WALLACE'S LINE: A RESULT OF PLATE TECTONICS[1]

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Wallace's line is one of the sharpest and first detected zoogeographical boundaries on earth. This line, running north to south through the center of the Malay archipelago, separates predominantly Asian faunas to its west from predominantly Australasian faunas to its east. The sharpness of the boundary differs from group to group, dependent on the dispersibility of the group under consideration. For rain forest plants Wallace's line is a less marked boundary. To its west Australasian plants occur mainly on oligotrophic podzolized sands in heath forest. Asian plants massively penetrate to its east and the Australasian element is perhaps most predominant in certain mid-mountain forests rich in *Nothofagus* or the conifers *Agathis* and *Araucaria*.

Malesia has an extremely rich flora, conservatively estimated to comprise 25,000 species of flowering plants (van Steenis, 1971) and this has contributed to the view that the 'cradle of the angiosperms' lies somewhere between Assam and Fiji (Takhtajan, 1969; Smith, 1970).

Until recently different viewpoints on the palaeogeography and biogeography of the Malay archipelago had to stand or fall on their ability to fit all known facts into a plausible hypothesis. There was no external point of reference. Biologists tended to make geographical reconstructions and geographers to use biological evidence.

The revolution in the earth sciences during the last two decades, which has resulted from the theory of plate tectonics, means that the palaeogeography of the globe during the Mesozoic and Cenozoic is now understood in general terms. Now biologists can for the first time work with a broadly painted background of established palaeogeographical facts, albeit still lacking much fine detail, rather than mere suppositions. The former dangers of circular argument, which have so often plagued discussions of biogeography, no longer befog the scene.

The major events of global geology that affect the biogeography of the region of Wallace's line are the progressive break up of Gondwanaland from about 140 m.y.a. (Jurassic/Cretaceous boundary) and the drifting north of the Indian fragment to collide with Laurasia at about 55 m.y.a. and of the Australia/New Guinea fragment to collide with the southeastern extremity of Laurasia at only about 15 m.y.a., the mid-Miocene. Before that the Malay archipelago did not exist.

Plants and animals could have reached modern Malesia from one of three sources, Laurasia, Gondwanaland via Australia, or Gondwanaland via India followed by southeastwards migration.

Before we look at some present-day phytogeographic patterns and see how

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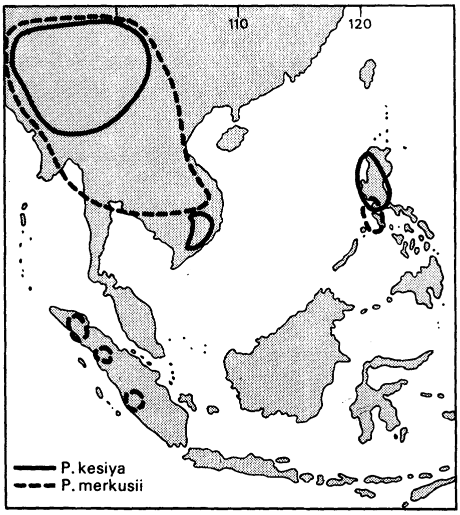

FIGURE 1. *Pinus* in Malesia. Reproduced from Whitmore, 1981, fig. 8.1.

they reflect this history we must first consider palaeoclimate. Both animals and plants are variously confined to particular habitats. Contemporary distributions are likely partly to reflect past differences in climate. The interpretation of range must penetrate this veil and take it as well as palaeogeographic dispositions of land into account.

It is now known that there have been major fluctuations in tropical climates. During ice ages sea-level was lowered by up to 180 m, rainfall was less and areas with a seasonally dry climate more extensive. In Africa and tropical America there was substantial desiccation. Rain forest was restricted to pockets, so-called refugia, set like islands in a 'sea' of seasonal forest and savanna. The rain forest patches were to some extent in contact through gallery forests along rivers. Today tropical rain forests are at or near their greatest extent, achieved for only a small fraction of the last two million years. In Africa and America centers of species richness and endemism have been detected within the rain forest and these are believed to represent the refugia.

