4. Phytogeography and evolution of the Ericaceae of New Guinea

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1. Introduction

The Ericaceae are among the ecologically most important families of the more open woody vegetation from about 1000 to 3750 m especially in the Upper Montane and Subalpine vegetation in New Guinea, but they also occur less frequently in other vegetation types from sea level to over 4000 m. There are over 400 species in six genera in our area alone (Table 1), and the Ericaceae are probably the most diverse woody family in this vegetation: none of the six genera is restricted to New Guinea, but all bar three of the species are. The main purpose of this paper is to examine the morphological and ecological variation of the New Guinea Ericaceae in the context of the variation pattern of the whole family. An attempt is also made to discuss the historical biogeography of the family in New Guinea.

The family is fairly well known taxonomically because of the conspicuous flowers of many of the species and the resultant interest in them in horticultural circles. Sleumer's comprehensive account of the family for the "Flora Malesiana" forms the taxonomic basis of this work (Sleumer 1966, 1967), changes since then being noted below (authorities are not mentioned after species' names except where they are not included, or differ from those given, in Sleumer's accounts). New Guinea as delimited here includes the main part of the East Malesian region (see van Balgooy 1976 for references), but to understand the evolution of the New Guinea Ericaceae one must look at species from the rest of Malesia and SE Asia, as well as tropical America.

The great majority of the family has pollen in tetrads and anthers that invert during the course of development, dehisce by pores, and often lack an endothecium, but, apart from the absence of stipules and the usually axile placentation, there is otherwise great diversity within the family. However, as is quite common (see van Steenis 1978), the coherence of the family is increased because of numerous polyphyletic "trends" or "tendencies" within it, for example, the presence of projections on the anthers, the occurrence of rhizomes and the winging of seeds. The evolution of the New Guinea Ericaceae will be discussed in the light of these and other tendencies, and so placed within the framework of the evolution of the family as a whole. Although the lack of detailed knowledge of cladistic relationships within the family and of the

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Table 1. General distribution of New Guinea Ericaceae and their immediate relatives in Malesia.

		West New Guinea only	East New Guinea only	Widespread New Guinea	Total New Guinea	Rest of Malesia	Pacific and NE Australia
Rhododendron subsection	*Pseudovireya*	8	3	4	15	13	0
	Siphonovireya	4	1	2	7	0	0
	Phaeovireya	19	19	3	41	2	0
	Malayovireya	0	0	0	0	13	0
	Albovireya	3	3	0	6	8	0
	Solenovireya	8	14	3	25	12	1
	Euvireya series						
	Linnaeoidea	7	1	3	11	0	0
	Saxifragoidea	0	0	1	1	0	0
	Taxifolia	0	0	0	0	1	0
	*Stenophylla**	0	0	0	0	1	0
	Citrina	0	0	0	0	1	0
	*Buxifolia/Javanica**	28	19	10	57	73	2
Gaultheria		4	1	1	6	18	0
Diplycosia		13	5	3	21	75	0
Vaccinium section	*Galeopetalum*	0	0	0	0	1	0
	Rigiolepis	0	0	0	0	23	0
	Oarianthe	29	7	5	41	4	3
	Neojunghuhnia	11	2	1	13	0	0
	Bracteata	36	34	4	74	79	1
Dimorphanthera section	*Pteridosiphon*	2	0	0	2	0	0
	Pachyantha	0	6	0	6	0	0
	Dimorphanthera	2	3	5	10	2	0
	Trochilanthe	23	25	5	53	0	0
Agapetes subgenus	*Paphia* section *Paphia*	0	14	0	14	0	4
Total		197	157	49	403	327	11

*For circumscription of these taxa, see text.

polarity of evolution of many of the characters discussed makes this task more difficult, the immediate relationships of most of the genera and supraspecific taxa are becoming clearer, as mentioned below.

It is concluded that New Guinea Ericaceae, and most tropical Ericaceae in general, seem to have evolved very much within the constraints within which the temperate members have evolved. More or less particularly tropical characteristics are the scandent habit, the epiphytic habitat, and some corolla types, especially those probably associated with ornithophily. The specific diversity in New Guinea is in part at least accompanied by the evolution of characteristics similar to those that have developed independently in the family elsewhere, both in the tropics and in the temperate zone.

This chapter is divided into three slightly overlapping parts. The general morphology and taxonomic relationships of the New Guinea Ericaceae and their probable nearest relatives are discussed first, and their general geographical distribution within New Guinea given. In the main section the characters of the Ericaceae in New Guinea are compared in some detail from a basically ecological point of view with those of the family elsewhere. In the third section the evidence presented is discussed in the light of what is known about the geological history of New Guinea.

2. The New Guinea Ericaceae: morphology, relationships, and current distribution

The genera and the main supraspecific taxa of the New Guinea Ericaceae are listed in Table 1. The main species concentrations in the New Guinea taxa are mentioned below, while overall patterns of distribution of the Ericaceae in New Guinea are discussed at the end of this section.

2.1 Rhododendron

All the New Guinea species belong to section *Vireya* which is overwhelmingly Malesian in distribution. A single species of subsection *Euvireya* is known from NE Australia, a few species of subsection *Pseudovireya* grow on the Himalayas and elsewhere in SE Asia, while subsection *Euvireya* is even more sparsely represented on the SE Asian mainland. *Rhododendron* section *Vireya* is currently placed in subgenus *Rhododendron* (Sleumer 1949; Cullen and Chamberlain 1978). It has scales, but no other multicellular hairs. Many members are epiphytes, a habit uncommon in the rest of the genus. The various subsections and series within section *Vireya* are distinguished by differences of indumentum, flower type, habit and leaf size (Sleumer 1966). A reevaluation of the limits of these taxa is necessary, and although this cannot be attempted here, the following points should be noted. Within subsection *Euvireya*, I have combined series *Buxifolia*, *Javanica* and the New Guinea species of series *Stenophylla*. In both flower and leaf type the New Guinea species of series *Stenophylla* differ considerably from *R. stenophyllum*, from Borneo, and are much more similar to species from series *Buxifolia* and *Javanica* (Stevens 1976; see also Woods 1978). These latter differ only in leaf size, and, as Sleumer (1973) noted, closely related species may be placed in different series because of this. The concentration of species of series *Linnaeoidea* and, to a lesser extent, those of subsection *Pseudovireya*, in Irian Jaya is noteworthy; the taxa involved have small leaves. Species limits in subsection *Solenovireya* are exceptionally difficult and the significance of the distributional pattern in this group is unclear.

2.2 Gaultheria

There are relatively few New Guinea representatives of this large, circum-Pacific genus, which can be recognized by its fleshy calyx that encloses a capsular fruit and its awned anthers. The New Guinea species seem most related to W Malesian species, with the possible exception of *G. mundula* (Sleumer 1967), which is superficially similar to some species from New Zealand (see also van Steenis 1934). The genus is in need of monographic work to ascertain infrageneric relationships.

2.3 Diplycosia

Diplycosia is close to *Gaultheria*, the two having similar fruits, and at least some members of both genera smell of methyl salicylate (wintergreen). *Diplycosia* may be distinguished by its consistently fasciculate inflorescence (very rare in *Gaultheria*), its anthers, which lack spurs but which have tubules, and by the presence of numerous fibers wandering throughout the mesophyll in all species that I have examined (this character is uncommon in *Gaultheria*). *Diplycosia* is also much more commonly epiphytic than *Gaultheria*. All these characteristics are probably derived, although, apart from stamen type, all also occur in *Gaultheria*. The center of diversity in *Diplycosia* is Borneo (Table 1), and the genus has only a foothold on mainland SE Asia; the New Guinea representatives are few and are not distinguished by any characters that set them apart as a group in the genus. The center of diversity of the genus in New Guinea is the Vogelkop Peninsula; there are 7 species there, and 6 are found nowhere else.

