botanists who think more in terms of autonomous evolution and distribution, modelled and modified by changes of physical and/or climatic environment.

It is clear, however, that if there have been land-bridges they have been used by both plants and animals. From this follows that 'botanical' land-bridges must not be in conflict with 'established' facts of zoogeography. For that reason I have yielded to the pressure of my zoological colleagues of the 'Rijksmuseum van Natuurlijke Historie' at Leyden to see in how far there is agreement or conflict respectively between the main trends of the chorology of plants and that of animals. They advised me to consult for the purpose the zoogeography of the Vertebrates by P. J. Darlington Jr (1957). I would have liked similar surveys on insects and land- and freshwater-molluscs, but they seem not available.

As already alluded to on p. 270 the *rapidity of evolution* in the animal kingdom seems in most groups to be much higher than in the more conservative and monotonous plant kingdom, and extinction more complete. This leads to a rather serious implication, because, whereas it seems reasonable to assume that the frame of the present plant-geographical pattern of the Ferns and Spermatophytes was mainly established in the Mesozoic, it seems, according to Darlington (1961, 597) "that the existing Vertebrates, except perhaps some fresh-water fishes, can tell little directly about Mesozoic geography. For the most part, their distributions are Tertiary or later. Zoogeographic evidence about the Mesozoic must therefore come mostly from fossils. But the evidence of fossils has to be interpreted by comparison with existing distributions, and interpretation is not an easy matter".

"The Mesozoic was the age of Reptiles. Dinosaurs were the most conspicuous, best-known, and therefore most significant land animals. The Mesozoic saw also the endings of several ancient groups of reptiles and the beginning of crocodiles, lizards, turtles, and snakes. There were reptiles in the sea and in the air as well as on the land. Of other Vertebrates, fishes and amphibians underwent complex evolutions and replacements during the Mesozoic. Birds arose in the Jurassic. The first mammals appeared in the Triassic. But most of these groups are too unimportant or too little known during the Mesozoic to be of much zoogeographic significance".

Relicts of the Mesozoic vertebrate faunas are apparently extremely scarce and so widely scattered that they are inadequate for zoogeographical reconstruction. For example: *Rhynchocephalia* were on most continents in the Early and Middle Mesozoic, but they are unknown fossil later than the Lower Cretaceous; the only living relict of this group is *Sphenodon,* in New Zealand.

Fossils also are sometimes extremely scarce. Of the Amphibians the suborder *Amphicoela* of the frogs has two living species, one in Western North America, the other in New Zealand. The only fossils known of this group are from the Upper Jurassic but only tentatively assigned to it (Darlington 1957, 164).

This lack of fossil data, and especially the lack of geographical fossil data seems to be appalling: it is possibly this vacuum which provides space for two possibilities of zoogeographic speculation (*l.c.* 580).

Darlington expressed this inadequacy of fossil pre-Cretaceous vertebrate faunas in his brief 'motion-picture history' of the fauna of the world: "during the Permian and early Mesozoic.... Africa and America had more than now in common, Dinosaurs would appear in the Triassic and would soon be on all continents, but the picture would not show how they got there. Not until the Cretaceous, still somewhat fragmentary, the fauna would begin to suggest the world as a whole" (*l.c.* 612).

The absence or extreme scarcity of the fossil record is also evident from the fact that for example on the question "as to how many Marsupials reached Australia, and when, the fossil record is mute" (*l.c.* 345).

However meagre the fossil record may be and however hypothetical deductions for the Mesozoic may be, it seems to me out of proportion to restrict one's reasoning to the *living* relict species which must be the chance survivors of once much larger, indubitably very ancient groups. At least in botanical reasoning we are accustomed to assume that such relicts are a sure sign that the group concerned made part of a much larger one in the past in the same area. We would never visualize an ancient Ranalian plant, in status comparable to *Sphenodon,* as *Degeneria* in Fiji, or another ancient plant of possibly similar affinity, *Lactoris fernandeziana* restricted to the Juan Fernandez Islands, as representing single advanced waifs or early single immigrants.

This inadequacy is the reason why Darlington could not give the important standing to some crucial relicts which they deserve in their historical setting. Their importance is so to say swamped by the Tertiary progressive and agressive, successful development of the dominant recent groups [1]) which, though they must root in or rest on a very long, immense former development, have conquered the world and made a 'new zoogeography of their own' nearly independent of the Mesozoic vertebrate fauna which entirely disappeared.