The Malesian rain forest occurs in two great blocks. The western or Sunda shelf block is centered on Sumatra, Malaya, and Borneo. The eastern, Papuasian or Sahul shelf, block is centered on New Guinea. Between the blocks lies a north-south belt of seasonal forests running through the western Philippines and Celebes to the Lesser Sunda Islands. The whole of each block is of comparable species richness and endemism to one of the rain forest refuges of Africa or America. There is as yet no geoscientific (geomorphological or pedological) or palynological evidence of more extensive seasonal climates in Malesia. Nevertheless these two blocks are likely to have been of reduced extent at the ice age maxima. We may speculate that seasonal forests developed mainly on land exposed by low sea level and which is now flooded, e.g. as the South China Sea (beneath which indeed true laterite and kunkur nodules are evidence of subaerial exposure and seasonality). There would probably also have been extensive forests under the

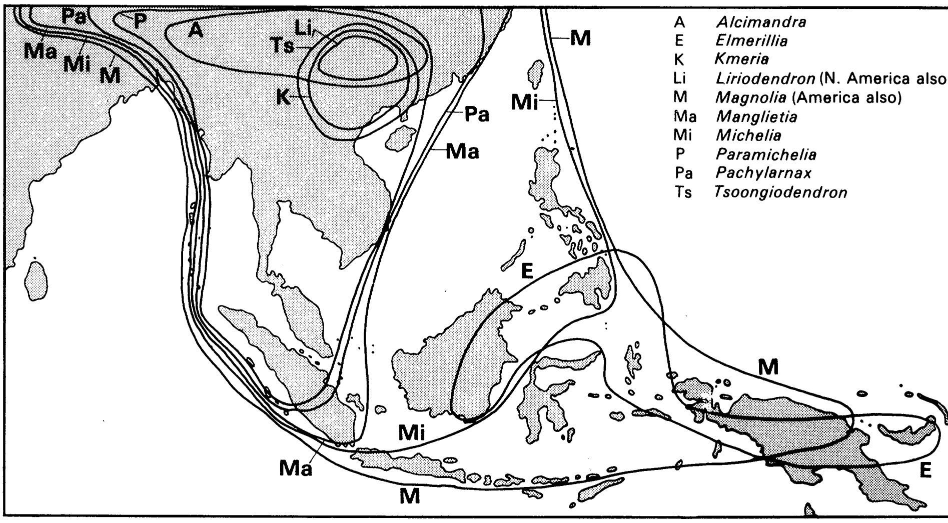

FIGURE 2. The ranges of the genera of Magnoliaceae in Malesia and southeast Asia. Reproduced from Whitmore, 1981, fig. 8.4.

influence of saline water on the low, exposed land (i.e. mangrove and brackish water swamp forests).

Thus, we may conclude that most of the present-day areas of rain forest have been continuously forested. Do the ranges of rain forest plants therefore reflect the palaeogeographical history?

LAURASIAN GROUPS

It is well established that the Coniferae divide into two great classes of northern and southern hemisphere range respectively (Florin, 1962). Both classes have representatives in Malesia. Amongst the northern conifers only *Pinus* (Fig. 1) extends into Malesia at the present day. It is represented by two species, *P. kesiya* and *P. merkusii,* of partly overlapping ranges. For both, the Malesian stations are the extremity of a wide range in seasonally dry continental southeast Asia.

Six genera of Magnoliaceae occur in Malesia and four more are endemic to the region of southern China and northern Indo-China (Fig. 2). Within Malesia *Elmerrillia* is endemic from eastern Borneo to New Britain. There is a very marked concentration in western Malesia. Magnoliaceae as a family are strongly concentrated in subtropical east Asia and extend into Malesia from this bastion becoming progressively less well represented eastwards. Magnoliaceae are accepted by most botanists to be a primitive family. The distribution contrasts strongly with that of Winteraceae, also regarded as primitive, which is described below.