2.4 Vaccinium

Vaccinium is a large and diverse genus, the New Guinea representatives of which can be characterized by their falsely 10-locular ovaries, small (usually less than 1 cm long) and usually urceolate to globose corollas, and fleshy fruit. (For the circumscription of the genus in Malesia, with section *Pachyantha* being transferred to *Dimorphanthera*, see Stevens 1974). Neither of the New Guinea-centered sections is much different from the polymorphic section *Bracteata*. Section *Neojunghuhnia*, with its very long calyx lobes, is endemic to New Guinea (Table 1); it is poorly known. Section *Oarianthe* is most diverse in New Guinea, only five species not occurring there. It has small leaves, often less than 1 cm long, and basically fasciculate inflorescences; both of these are derived characteristics, although neither is unique in the genus, even within Malesia. Despite the apparent distinctness of section *Oarianthe*, species like *V. summifaucis* and the recently described *V. morobense* Kloet, both placed in section *Bracteata* yet having small leaves and reduced inflorescences, makes one pause for thought.

Species limits in *Vaccinium* will doubtless need emending when more material becomes available, and the local nature of many of the species currently recognized may change. The concentration of species of sections *Oarianthe* and *Neojunghuhnia* in Irian Jaya is perhaps worthy of note, although 11 of the 13 species recognized by Sleumer (1967) in the latter were known to him from only one or two collections, and little more is known about them now.

2.5 Dimorphanthera

Dimorphanthera is characterized by its usually 5-locular ovary; flowers usually over 1 cm long; its relatively short, usually strongly dimorphic, woody stamens, the filaments of which are free (there may appear to be only five stamens, since the larger stamens overarch the smaller); and numerous anatomical features. Available evidence suggests a relationship to *Satyria* and other tropical American genera (Stevens 1972, 1974, ms).

Of the four sections of *Dimorphanthera*, section *Pteridosiphon*, with its conspicuously ribbed calyx, is poorly known. Section *Pachyantha*, with its campanulate, very thick-walled, apparently two-layered corolla less than 1 cm long, is distinct, while section *Dimorphanthera*, with a large, campanulate, usually deeply-lobed corolla, and section *Trochilanthe*, with a basically tubular, usually more shallowly-lobed corolla, are sometimes not easy to distinguish.

Dimorphanthera section *Pachyantha* is restricted to the eastern half of New Guinea. Section *Dimorphanthera* extends to the Philippines and has several wide-ranging species, while section *Trochilanthe* has more numerous, sometimes narrowly distributed species, and further species are still being discovered (Fig. 3).

2.6 Agapetes subgenus Paphia

Agapetes subgenus *Paphia* is anatomically similar to *Dimorphanthera*, but is very different from the other subgenus, *Agapetes*, and may be closer to American taxa (Stevens 1972). It has large, usually rather strictly tubular flowers, and stamens that are almost as long as the corolla, but which are not notably woody or dimorphic. Section *Pseudagapetes* is monotypic, with a single species on the Malay Peninsula, while section *Paphia* is centered in New Guinea, but also occurs in New Caledonia, NE Australia and Fiji. Thirteen of the 14 New Guinea species of subgenus *Paphia* grow on the mountains between Mt Amungwiwa and Mt Victoria in the SE, a distance of only some 250 km, and 11 of them are restricted to this area. Although there is a considerable amount of variation in habit, floral characters, etc., between these species, there are no discontinuities obvious enough on which supraspecific taxa could be based.

2.7 General distribution patterns of New Guinea Ericaceae

About 12% of the species can be called widespread, that is, found along half or more the length of the island (Table 1). Although the figure was arrived at simply by recording as widespread all species which grow in both Irian Jaya and Papua New Guinea, species which just straddle the boundary (e.g., *Vaccinium sanguineum*) are probably balanced by those which have a very wide distribution within one half of New Guinea (e.g., *Dimorphanthera elegantissima*). About 40% of the species are apparently local — restricted to a single mountain or to two adjacent peaks, but this may be an over-estimate (see below). About 26% of the species in the eastern part of the island are local; over a third of these species occur around the Sepik Basin, a very poorly collected area. About 44% of the species from Irian Jaya are local, of which slightly under a quarter are restricted to the Vogelkop.

Ericaceae are poorly represented on the Bismarcks and the Solomons. One species of *Vaccinium* section *Bracteata* occurs on New Britain, one on Rossel Island (and one of section *Oarianthe* on Bougainville) and two species of *Dimorphanthera* on New Britain and one on New Ireland. A few species of *Rhododendron* belonging to several groups also occur on New Britain and New Ireland (Figs. 1–3).

Serious problems arise when discussing details of the distribution of individual species. Although the Ericaceae are among better collected montane families, much more collecting off the beaten track needs to be done, especially in Irian Jaya; novelties are still being collected, and infraspecific variability and species limits and relationships need to be assessed more accurately. Using any species as an example of a particular distribution pattern can be hazardous. Thus *Dimorphanthera calodon* had a restricted geographic range, being known only from the Murray Pass, in the Central Province (Sleumer 1967), until it turned up rather abundantly along the Bulldog Road, Morobe Province (Stevens 1977); *Rhododendron wrightianum* var. *wrightianum* had a disjunct distribution, being known only from Irian Jaya and Milne Bay Province (Sleumer 1966), until it was reported from Western, Morobe and Central Provinces (Sleumer 1973). Hence it is considered premature to analyze species distributions more closely. Kalkman and Vink (1970) discussed the geographical distribution of Ericaceae on the mountains in the well-collected central highlands of Papua New Guinea; they concluded that, although few species there were single mountain endemics, many species occurred on fewer mountains than their overall distribution might have suggested.

3. Characteristics of New Guinea Ericaceae compared with those of the rest of the family

It seems that an explanation of at least some of the variation in New Guinea and other tropical Ericaceae may be sought in terms of adaptive radiation in rather

