

## Mount Kinabalu: Hotspot of plant diversity in Borneo

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An overall programme of research on the flora of Mount Kinabalu has four major objectives as outlined below. (1) Inventory of vascular plants. The Kinabalu flora, with approximately 5,000 taxa recognized, is now completely enumerated and published. The database includes over 62,000 specimen records representing 218 families and 1,070 genera. The final part of the inventory (dicot families Magnoliaceae to Winteraceae) was published in 2004. The enormous diversity of Kinabalu occurs in an area of only 1,200 km<sup>2</sup>, making this flora one of the richest in the world. Analyses of the general geographical distribution in four exemplar families involving 143 taxa indicated that floristic relationships are strongest with Borneo, the rest of West Malesia and continental East and Southeast Asia. Weaker affinities were found east of Wallace's line in Central and East Malesia, Australia and the Pacific islands. Floristic similarities between Kinabalu and a few other Malesian high mountains are briefly considered. A website (<http://herbarium.lsa.umich.edu/kinabalu>) provides searchable databases on pteridophytes, gymnosperms, monocots, and dicots. (2) Geographic information system. A geographic information system (GIS) is being used in the floristic, phylogenetic and ethnobotanical studies. Over 500 locally named landforms and villages, most of which were not previously mapped, are included on a coloured topographic map that is ready for publication. Three components are an introduction and gazetteer, the map itself, and a Landsat TM image of the area. Maps also are being prepared for areas around nine villages where ethnobotanical studies have been concentrated. The GIS technology additionally has been applied to investigating complex phylogenetic and biogeographic relationships. (3) Phylogenetic analyses. Various exemplar taxa in such unrelated groups as the ferns, orchids, stone-oaks (*Lithocarpus*), and nettle relatives (*Elatostema*) have been subjected to phylogenetic analysis. Among the conclusions resulting from these independent studies is that some high-elevation, endemic species have been derived from neighbouring species of lower elevations, rather than having originated by dispersal from distant geographical sources. (4) Ethnobotany. An ethnobotanical project (*Projek Etnobotani Kinabalu [PEK]*) has given special attention to the collection and description of plants that are economically valuable, ecologically important, and threatened by human activities. Seventeen local collectors worked extensively around their home villages, contributing some 9,000 specimens that document names, uses, and localities for both used and currently unused plant resources. A team including local people, Kinabalu Park personnel and visiting researchers is studying patterns of Dusun knowledge of plants. During the project, research and capacity-building opportunities have been provided for students from Malaysia and other Asian countries, particularly through a series of certificate training courses. The results of the floristic inventory will be returned to local communities in the form of a *Dusun Ethnoflora*. These efforts should provide a continuing incentive to the communities to carefully manage unprotected forests in buffer zones around Kinabalu Park and to promote the viability of Dusun botanical and ecological knowledge.

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## Introduction

Mount Kinabalu, located on the island of Borneo in the Malaysian state of Sabah, is one of the world's most remarkable landforms. Of origin in the late Pliocene-Pleistocene, Kinabalu rises from near sea level to nearly 4,100 m and is isolated by vast distances from other mountains of comparable elevation. Its exceedingly diverse biota offers outstanding opportunities for research on evolution and diversification of species and vegetation types. In 2000 Kinabalu Park was inscribed on the World Heritage List. Considering that the symposium deals in part with local plant diversity and complexity problems, this account represents an especially local example; the area of Mount Kinabalu has an extent of only *c.* 1,200 km<sup>2</sup>.

A discussion by van Steenis (1964) on plant geography of the mountain flora of Kinabalu established a foundation upon which much subsequent biogeographical and evolutionary research can be built and argued. van Steenis suggested that the interest and uniqueness of Kinabalu lies largely with its mountain flora (as distinct from that of the lowlands). He further noted that interpretation of a mountain flora requires recognition that some species may have evolved *in situ* and can be called autochthonous or centric, while others have migrated from remote centers of development and are called allochthonous or eccentric. This problem of biogeography and evolution presents a marvelous opportunity to employ phylogenetic analysis of morphological and molecular data to enhance understanding of the origin and evolution of species in the Kinabalu flora.

Many of the techniques and data van Steenis needed to better understand the phytogeography of Mount Kinabalu have only become well developed in the past 15 years, particularly those offered by molecular and morphological phylogenetic analyses and GIS. He lamented

that there was no complete plant list of Mount Kinabalu, a situation that is now nearly remedied. He further indicated that the north and east slopes of the mountain were almost completely unexplored. Since 1992 a team of ethnobotanical collectors has made over 9,000 new collections on the lower slopes of Kinabalu, mainly on the north side. These are contributing significantly to a fuller understanding of the composition and distribution of the flora.

Fourteen years ago it was suggested (Beaman & Beaman 1990) that this flora included about 4,000 species of vascular plants. A few years later the figure was revised to about 4,500 species, and now we know that the total is around 5,000 species. This extraordinary diversity in an area of only 1,200 km<sup>2</sup> is particularly remarkable considering that the analysis by Barthlott *et al.* (1996) of the global distribution of species diversity identified the six highest global diversity centres in the world as having more than 5,000 species per 10,000 km<sup>2</sup>. Our data indicating that 5,000 species occur in an area of less than 20 percent that unit size point to the extraordinary richness of the Kinabalu flora.