PAPUASIAN GROUPS

Phyllocladus, the 'Celery Pine' is a small genus of the big southern conifer family Podocarpaceae. There are three species in New Zealand, one in Tasmania,

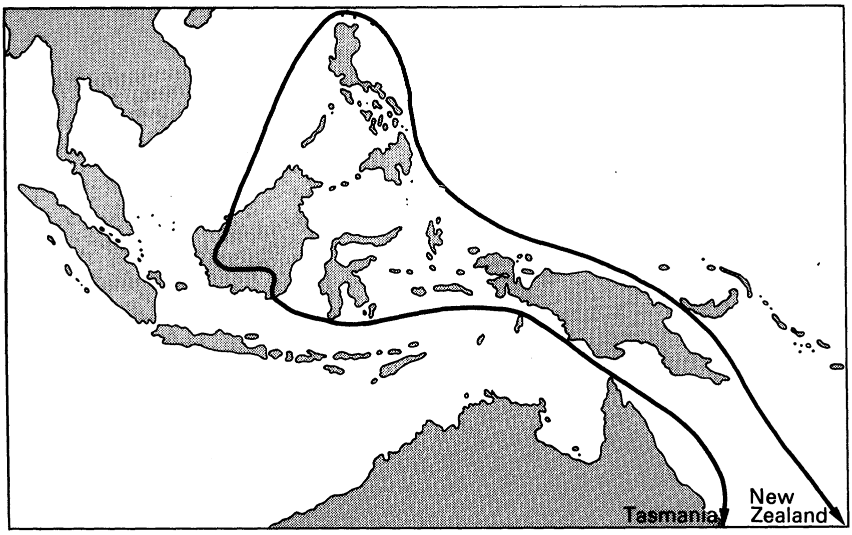

FIGURE 3. The range of *Phyllocladus,* Podocarpaceae. Reproduced from Whitmore, 1981, fig. 8.6.

and one, *P. hypophyllus,* in montane rain forests in Malesia extending west as far as Philippines and eastern Borneo (Fig. 3). The range is strongly Gondwanic. It is of interest that in pollen profiles from northern Borneo, which extend from the Oligocene (30 m.y.a.) onwards, *Phyllocladus* pollen suddenly appears at the Plio-Pleistocene boundary, 2–3 m.y.a. (Muller, 1966). *Podocarpus imbricatus* pollen appears at about the same time.

The primitive family Winteraceae is strongly centered on the islands of the southwest Pacific (Fig. 4; Smith, 1943; Vink, 1970). There are three genera in eastern New Guinea, of which *Drimys* extends westwards to cross Wallace's line into the Philippines and eastern Borneo. Winteraceae is the southern counterpart of Magnoliaceae.

MALESIAN GROUPS OF APPARENTLY DUAL ORIGIN

There is not much doubt that the families so far considered entered Malesia from either Laurasia or Gondwanaland. Any alternative hypothesis would offend Occam's razor. It is more difficult to identify families that have arrived from both directions as this presupposes a very thorough understanding of the group in question.

Proteaceae have been the subject of very detailed investigation (Sleumer, 1955; Johnson & Briggs, 1975). The family is concentrated in the southern hemisphere and strongly concentrated on Australia and the southern tip of Africa. The ranges of seven Australian genera extend into Malesia (Fig. 5) and one genus, *Finschia,* is endemic to east Malesia and the southwest Pacific. However, the genus *Heliciopsis* presents an anomaly. This is endemic to Malesia and adjacent Asia. Johnson and Briggs believed that *Heliciopsis* could have reached southeast Asia from West Gondwanaland by the 'Noah's Ark' medium of India in which it subsequently died out. Proteaceous pollen has been found in the Eocene of India.