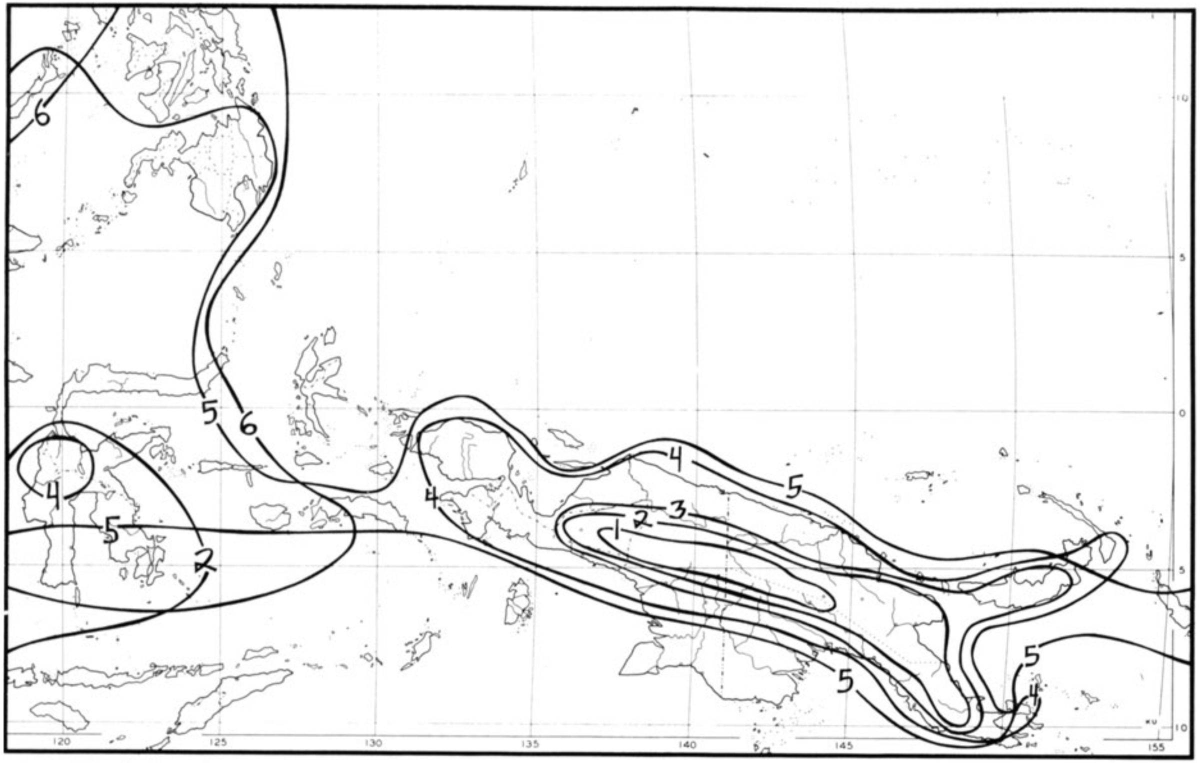

Fig. 1. Distribution of some groups of *Rhododendron* in East Malesia. 1, *Rhododendron* series *Saxifragoidea*; 2, series *Linnaeoidea*; 3, subsection *Albovireya*; 4, subsection *Phaeovireya*; 5, subsection *Solenovireya*; 6, subsection *Malayovireya*.

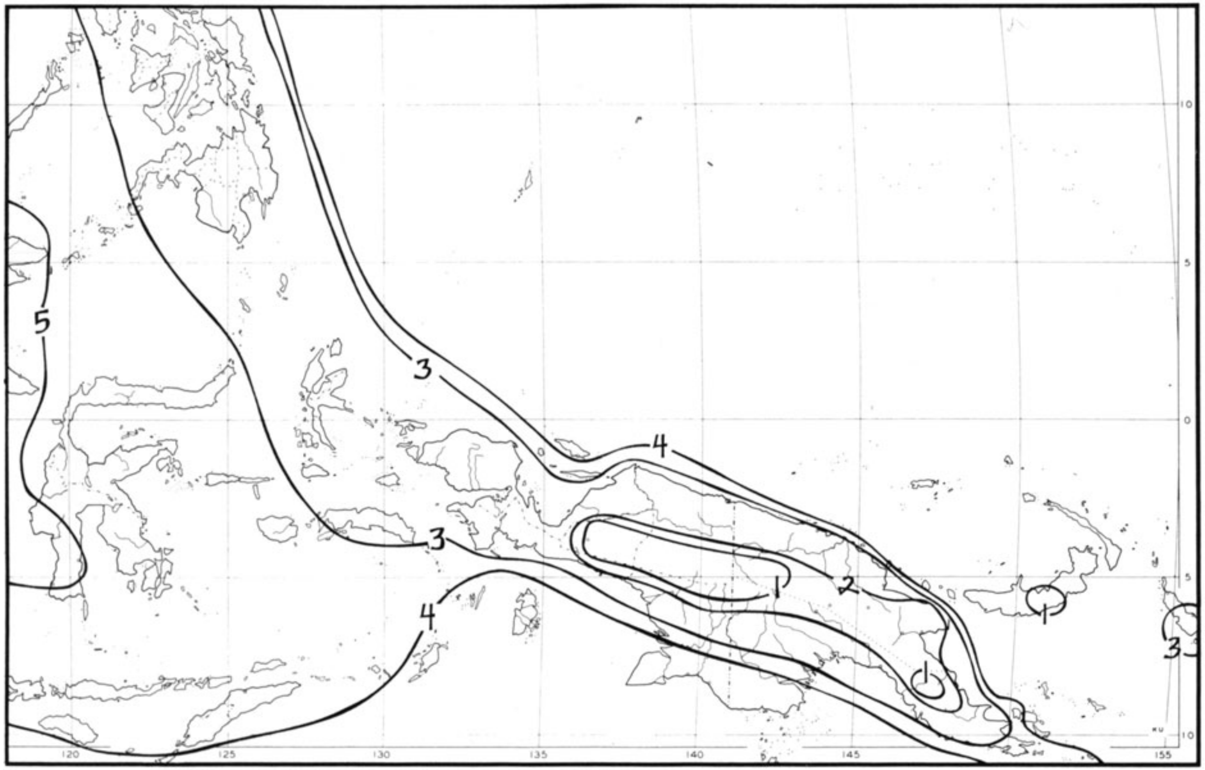

Fig. 2. Distribution of some groups of *Rhododendron* and *Vaccinium in* East Malesia. 1, *Vaccinium* section *Neojunghuhnia*; 2, *Rhododendron* subsection *Siphonovireya*; 3, *Vaccinium* section *Oarianthe*; 4, *Vaccinium* section *Bracteata* (the record from New Britain should be referred to this section); 5, *Vaccinium* section *Rigiolepis*.

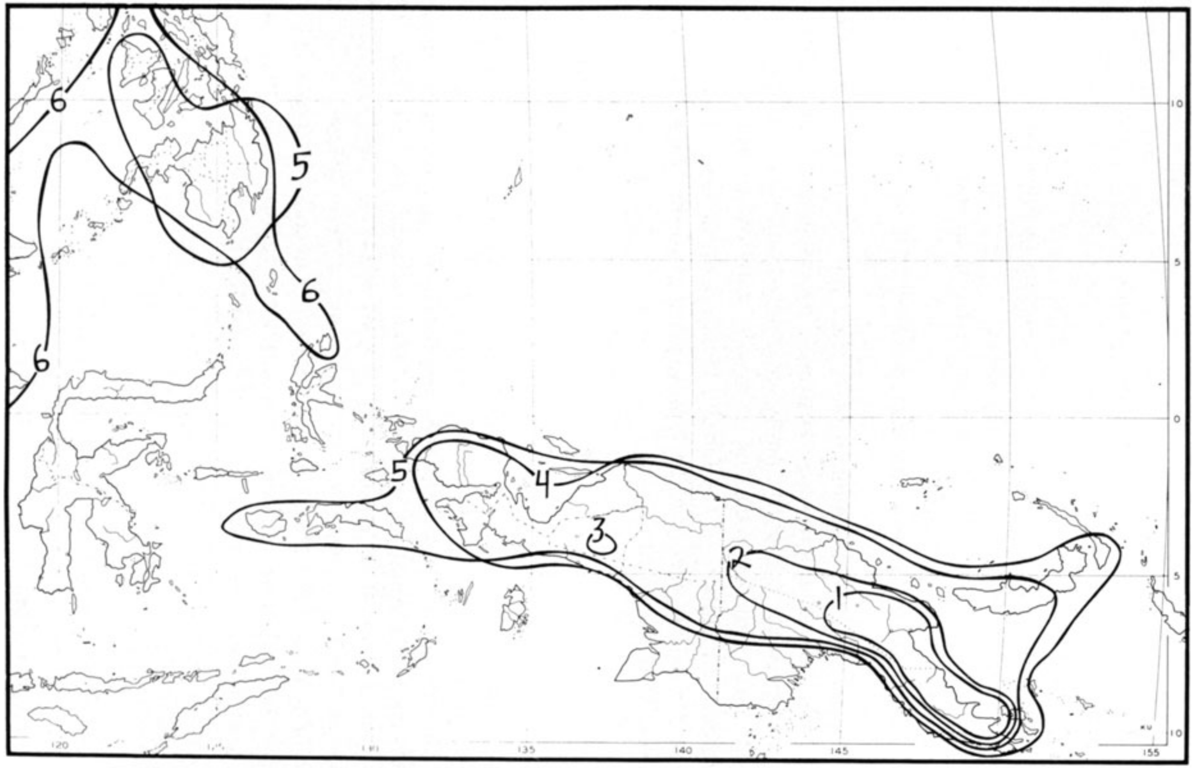

Fig. 3. Distribution of some Vaccinieae in East Malesia. 1, *Agapetes* section *Paphia*; 2, *Dimorphanthera* section *Pachyantha*; 3, *Dimorphanthera* section *Pteridosiphon*; 4, *Dimorphanthera* section *Trochilanthe*; 5, *Dimorphanthera* section *Dimorphanthera*; 6, *Costera*.

particular ecological situations (see also Stevens 1976). In this section, the general ecological constraints within which the New Guinea Ericaceae seem to have evolved will be compared with the ecological characteristics of members of the family. Reference will be made to more specific morphological and anatomical characteristics of the family where necessary. The ecological characteristics are listed below.