He treats the few but extremely interesting relict Vertebrates of New Zealand along the line derived from the progressive groups of the Tertiary, for example: "Frogs have reached Australia several times, and New Zealand once, but they have apparently done so with difficulty and at long intervals. The family that has reached New Zealand no longer exists in Australia or the Orient. Ceratodontid lungfishes may be the only strictly fresh-water fishes that reached Australia even in ancient times. Leptodactylids and *Hyla,* which have reached Australia, no longer exist in the Oriental Region. Of Reptiles, *Sphenodon* has reached New Zealand and survived there in isolation while its relatives have disappeared from the rest of the world, everywhere and abruptly at the end of the Cretaceous" (*l.c.* 572; see also *l.c.* 345 line 3 from top).

The zoogeography of mammals and birds seems entirely bound up to the Tertiary. Reptiles contain probably patterns comparable to plant-geographical areas and are rather well known in the fossil state, but the groups

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[1]) The rapid evolution among the Vertebrates has led Darlington to the premise (*l. c.* 580) "that animals have great power of movement and that they have been continuously dispersing (spreading and receding over the world)" which makes "the past more difficult to read". In his opinion dominance, success and competition are the driving forces of evolution, hence responsible for the shaping of zoogeography (*l. c.* 552—554). In this light it seems strange that though mammals date from the Triassic, Dinosaurs reigned supremely over the Mesozoic animal world, became suddenly and completely extinct for an unknown reason, and mammals only then could take this dominant position. Could they do only so, because the Dinosaurs became extinct?

are, it seems, seldom strictly megatherm, and besides mostly extinct. The relatively modern group of the snakes is largely tropical in ecology; there are certain patterns in this group which are pantropical, amphi-transatlantic or amphi-transpacific, similarly as in some families of lizards.

Recent amphibians are rather well tolerant to very varied temperature conditions. Strict freshwater fishes are certainly very old as a whole, but the main geographic pattern of today is formed by rather recent groups; their dispersal especially along (interrupted) land-bridges would, moreover, seem much more difficult than that of plants or land animals.

Among invertebrates biogeographic similarity with plants can possibly be found among land- and freshwater-mollusks which as a group are very old, are rather well-known recent as well as fossil, and have a slow dispersal. Another promising group in this respect are the insects, the dispersal of which is probably comparable to that of plants and whose evolution is in some groups presumably largely tied up with that of the Spermatophytes.

After these introductory remarks which show the limitations of Vertebrates for the zoogeographical history, especially in the Mesozoic, I will go into more detail on some specified points.

First, the zoogeographical data on the Vertebrates have led Darlington to accept the 'steady state', as I have called it, (i) geographically, by rejecting continental drift at least onwards of the Mesozoic (*l.c.* 601—606), and (ii) climatically, in rejecting the idea — sometimes loosely accepted by some geologists — of former uniform, worldwide megatherm climates with high rainfall (*l.c.* 8, 596). He strictly adheres to permanence of climatic zonation (*l.c.* 595) in the past, and agrees with Barghoorn (in Shapley *et al.*) (*l.c.* 598): "that it is unlikely that truly tropical conditions occurred in midlatitudes; more likely, an absence of winter freezing allowed extensions northward of tropical plants". And further: "Even early in the Tertiary, however, zonation of climate would limit exchange, blocking strictly tropical groups" (*l.c.* 595).

Second, in conformity to my conclusion on the Angiosperms, he accepts a tropical origin of most Vertebrates: "fresh-water fishes, amphibians, reptiles, birds, and mammals seem to have dispersed from the tropics in the north-temperate zone more than the reverse" (*l.c.* 556); the same happened towards the southern hemisphere (*l.c.* 572).

Third, it appears that vertebrate zoogeography can mostly be explained by the development from the fossil Tertiary fauna which developed under proportionally stable conditions, with intermittent fluctuations, and a gradual cooling at middle and higher latitudes till the Pleistocene, all the continents being connected by two land-bridges, *viz* the Bering and Panama isthmuses which are both essential (*l.c.* 591). Since the Cretaceous there have been no other major land-bridges, that in Malaysia (connecting Asia and Australia) having remained 'insular' (*l.c.* 494—495). "Lemuria did not exist in the Tertiary" (*l.c.* 591). This is in entire agreement with the phytogeography of the Tertiary. See my *map 23.*