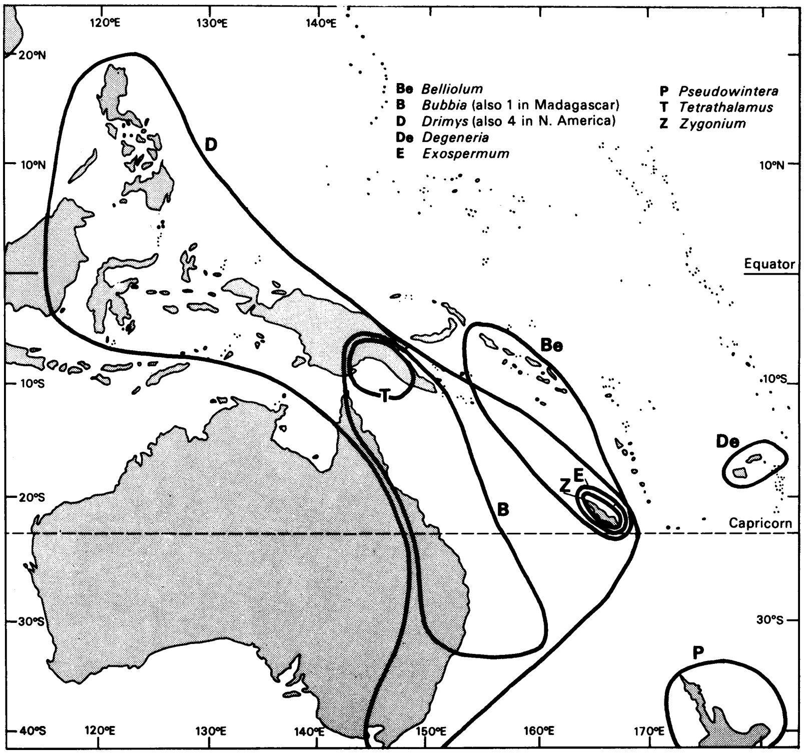

FIGURE 4. The ranges of the genera of Winteraceae in Malesia and the southwest Pacific. Reproduced from Whitmore, 1981, fig. 8.9.

Nastus, a small genus of ca. 15 species of bamboos that scramble through the canopy of tropical forests, occurs in Java, Sumba and Flores, and possibly Sumatra. It is also in New Guinea, the Bismarcks, and Solomons. *Nastus* also occurs on the south India Ocean islands of Réunion and Madagascar (S. Soenarko—Dransfield, pers. comm.). This range suggests a West Gondwanic origin followed by arrival in Malesia via both Laurasia and Australia/New Guinea. *Livistona* is a genus of fan palms of the rather primitive Coryphoid group. It is strongly represented at the western and eastern extremities of Malesia with few species in the center (Fig. 6). There is a series of species of great morphological diversity and relict distribution in Australia and a scarcely distinct related genus (*Wissmannia*) in the Horn of Africa. The picture may represent a relic of a much wider distribution that could have come from a west Gondwanic origin arriving in Malesia from both ends (Dransfield, 1981).

THE REMAINING ENIGMA

Fagaceae instance one of the great remaining puzzles of phytogeography. Subfamily Fagoideae have two genera. The true beech *Fagus* has a northern hemisphere range extending to southern China. The other genus, *Nothofagus,* the southern beech, reaches northwards from Australia and New Zealand to