1. A preference for cool, rather than hot, climates.
2. A preference for acid habitats.
3. A strong tendency to be heliophilic.
4. A shrubby habit, but with considerable variation in physiognomy.
5. A diversity of leaf size and especially shape.
6. A conspicuous corolla and considerable variation in stamen type.
7. A small fruit with numerous seeds.
8. An accumulation of tannins and sometimes other toxins.

There is a danger of circular argument here, since the New Guinea Ericaceae must have the family characteristics. However, by discussing temperate and other tropical representatives of the family separately, some idea can be given as to how the New Guinea members compare with West Malesian/other tropical/temperate members of the family. Hence a distinction can be drawn between characteristics general in the family, peculiar to the tropical environment, or peculiar to New Guinea.

3.1 Climatic preferences

The Ericaceae are well known for being plants predominantly of arctic to warm temperate conditions (e.g. see Sleumer 1941); in Africa, America and Malesia they occur mostly on mountains as they approach the equator. Throughout Malesia, few species habitually grow below 1000 m (see Stevens 1976, Figs. 2A, 3B–3D for *Rhododendron* in Malesia; van Steenis 1934). In New Guinea, *R. zoelleri* grows from sea level to 2000 m, and a few species, such as *Dimorphanthera tedentii* P. F. Stevens, have not yet been collected above 100 m. The family prefers well-watered conditions, the main exceptions being two warm temperate groups, the Arbuteae in California and the Ericoideae in S Africa.

3.2 Acid habitats

The combination of cool climate and high rainfall often results in the soils becoming acid, even over a base-rich rock (see pp. 118–120 in Whitmore 1975 for a discussion on the montane soils of Malesia), or in the development of peat bogs. The Ericaceae prefer such habitats; as Sleumer (1966, p. 470) notes, it is not clear whether Ericaceae reported as growing on limestone or other base-rich substrates were actually rooted in the rock or growing in a humus pocket. Epiphytic Ericaceae often grow in tree crotches where characteristically often very acid humus accumulates (Grubb and Edwards 1977 recorded a p.H. of

3.9–4.0 for the humus from a tree crotch at Marafunga, Papua New Guinea).

Many temperate Ericaceae are known to have a mycorrhizal association which is believed to help in obtaining nutrients in such base-poor environments (see also Leiser's 1968 report on the mucilaginous root sheath occurring in at least some Ericaceae). However, the study of nutrient cycling in the habitats that Ericaceae favor is only just beginning.

3.3 Heliophilic tendencies

The preferences of most Ericaceae for well-lighted habitats are well known (Camp 1942; Sleumer 1965, 1966). All New Guinea Ericaceae grow in rather open, often stunted forest, clearings, forest margins, or in open habitats such as bogs, grassland, and rock outcrops, or as epiphytes or lianes in the crowns of trees. Sleumer (1965) noted that if they grew in shady habitats they tended to be sterile.

3. 1–3 Combined:

The effects of climate, acidity of the habitat, and insolation are interconnected. Ericaceae are predominantly epiphytic in the crowns of trees at low altitudes in New Guinea, although they sometimes occur on acid sands with open vegetation (more frequently elsewhere in Malesia) or on rock outcrops, i.e., acid, well-insolated, but not notably cool, habitats. Thus in the Kiunga area (Western Province, Papua New Guinea), which is about 300 km from the sea and experiences very heavy rainfall, *Dimorphanthera intermedia*, *D. tedentii* and *Vaccinium* sp. are not infrequent epiphytes, although they are at less than 100 m elevation. In the same area are species of *Podocarpus*, *Lithocarpus* and *Calophyllum*, all either species of other basically montane genera or species which elsewhere grow at higher altitudes. This suggests that there are factors of the ecology, probably climatic, at Kiunga that favor such apparent altitudinal irregularities. At intermediate elevations the family occurs in similar habitats, and also in the often rather dwarfed and open vegetation on sharp ridges; they also invade road cuttings, grassland, etc. At still higher altitudes, subalpine shrub may be locally dominated by Ericaceae, and the vegetation is low and often partly open.

There is often infraspecific variation in habitat, a species that is epiphytic and/or lianoid (see below) at lower elevations being shrubby and terrestrial at higher elevations. On Mt Strong *Dimorphanthera amplifolia* (F. Mueller) P. F. Stevens was a very common shrub in Subalpine forest growing on peaty soil; at lower elevations it was an epiphyte. On Mt Suckling the variable *Rhododendron truncicola* grew in open vegetation in acid, sandy, riverine flats, on the forest floor in rather open vegetation on sharp ridges, and as an epiphyte in giant *Araucaria cunninghamii* trees which overtopped the closed forest below. Further examples are given by Sleumer (1966, 1967). In the New World tropics, Ericaceae sometimes grow as epiphytes in mangrove forest and also at low altitudes terrestrial on acid, sandy soil. Infraspecific variation in habitat comparable to that described above is reported from New World Vaccinieae (Camp 1945), and in *Rhododendron* section *Maddenia* from the Himalayas (Cant 1937).

3.4 Habit and architecture

Ericaceae throughout the world are generally small to large shrubs, or sometimes smallish trees, as in *Rhododendron*, *Agauria* and *Oxydendrum*. Herbs or near herbs occur in the predominantly temperate Monotropoideae, Pyroloideae and Wittsteinioideae. Growth patterns of New Guinea Ericaceae are dealt with in some detail here; those of the whole family are little known, although the preliminary findings of Temple (1975) indicate considerable diversity (Fig. 4 see Hallé *et al.* 1978 for definitions).

From admittedly casual observations, many, if not all, the species of *Rhododendron*, as well as *Gaultheria pullei* (frequently!), seem to belong to Leeuwenberg's model: there is no trunk, and overall construction is modular, the sympodial axes being terminated by inflorescences. This model has been reported for *R. aurigeranum* by Temple (1975), who notes that it, as well as Scarrone's model, which differs only in having a monopodial main axis, are common in the Ericaceae, intermediates also occurring.

Many other New Guinea Ericaceae are similar, except that the axes are determinate because of the death of the apex, e.g., *Gaultheria mundula*, *Vaccinium amblyandrum* var. *pungens*, *Diplycosia rupicola*, *Dimorphanthera microphylla* and *Agapetes vitis-idaea* (see also below). This growth pattern is probably common in erect Malesian members of these genera.

The lianoid New Guinea Ericaceae also have determinate axes that abort at the apex, but the axes cannot be supported by the lignification that they develop; the sprawling, vine habit is the result. These vines tend to bear their flowers along the leafless, older part of the stem. Plants with this type of growth are probably referrable to the ill-defined Champagnat's model, which has also been reported from a tropical American genus of the Vaccinieae, *Sphyrospermum* (Temple 1975) and probably occurs in *Gaultheria adenothrix* (Miq.) Maxim. (Fig. 4, H).