Fourth, to my great satisfaction Darlington (*l.c.* 597—598) made some critical remarks about the caution we should have in assigning a restricted thermo-ecological range to extinct groups (see p. 286). In the discussion following a lecture which I held at Amsterdam in November 1961 on the subject of tropical land-bridges, the geologists and palaeontologists derived a supposed tropical climate of Mongolia and Beringia from Mesozoic Dinosaur fossils which, as my opponents said, "are by common consent and judging from size and physiology indubitable indicators of a tropical climate". It is a great relief to find that my layman's doubt about the exclusively megatherm habit of the reptiles is supported by Darlington who wrote: "Ancient animals and plants may have had capacities and tolerances different from those of existing ones. The possibility of this increases with remoteness of time. The relation of reptiles to climate in the Mesozoic may have been very different from now — basically different, not just different in species' adaptations. *Sphenodon* hints at this. It lives in cool-temperate New Zealand without any apparent special adaptations for withstanding coolness or securing heat. It has not become ovoviviparous as modern lizards, both geckos and skinks, have done in New Zealand, and it has not even become diurnal but is active in the cold of the night, at temperatures uncomfortably low for clothed men. Perhaps it and its Mesozoic contemporaries were less susceptible to cold than modern reptiles. Another hint of past difference in relation to climate comes from the American alligator, which has 'surprising' tolerance for cold. Alligators might be able to live far north of their present limits, if temperature were the only limiting factor. But there is another factor now which did not exist in the Mesozoic — the presence of many warm-blooded mammals. In the absence of effective warm-blooded competitors, a diversity of reptiles may have existed in cool northern regions, and whole faunas of them may just have suspended activity in cold weather" (*l.c.* 211, 597).

Fifth, Darlington's remarks (*l.c.* 30) on the 'functioning of land-bridges' (in casu the Panama isthmus, but the same for Beringia) are fully in accordance with my opinion on their effective functioning for plants (see p. 332). He wrote: "According to Simpson, just before North and South America were united towards the end of the Pliocene they had respectively about 27 and 29 families of land mammals. With one or two exceptions, they did not then have any families in common. After their union, the two continents exchanged mammals very extensively. In the Pleistocene they had 22 families in common, and further movements have occurred" (*l.c.* 30).

Sixth, in his zoogeography the two present land-bridges (Beringia and Panama) play a very important role. About land-bridges in the Mesozoic Darlington is, wisely, more cautious and vague, because the fossil evidence for them is extremely scant (*l.c.* 602—606). He is not opposed to postulate them as he wrote: "As the facts now stand, it is a reasonable hypothesis that mid-Triassic Vertebrates reached South America from Africa by a direct connection, but more facts are needed. At some time during the Triassic, land vertebrates apparently had access to all continents" (*l.c.* 611). Continents were occasionally connected by land-bridges of a volcanic nature (*l.c.* 614). These statements are all in agreement with my *map 23.*

In the Cretaceous he found no indications for a land connection between South America and Africa (*l.c.* 603); on my *map 22* this connection had by that time crumbled to an insular condition. As to the South Pacific he wrote (*l.c.* 605) that there was no land-bridge in the Tertiary, which agrees with my *map 23,* in which the South Pacific land-bridge is shown in almost decayed form.

On the whole, however, he is not in favour of a South Pacific land connection, but he is rather in doubt about it, which appears from other quotations: South American-New Zealand-Australian bird groups "which were once thought to be related, are now usually considered independent, convergent groups" (*l.c.* 257). "No land or strictly fresh-water vertebrates seem to have crossed an antarctic bridge" (*l.c.* 603). "Marsupials, once thought to be the best evidence of an antarctic bridge, are now thought to have reached South America and Australia separately and to have evolved parallel specializations there. However, some plants and insects.... do show what seem to be direct relationships between S. America, S. Australia, and New Zealand too. Why should the vertebrates tell one story, and the plants and insects another?" (*l.c.* 604). He then offers three explanations, *viz* (i) that the dispersal of the plants and insects preceded that of the Vertebrates, which is declined, (ii) that they have different powers of dispersal, (iii) that they may have been dispersed in the same ways but behaved differently afterward; though there may have been no Tertiary antarctic bridge, there might have been a pre-Tertiary connection used by both groups, "but that only the plants and invertebrates have been able to survive upon it.... But I think they probably did so across water gaps and not by continuous land" (*l.c.* 604—605).

Though he attaches great importance to long-distance dispersal by rafting (*l.c.* 15—16), obviously following Wallace (1880) and Matthew (1915), he does not let this interfere with his land-bridges, but he does obviously accept it for explaining island faunas. "The most important fact about island vertebrates is that most of them seem to be fairly recent immigrants, not ancient relicts" (*l.c.* 533) and "the possibility to reach island distribution depends on their capacity to spread over salt water surfaces, but is not correlated with geological age". This latter point is the only real discrepancy I can find with phytogeography.

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INDEX

Scientific names (synonyms in italics)

Personal names

Selected subjects