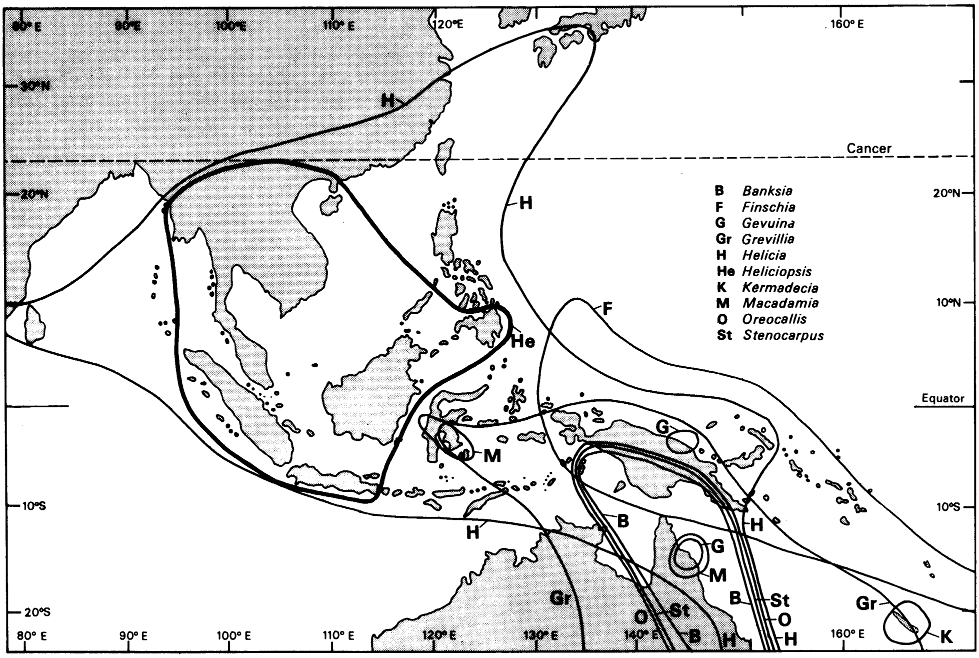

FIGURE 5. The ranges of the genera of Proteaceae in Malesia and southeast Asia. Reproduced from Whitmore, 1981, fig. 8.11.

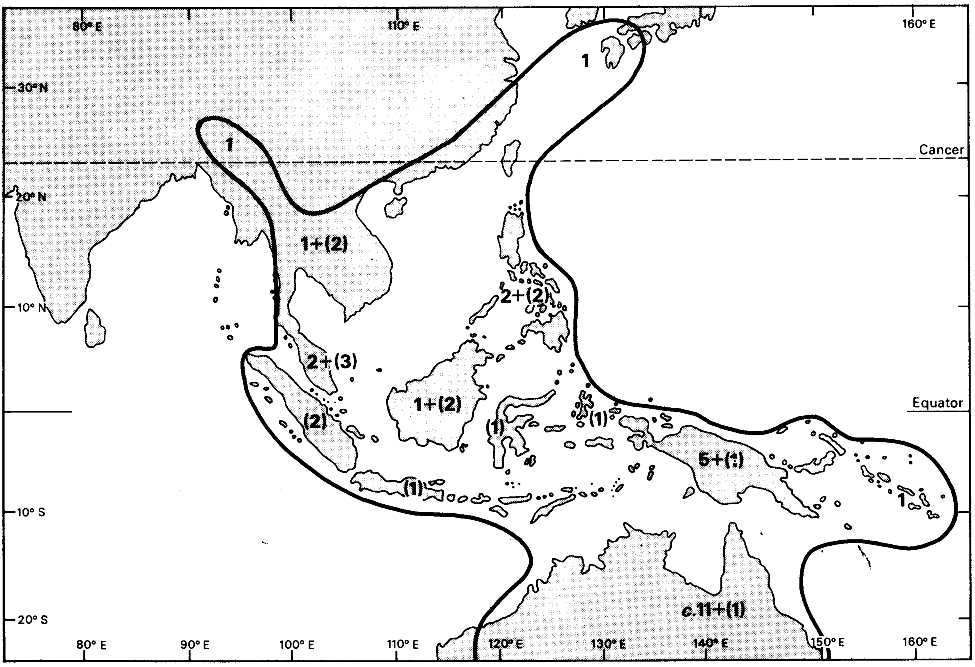

FIGURE 6. The distribution of the species of *Livistona*. Numbers of endemic and, in parentheses, non-endemic species shown. Reproduced from Dransfield, 1981, fig. 6.9.