Mangenot's model, in which the main axes are mixed, the basal part being orthotropic and the apical part plagiotropic, occurs in a temperate shrubby species of *Vaccinium* (Hallé *et al.* 1978), as well as other species of *Vaccinium* and *Leucothoe* (pers. obs.); it should be looked for in lianoid or pendent New Guinea Ericaceae.

There are two complicating factors in the analysis of New Guinea and other Ericaceae in terms of architectural models. The first is that several species have subterranean rhizomes that turn up at the end and produce above ground shoots which, in the cases known, conform to one of the subtypes of Leeuwenberg's model as defined above; however, growth by rhizomes is accommodated neither in currently accepted models nor by reiteration as currently understood. Such rhizomes are known in *Rhododendron anagalliflorum*, *Vaccinium amblyandrum* especially var. *amblyandrum*, *V. crassiflorum*, *V. decumbens*, *V. oranjense*, *Gaultheria mundula* (probable), *Agapetes prostrata* P. F. Stevens, *A. rubrocalyx* and *A. vitis-idaea* from New Guinea, and *G. borneensis*, *G. pernettyoides*, *Diplycosia elliptica* and *D. kinabaluensis*, all from Borneo. They are probably more common, although our field knowledge is poor and collections so often lack the underground parts of the plant that Sleumer (1966, 1967) did not mention rhizomes in his descriptions. Many species layer, especially in moss forest, and ordinary shoots may then become difficult to distinguish from rhizomes, since all Malesian Ericaceae that I know have scales at the bases of the innovations. Short rhizomes occur elsewhere in *Rhododendron* and *Ledum*, and longer rhizomes are common, e.g. *Cassiope*, *Gaultheria*, *Gaylussacia*, *Lyonia*, *Vaccinium* and *Zenobia*.

The second problem is that a number of species may be erect shrubs, trailing shrubs, or vines, depending on the habitat, as anyone who has commonly collected Ericaceae soon realizes. This is also clear from Sleumer's descriptions of the species. Many species of *Agapetes*, *Dimorphanthera*, *Gaultheria* and *Vaccinium* have rather slender, albeit wiry, stems, and the transition to the vine habit given the right genotype or environment seems to be easy. Thus there may be species that are intermediate between 2 models, as well as infraspecific variation in model type. (Hallé *et al.* (1978) note similar examples in their discussions of Champagnat's model; since the final form of the model is not the result of active growth processes, this is to be expected here.)

Thus many Ericaceae, both temperate and tropical, do not lend themselves readily to an attempt at categorization in terms of models; this was also made clear by Temple (1974). It is perhaps more useful to note that New Guinea Ericaceae have determinate axes, and at least the majority have spirally arranged leaves. One can then consider the variation in habit and physiognomy seen and its possible ecological significance, bearing in mind that the particular aspects singled out for attention are part of almost a continuum of variation.

More or less parallel physiognomic series occur in *Rhododendron*, with terminal inflorescences, and the other genera, which, for the purposes of discussion, all have aborting stem apices (Fig. 4). In both there are phanerophytes with more or less steeply ascending branches, either shrubs or small trees. In rather open, Subalpine forest, forms with rather few, steeply ascending branches occur, as well as those with more numerous and widely spreading branches; the branches may be decurved as in *Vaccinium oreites* and *V. kostermansii*.

With increasing plagiotropy of the branches in *Rhododendron*, at least, dwarf, spreading forms may result; these chamaephytes (less than 30 cm tall) may grow as epiphytes, e.g. *R. caespitosum*, or sprawling over rocks, e.g. *R. gracilentum*. The angle at which the branches spread may to a greater or lesser extent be accentuated by environmental conditions. In the chamaephytic species of *Vaccinium* section *Oarianthe* and *Agapetes* subgenus *Paphia* the low stature of the above-ground parts is probably due to environmental pruning and small growth increments; the shoots themselves are usually strictly orthotropic (c.f. the tripartite division of chamaephytes in Raunkiaer 1934). Chamaephytes are not known in *Gaultheria* and *Diplycosia* in New Guinea.

Species of *Vaccinium*, *Gaultheria* and *Agapetes* with rhizomes grow in open, often grassy habitats at high altitudes; the rhizomatous, chamaephytic habit seems suited to such conditions. Thus on Mt Giluwe *V.* c.f. *amblyandrum* grows above the tree limit in tussock bogs; the rhizomes grow in and amongst the dense tussocks, and the exposed, leafy shoot is less than 3 cm long.

Rhododendron anagalliflorum is a plant of lower altitudes. *R. saxifragoides* is the only New Guinea member of the family that forms sometimes quite prominent tussocks in bogs or wet grassland. Growth increments are small, the leaves are steeply ascending, and old foliage persists along the stems. Its architecture, Leeuwenberg's model, is similar to that of other New Guinea species of *Rhododendron*, but its physiognomy and habitat are different. The tendency of the more erect growing species to flop over and layer is best shown in the mossy forest in which so many species grow; branches or fallen trunks may develop roots.

Vaccinium varingaefolium, from W Malesia, persists after a fire because shoots develop from the base (Sleumer 1967). *V. striicaule*, from New Guinea, may also persist after fire (Lane-Poole 1925, p. 179, as *V. blepharocalyx*), and there are *Vaccinium*-dominated shrubberies at high altitudes on the much fired Mt Giluwe. Similar behavior occurs also in the closely related Afro-American

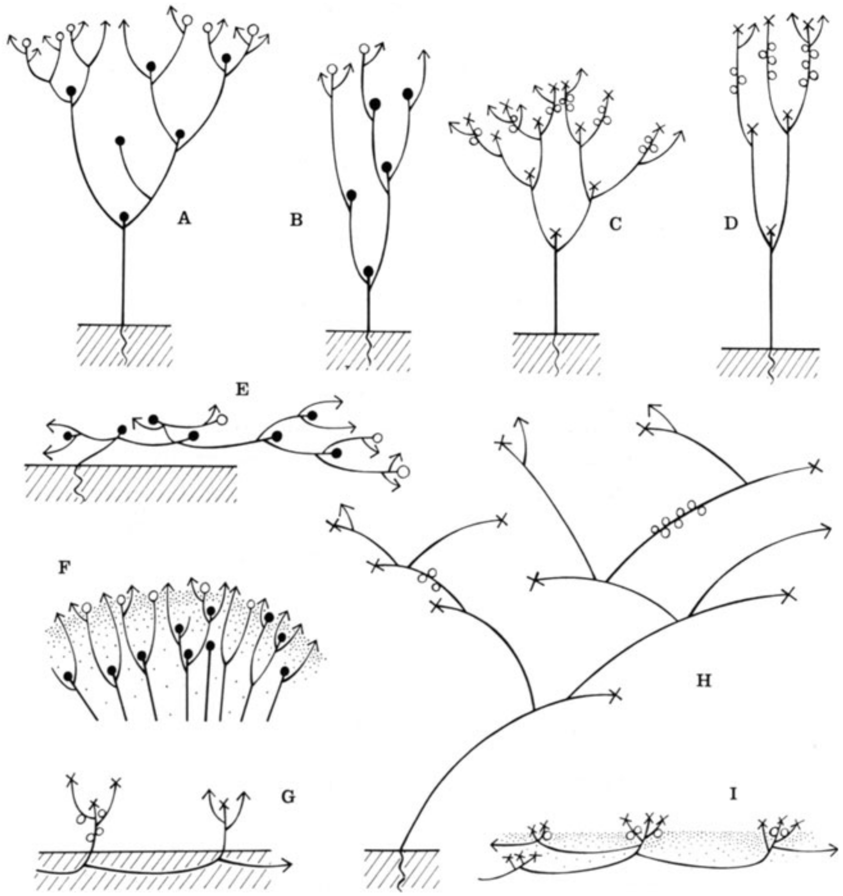

Fig. 4. Growth types in some New Guinea Ericaceae. A, *Rhododendron culminicola*; B, *R. wormersleyi*; C, *Vaccinium striicaule*; D, *Diplycosia rupicola*; *E*, *Rhododendron gracilentum*; F, *R. saxifragoides* — single plant; G, *Agapetes vitis-idaea*; H, *Dimorphanthera anchorifera*; I, *Vaccinium amblyandrum* var. *amblyandrum*. Arrows = growing innovations; x = aborted stem apices; ● = old (terminal) inflorescences; ○ = current inflorescences; diagonal hatching = ground; stippling = organic matter. N.B. Young stages before flowering omitted; those of *Vaccinium*, *Agapetes*, *Dimorphanthera*, and *Diplycosia* probably sympodial, those of *Rhododendron* probably monopodial.

pair of genera *Agauria* and *Agarista.* Roots, burls, swollen stems and associated roots, from which shoots may develop after fire damage to the above ground parts of the plant, occur in genera such as *Arctostaphylos* (Jepson 1916) and *Lyonia* (Judd 1981). The stem bases, and often the adjacent roots, of epiphytic species in all genera are quite frequently more or less swollen. This is common in epiphytic Ericaceae, and is known from tropical American Vaccinieae (Camp 1945), *Rhododendron* section *Maddenia* (Cant 1937), and *Agapetes* subgenus *Agapetes.* Sleumer (1967, p. 476) notes that the roots of *Vaccinium, Dimorphanthera, Agapetes* (and *Costera*) may be swollen. This swelling is perhaps associated with a swollen stem base.

Scandent forms occur in *Dimorphanthera, Agapetes* subgenus *Paphia* (common in both), *Vaccinium* (uncommon); some grow up to 30 m long, e.g. *A. stenantha*, and may be either epiphytic or terrestrial. Some species of *Gaultheria* and *Diplycosia* sprawl, rather than being properly scandent; *Rhododendron* shows the least tendency to be a vine.

It is clear that this whole subject would repay careful study. Differences in Ericaceae growing in cold temperate areas, many similar to those described above, show close correlations between method of growth and habitat (du Rietz 1931).

3.5 Leaf type

Variation in both leaf size and shape within New Guinea Ericaceae is considerable. Generally speaking, the leaves tend to be smaller and thicker, and sometimes with more prominent indumentum, at higher altitudes. Some species of *Rhododendron*, e.g. *R. purpureiflorum*, have narrowly elliptic to sublinear leaf blades, but none has linear leaves like those of some West Malesian species in *Rhododendron* subsection *Pseudovireya* and subsection *Euvireya* series *Stenophylla* and *Taxifolia.* In neither *Gaultheria* nor *Diplycosia* is there great variation in lamina shape; that within *Vaccinium* is moderate, and within *Dimorphanthera* and *Agapetes* subgenus *Paphia* rather little.

The Ericaceae as a whole is noted for diversity in leaf shape, and this sometimes occurs within a genus, as within West Malesian *Diplycosia* and *Rhododendron*, and also the temperate to arctic genus *Cassiope* and the tropical American montane genus *Agarista* (Stevens 1970). Infra- and intergeneric variation in leaf shape in the Vaccinieae is generally less than in other tribes of the Vaccinioideae and Rhododendroideae. New Guinea Vaccineae are as variable as other tropical representatives, but overall, New Guinea Ericaceae are not notably variable in leaf shape. As might be expected, marginal serrations are usually inconspicuous.

The leaves in *Rhododendron* section *Vireya* are scattered or arranged in false verticils. Although prostrate species of *Rhododendron* in New Guinea apparently always have pseudoverticillate leaves, erect species may have scattered to pseudoverticillate leaves. Some species of *Agapetes* subgenus *Agapetes* and the related *Vaccinium* section *Epigynium*, both commonly epiphytic groups, also have pseudoyerticillate leaves, and there is a common tendency in the family for the expanded leaves to be borne mainly in the uppermost part of an innovation.

Another variable of possible ecological significance is the angle at which the leaves are held. Thus, *R. womersleyi* has small, spreading leaves, while the larger leaves of *R. atropurpureum* are often strongly ascending; both species grow in well-lighted conditions. There is comparable variation in the angles at which the leaves are borne in other genera.

3.6 Corolla and stamen

In general stamen type and development, in the occurrence of pollen tetrads in all genera, and in the ubiquitous occurrence of sympetalous corollas, New Guinea Ericaceae agree with the rest of the family, both tropical and temperate. In *Rhododendron*, *Gaultheria*, and *Diplycosia* at least the pedicel is erect in fruit, whatever its position in flower, a change common elsewhere in the family. New Guinea species of *Rhododendron* have viscin threads, like the majority of the Rhododendroideae. However, some details of the variation in corolla and stamen are important in understanding the evolution of the family in New Guinea.

Species of *Gaultheria*, *Diplycosia* and *Vaccinium* have small (usually less than 1 cm long) urceolate to campanulate, rarely tubular, white to red corollas and are more or less similar in this to other members of the genus both elsewhere in Malesia and to many other genera throughout the world. In Java pollination by short-tongued insects or self pollination seems likely for some species of *Gaultheria* and *Vaccinium* (Doctors van Leeuwen 1933).

Most members of *Dimorphanthera*, *Agapetes* subgenus *Paphia* and *Rhododendron* have large flowers more than 1 cm long and tubular to infundibular in shape; corolla colors are red, white or yellow, and there is no asymmetry in the color patterning that occurs in a few of these species. Details of the variation in the Papuasian species of *Rhododendron* has been dealt with in some detail (Stevens 1976). The long, tubular, often bright red, thick-walled corolla so common in *Dimorphanthera* section *Trochilanthe*, *Agapetes* subgenus *Paphia*, and *Rhododendron* (Stevens 1976, Type 1D) seems to be associated with bird pollination (Stevens 1976, 1977), and is known from West Malesia, the Himalayas (*Agapetes* subgenus *Agapetes*), Africa (*Erica*) and the Americas (commonly in the Vaccinieae, but also some members of the polypetalous *Bejaria*, of the Rhododendroideae, where the edges of the broad petals overlap). The diversity in details of shape and coloring of the New Guinea Vaccinieae with this corolla type is less than that of their tropical American relatives, and the variation in mainland Asian representatives of *Agapetes* subgenus *Agapetes* is also considerable. Long, tubular, red corollas occur in some W Malesian species of *Rhododendron*, but they are very uncommon in the Vaccinieae there. Another ornithophilous flower type, with a curved tube and the anthers and stigma positioned on the adaxial side of the tube (Type 1A) is known only in New Guinea, where it occurs in about 38 species of Rhododendron; it seems to be unique in the family.

The large, white, campanulate-infundibular, very sweet-scented flowers found in 10 New Guinea species of *Rhododendron* (Type 2B) seem to be restricted to E Malesia (4 species with a flower type like, or similar to, this type occur in the Celebes-Moluccas region); it is possible that such flowers are pollinated by bats. I do not know of similar flowers elsewhere in the family.

The predominantly white, scented, long-tubular flowers (Type 2A) so common in *Rhododendron* subsections *Solenovireya* and *Siphonovireya* that are probably pollinated by sphingid moths also occur in species of the genus in W Malesia, albeit less frequently. S African species of *Erica* and North American species of *Rhododendron* have a similar floral syndrome, but it is as yet unknown from other tropical areas.