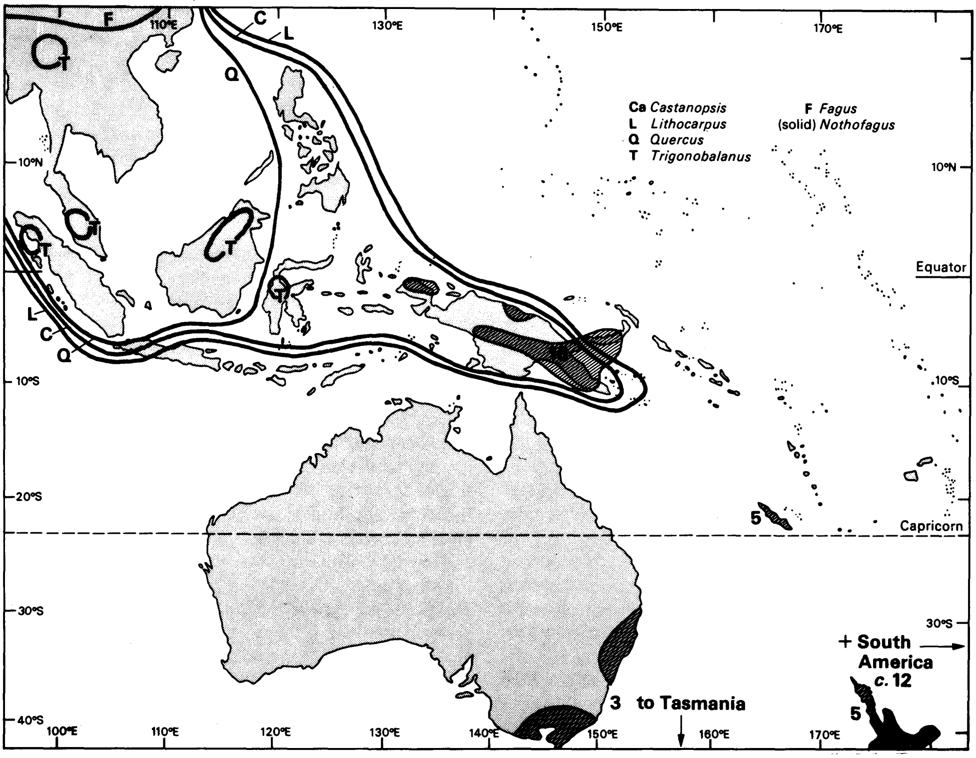

FIGURE 7. The ranges of the genera of Fagaceae in southeast Asia, Malesia, and the southwest Pacific. Reproduced from Whitmore, 1981, fig. 8.13.

eastern New Guinea (Fig. 7). The region of Southeast Asia and Malesia is where the ranges of the two genera of this undoubtedly natural subfamily came closest together. Magnoliaceae of the northern hemisphere and Winteraceae of the southern hemisphere are both families widely believed to be primitive and related. Their ranges overlap only in Malesia. Other pairs of northern and southern families that similarly overlap are Ericaceae and Epacridaceae (*Styphelia*), Staphyleaceae and Cunoniaceae, and Saxifragaceae and Escalloniaceae.

Botanists have attempted to account for these bihemispheric pairs, though controversy is likely to continue to rage in the absence of either a fossil record or an accepted view of evolutionary relationships within the group under discussion. Many angiosperm families appear to have originated in western Gondwanaland and moved out simultaneously with the break up of that great southern continent (Raven & Axelrod, 1974).

Malesia is the region where these groups come closest at the present day. In some cases their ranges overlap. What is known of evolutionary rates and the evidence of micro and macro fossils (Muller, 1974) makes it improbable that these pairs could have evolved in the last 15 million years or that they could have evolved on either the Laurasian or Gondwanan margin and spread throughout the globe since the collision. This enigma was recently pinpointed by van Steenis (1979), who postulated there must have been contact between north and south long before the mid-Miocene collision. Close examination of the geological record shows that there is the possibility of an earlier connection and this has recently been explored by Audley-Charles et al. (1981). About late Jurassic or early Cretaceous the northwest continental margin of Australia was block faulted. The continental block that is believed to have separated from the Australian continent has not been identified. It could perhaps have been subducted at the Java trench or its ancestor. Alternatively it could be extant and lying somewhere northeast of present-day India, for at the time of its separation from Australia northwest Australia lay close to northeast India. Very recently Mitchell (1981) has identified south Tibet and Burma-Thailand as former parts of Gondwanaland that were rifted away from that continent in the later Permian or early Mesozoic (ca. 200 m.y.a.). However, the evidence for dating the separation is sufficiently uncertain to allow them to be considered tentatively as the missing fragment of northwest Australia.

This interpretation must at present be tentative. It rests on two areas of uncertainty. We need to know more, firstly, on the date of drift of Mitchell's continental fragment. Secondly, we have as yet inadequate knowledge on the timing and course of evolution of flowering plants. Fossils are sparse.

In conclusion, despite the revolution in the earth sciences of the last two decades, which has led to a total reappraisal of the biogeography of the Malay archipelago, Wallace's Line remains today, as for the past 120 years, a cogent influence, powerfully able to generate hypotheses subject to further test. It is still a challenge to biogeographers and geologists.

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