The large, red to orange, campanulate corolla that occurs in *Rhododendron* (Types 1G and 3A) and *Dimorphanthera* section *Dimorphanthera* occur in the former genus throughout Malesia, although the strictly red, scentless flowers occurring in the latter are particularly common in New Guinea. Flowers of this general type are uncommon elsewhere in the family, although they may occur in some species of *Rhododendron* from the hills of SE Asia. The flowers of *Dimorphanthera* section *Pachyantha*, which vary from whitish to red in color and have very thick walls, are also scentless and campanulate, although they are less than 1 cm long. There is circumstantial evidence that both sections of *Dimorphanthera* are visited by birds (Stevens 1976, 1977). Other flower types in both New Guinea and W Malesia are found in only a very few species (Stevens 1976). Nothing is known of their function in pollination; some of these types seem restricted to one of the two areas.

In general terms, much of the variation in corolla characters in New Guinea Ericaceae, especially *Dimorphanthera*, *Agapetes* subgenus *Paphia* and *Rhododendron* seems associated with pollination by large animals. Almost twice as many species with corollas which appear adapted to such pollination occur in New Guinea as in the rest of Malesia.

The stamens of *Agapetes* subgenus *Paphia* and *Dimorphanthera* are rather different to those of Malesian *Vaccinium* and other strictly temperate Vaccinieae, being larger, and in *Dimorphanthera* much more woody and the two whorls more obviously dimorphic. However, the stamens of *Dimorphanthera* are similar to those of the probably related American genus *Satyria*, and the connate filaments that occur in some species of *Agapetes* subgenus *Paphia* are quite common in some American genera and also rarely occur in the not immediately related *Agapetes* subgenus *Agapetes*. A more detailed analysis of the variation of floral (and other) characters in the Vaccinieae confirms this general reticulate pattern of variation (Stevens ms).

3.7 Fruit and seed

Although the general fruit types of the New Guinea Ericaceae are well known, relatively little is known about seed structure, especially in the Vaccinioideae, and practically nothing is known of the details of dispersal.

All genera, except for *Rhododendron*, have colored, fleshy fruits, which are similar to fruits of both tropical and temperate representatives. The seeds, so far as is known, have a single layer of cells of which the outer periclinal walls (and sometimes also the inner) are unthickened, while the rest are thickened, again a common pattern in seeds of fleshy-fruited Ericaceae. Although endozoic transport, probably by birds, of the seeds is presumed, there is little direct evidence that this is so. *Gaultheria* and *Diplycosia* also have capsules, so there may be some local wind dispersal as well. A rather interesting seed type, with testa cells with longitudinally reticulate/scalariform thickening, which become mucilaginous on wetting and an often green embryo, occurs in a number of Vaccinieae from tropical America and mainland SE Asia; it has not been observed in any of the 35 New Guinea species of *Vaccinium*, as well as a few species of *Agapetes* and *Dimorphanthera* examined, although some species have green embryos.

Rhododendron has a capsular fruit and small seeds with long tails. The tails of the seeds are made up of cells similar in shape to those of the rest of the seed. Although such seeds are an extreme type in the genus and family, this is a matter of degree only, and there are other types of winged or tailed seeds. These small, tailed seeds would seem suitable for the epiphytic habitat of many of the species, and also may help dispersal into the open, geologically transient habitats that the genus also favors (see below).

3.8 Chemical constituents

Unfortunately little is known about the chemical constituents of tropical Ericaceae. Methyl salicylate is known from species of both *Gaultheria* and *Diplycosia* in New Guinea (see also Sleumer 1967), but it also occurs in several temperate members of the family (both immediately related, as well as in the Pyroloideae). Casual observation suggests that the Ericaceae are not much eaten, although in the Subalpine region on Mt Strong, Central Division, extensive damage to the leaves of a large population of *Rhododendron culminicola*, probably caused by the weevil *Gymnopholus* (*Symbiopholus*) *symbioticus* Gressitt, was observed (Coode and Stevens 1972). *Rhododendron macgregorii* is toxic to small mammals, and can be used to kill rodents (Henty and Pritchard 1975).

The temperate members of the family are noted for an accumulation of polyphenols and tannins, and sometimes other more specific toxins as well (see Hegenauer 1966 for references). McKey *et al.* (1978) noted that tannins might be implicated in protection against herbivores of vegetation in forest in Africa growing in poor, rather acid conditions, so knowledge of the chemical spectrum of the vegetation types in which the Ericaceae are so prominent would be of more than passing interest (see also Janzen 1974). Tannins may also help to generate the soil conditions that the family likes.

3.9 Other characters of New Guinea Ericaceae

Rhododendron subsection *Phaeovireya* has distinctive scales (Seithe 1960), but the scales throughout section *Vireya* are of the same general type that occurs elsewhere in the genus. The small, glandular hairs of many of the New Guinea Vaccinieae are also similar to those of other Vaccinieae throughout the tropics; the indumentum of New Guinea species of *Diplycosia* and *Gaultheria* is not remarkable.

Anatomical details as far as known also suggest no uniquely New Guinean features. *Vaccinium*, as noted above, is similar to other Malesian representatives of the genus, while *Dimorphanthera* and *Agapetes* subgenus *Paphia* have a number of characteristics in common with American genera. However, in general Ericaceae in tropical (to subtropical) montane areas are more likely to have a single or multiple hypodermis as well as some sort of lignification of the epidermis and/or hypodermis and/or mesophyll. The relatively large vessels and vein endings of *Agapetes* subgenus *Paphia* and *Dimorphanthera* and their American relatives occur in commonly epiphytic groups, however, these characteristics are neither restricted to New Guinea taxa in the Ericaceae, nor, even when considering New Guinea, are they the only anatomical syndrome compatible with the epiphytic habitat. Anatomical characteristics of *Rhododendron* and *Diplycosia* in New Guinea, although distinctive, are found in all Malesian representatives of these taxa as well as in other taxa elsewhere.

4. General discussion

Too little is known about the relationships of New Guinea Ericaceae to make more than suggestions as to their history and origins, and there is little fossil evidence for the whole of Malesia. Also, some of the statements made below are based on questionable assumptions.

Most authors agree over the outline of the plate tectonic history of the New Guinea region (Raven and Axelrod 1972, 1974; Doutch 1972; Nix and Kalma 1972; Walker 1972; and van Balgooy 1976; together with papers cited therein). The Australian plate, New Guinea not yet being recognizable, moved north in the early Tertiary and emergent land on the northern part of the plate entered the tropics somewhat before the Miocene, 25 million years ago. Uplift began as the Australian plate approached SE Asia. Much of New Guinea finally became emergent only in the Pliocene; tectonism probably began in the middle to late Miocene, but mountain uplift may not have been substantial much before the Pliocene, 5 million years ago. By this latter time New Guinea seems to have reached substantially its present position. Mountain uplift and vulcanism are still very active in parts of New Guinea, and Quaternary climatic changes have led to considerable vertical movements in the position of the Upper Montane and Subalpine vegetation which the Ericaceae favor. Despite changes in the sea level, the Moluccas, some islands in Geelvink Bay, and the Bismarck Archipelago remained separate from the New Guinea mainland.

It is unlikely that *Rhododendron*, *Vaccinium*, and at least most of *Gaultheria*, were on both halves of Malesia in the earlier Tertiary. The distinctions between the subsections and series of *Rhododendron* are slight, being based mostly on differences in leaf shape and size, details of scales, and corolla type. It has been known since the days when Malesian rhododendrons were popular as stove plants in the last century that it is easy to cross even the most dissimilar-looking plants and to obtain fertile hybrids (Henslow 1891 — W Malesian species), and this has been abundantly confirmed since then (e.g. Sleumer 1966 (esp. pp. 476, 478), 1973; Stevens 1974 — New Guinea species; E and W Malesian crosses — J. J. Rouse, pers. comm.). Chromosome counts from Malesian species are diploid, 2n = 26, except for a single triploid (Jones and Brighton 1972); the species counted came from several subsections and various altitudes. Indumentum and many floral characters in *Rhododendron* section *Vireya* are derived. Although many of the species of *Rhododendron* subgenus *Rhododendron*, to which section *Vireya* belongs, are polyploid (Janaki-Ammal *et al.* 1950), there are also diploids, and *Rhododendron* section *Vireya* is much related to other groups in montane SE Asia.

Rhododendron is clearly very diverse on the SE Asian mainland. The diversity of section *Vireya* in W Malesia is greater than in E Malesia in all characteristics except, perhaps, floral types and habit. Despite the abundance and diversity of *Rhododendron* in New Guinea, only three species occur south and east of the area, although there is no obvious ecogeographic reasons for such an abrupt cut-off (see also van Steenis 1934). Hence it seems reasonable to postulate movement from west to east through Malesia. In Malesian *Vaccinium* as well, the distinctions between the sections are slight, and all sections have substantial similarity in derived floral and anatomical characteristics. Little is known of their cytology and ability to hybridize, although on Mt Wilhelm, Papua New Guinea, *V. amblyandrum* (section *Oarianthe*) and *V. cruentum* (section *Bracteata*) hybridize. Relatives of the Malesian species occur in SE Asia; there is as yet no compelling evidence of a transpacific relationship (c.f. Sleumer 1941).

The diversity of the relatives of the Malesian species of *Vaccinium* is greatest on the SE Asian mainland. Much of the variation there is probably of a derived nature, e.g. inflorescence and flower type, indumentum, leaf arrangement, seed type (Stevens ms., c.f. Sleumer 1941), but there are also less obviously specialized groups. Again, there are few species occurring to the south and east of New Guinea. It is suggested that *Vaccinium* also entered New Guinea from the west.

The history of *Dimorphanthera* and *Agapetes* subgenus *Paphia* in Malesia is unclear. Both have representatives in W Malesia (see above), and they are probably closer to the W Malesian genus *Costera* and to tropical American genera than to Malesian *Vaccinium*. Their history in Malesia may be quite different than that suggested for the above genera, and their immediate ancestors outside Malesia may have been adapted to the tropical montane habitat. (If, as Maguire *et al.* (1978) believe, *Dimorphanthera* and *Satyria* are not close, the problem may be of a different order, but with yet more examples of convergent evolution in characters of anatomy and stamen).

Diplycosia is probably a genus that has evolved wholly in the Old World montane tropics and has also entered New Guinea from the west. As mentioned above, the diversity of the genus is clearly greatest in W Malesia, especially Borneo. In addition, some of the species of *Gaultheria* in West Malesia, notably the curious *G. pernettyoides*, have both the facies and anatomy of *Diplycosia*, although differing in stamen type.

I suggest that diversification of the Ericaceae in New Guinea has occurred since late Miocene at the earliest, some 10 million years ago, and has been dependent on the arrival of probably only a few ancestors, mostly from W Malesia (note that the little evidence we have — Muller 1972 — suggests that in NW Borneo Ericaceae occurred more frequently in Pliocene than in older sediments). The family in New Guinea has always been predominantly montane, since there the conditions that the family favors are most widespread; the occurrence of species in the lowland is a secondary phenomenon. The isolation, youthful topography, and ecological diversity of the abundant montane habitats of New Guinea would seem ideal for speciation. The plasticity shown by many species in their growth form, their frequent ability to grow both as epiphytes and on the ground, and the probable dispersal of their seeds by wind and animals which, on occasion, may result in dispersal over quite considerable distances, might all be expected to give a species rather greater chance of survival than the transient nature of the habitat in which the individual grows might suggest.

Although little is known about the selective value of much of the variation discussed above, it seems clear that much of the variation in form of the plant, coupled with variation in leaf size, has allowed species in *Rhododendron* and *Vaccinium* section *Orianthe* at least to exploit particular micro-habitats on the mountains at the upper limit of woody plant growth; species with these characteristics are concentrated in the Snow Mountains of Irian Jaya, where conditions suitable for their growth are most common. The concentration of species of *Agapetes* subgenus *Paphia* on the mountains of SE New Guinea is accompanied by some similar variation; no other genus in New Guinea has a similar distribution pattern.

Another important factor in the diversification of *Rhododendron* in particular has been variation in flower type, which, coupled with geographical and other aspects of ecological isolation, may have aided speciation. However, there are no obvious internal barriers to hybridization in *Rhododendron*, and the variety of hybrids found in disturbed habitats in the wild suggests that any ethological isolating mechanisms can be readily broken down (Stevens 1974). The adoption of ornithophily seems to have been a factor in the evolution of the Ericaceae in the cool, cloudy conditions of the Upper Montane and Subalpine forest (Stevens 1976), although it should not be forgotten that several species of *Vaccinium*, usually with small, urceolate corollas, also grow there. Clearly other factors must be involved; for example, we know little about how much self pollination and inbreeding takes place or about details of flowering times in different species (for possible differences, see Kores 1978).

It is obvious that the characters discussed above that occur in the New Guinea Ericaceae are paralleled in a general or even quite specific way by Ericaceae elsewhere in the tropics and often in the temperate zone as well. A few characters, like superficial phellogen, may have evolved only once in the family, but this character is found in numerous species through the SE Asian tropics and subtropics. Some of the characters more particularly associated with the tropics, and in part at least involved in the diversification of the family in New Guinea, such as the development of certain flower types, the adoption of the epiphytic habitat, the vine growth form, and possibly some anatomical characteristics, have also clearly evolved repeatedly in the family; it is hard to imagine the monophyletic origin even of the distinctive zygomorphic ornithophilous flower type so common in New Guinea rhododendrons. The possibly bat-pollinated and the zygomorphous bird-pollinated flower types, and the deeply laciniate scales of *Rhododendron* subsection *Phaeovireya*, are the only major characters or character complexes which probably evolved in the New Guinea Ericaceae and nowhere else.

Many of the supraspecific taxa recognized in the Malesian Ericaceae reach their eastern or western limits somewhere between Borneo and New Guinea, although both *Dimorphanthera* section *Dimorphanthera* and *Vaccinium* section *Orianthe* extend to the Philippines (Figs. 2 and 3). That the area between the New Guinea mainland and Borneo and Java is one in which there is considerable quantitative and qualitative change in many elements of the flora and fauna has long been known (e.g. Wallace 1869; Raven and Axelrod 1972). These distribution patterns in the Ericaceae are probably due to factors like the isolation of the two main land masses in Malesia and possible biotic differences on these land masses, which in turn may reflect events associated with plate movements. Biotic differences seem to be an immediate possibility only when considering some pollination syndromes. Even here, although many New Guinea Ericaceae are probably pollinated by the overwhelmingly Australasian group, the Meliphagidae, their floral syndromes do not seem unsuited for pollination by the Nectarindae, which are more common in W Malesia. The two examples of a New Guinea-Philippines distribution (*Dimorphanthera* section *Dimorphanthera* and *Vaccinium* section *Oarianthe*) represent examples of a fairly frequent distribution type which cannot be satisfactorily explained, unless it represents migration along the New Guinea and Philippines montane tracks (van Steenis 1934).

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Note

A specimen of *Dimorphantera*, *LAE 59446*, was recently collected in the Star Mountains. It apparently represents an undescribed species, and is particularly notable in that the filaments are connate into a tube, i.e., it has the key character of the tropical American genus *Satyria*. This is another example of convergent evolution in this character in the Vaccinieae.