Five volumes are now published enumerating the groups of vascular plants on Mount Kinabalu (Parris *et al.* 1992; Wood *et al.* 1993; Beaman & Beaman 1998; Beaman *et al.* 2001; Beaman & Anderson 2004). A website (<http://herbarium.lsa.umich.edu/kinabalu>) provides searchable databases on pteridophytes, gymnosperms, monocots, and dicots.

It is now desirable to examine salient biogeographic, evolutionary and ecological principles that emerge from the enumeration. This could not be effectively done on a piece-meal basis with limited segments of the flora (*i.e.*, groups such as pteridophytes, gymnosperms, monocots, etc.), a circumstance that prevailed until three weeks before this symposium, because until then the database had been maintained



as separate components by major taxa. A new phytogeographic analysis comparable to that of Stapf (1894) should now be made, but more than a century of additions to our knowledge of the flora make this a daunting task. Stapf's analysis considered less than 15 percent of the currently known flora. With the completed inventory various other applications will be possible. For example, information could be provided, perhaps through the Internet, to facilitate field identification of species. In view of the present lack of up-to-date keys and species descriptions for many taxa, images of line drawings, photographs and herbarium specimens hold promise as identification aids.

In a general view of the vegetation, Kinabalu can be thought of as having four major zones dominated by trees: lowland tropical rain forest from the foot of the mountain at about 300 to 600 m (now mostly substituted with various kinds of secondary vegetation), hill forest, from about 600 to 1,400 m, in which the Dipterocarpaceae are especially important dominants, lower montane forest, from about 1,400 to 2,200 m, with families such as the Fagaceae, Lauraceae, Moraceae, Myrtaceae and Rubiaceae having special prominence, and upper montane forest, from about 2,200 to 3,400 m, in which gymnosperms and a few angiosperm genera are conspicuous. A fragmented sub-alpine scrub extends up to about 3,700 m. Above that level is a summit zone of alpine rock-desert with scattered communities of alpine scrub. Edaphic factors, ridges, valleys, slope, and exposure all influence the vegetation, giving rise to a highly diverse mosaic of vegetation types. It should be noted that the vegetation zones indicated above do not correspond to those designated by Whitmore (1984, fig. 18.1; 1998, fig. 2.7) for the mountains of Malaya. Mount Kinabalu is almost twice as high as any of the mountains on the Malay Peninsula, so it is not to be expected that there would be altitudinal correspondence. His dia-

grams show lowland forest extending to about 700 m, lower montane forest from 700 to 1,500 m, and upper montane forest from 1,500 to 2,100 m.

Detailed long-term ecological studies of the vegetation are being conducted by Kanehiro Kitayama and a number of collaborators. Kitayama has established permanent plots at various altitudinal levels and on different geological substrates to examine species composition and species-area relationships (see especially Kitayama 1991; Kitayama 1992; Aiba *et al.* 2002; Takyu *et al.* 2002). Along with the plots he has recorded extensive weather records from stations at various elevations (Kitayama *et al.* 1999).

The geology of Mount Kinabalu has received considerable attention over the past half century. Among the most important geological publications are those by Collenette (1958) and Jacobson (1970). The lower slopes of the mountain have thick layers of late Cretaceous to Tertiary sandstones and shales of the Trusmadi and Crocker Formations. The core of the mountain is a pluton of mainly hornblende and (granitic) adamellite diapirically emplaced into the complex of older rocks. The core is part of a large batholith underlying the area. The central part of the batholith was uplifted in the Pleistocene, forming the present mountain, and making it one of the youngest major mountains in the world. Pleistocene glaciation produced the present ice-carved topography of the summit area. Intrusive ultramafic rocks were uplifted with the core and appear rather like a collar around the mountain at lower and middle elevations.

### Geographical distribution, endemism

Stapf (1894), on the basis of the facts available to him at the time, gave a brilliant explanation of the history of the flora of Mount Kinabalu (J.H. Beaman 2001). This, however, was devel-

oped half a century or more before the concept of plate tectonics was elaborated. Thus he did not realize that Kinabalu was a very young mountain, whose flora could not have been so ancient as he imagined. Nor was he aware that New Guinea was part of the Australian continental plate, and that there had not been a continuous land connection between New Guinea, Borneo and Malaya at a time that would have allowed movement of the highland floras among these areas. His ideas on "land bridges" to explain phytogeographic relationships in the floras of Southeast Asia and Austral-Asia were taken up and vigorously elaborated some 40 years later by van Steenis (1934-1936), but these hypotheses must now give way to the recent information on the tectonic evolution of Southeast Asia as discussed by Hall (1996) and many other recent authors. Notwithstanding some of the currently unsupported conclusions reached by Stapf, his phytogeographical concepts of floristic relationships among the various regions are elegant and unassailable, and his explanation of the origin of the secondary vegetation as a product of human influence is all too evident today.

The overall distribution of the majority of species in the Kinabalu flora is not well documented, but we have more detailed knowledge of orchid distributions than for any other family. Among the total of 856 Kinabalu orchid taxa, 706 are fully determined. Eighty-six of these (12.2%) are known only from Mount Kinabalu. Among other taxa that have been analyzed, Beaman & Beaman (1998) considered the phytogeography of the Kinabalu Cyperaceae. This family was used because they had been treated in *Flora Malesiana* (Kern 1974; Kern & Nooteboom 1979) and they appeared representative of monocots in general. The predominant geographical affinity of the Kinabalu Cyperaceae is with Asia (45 taxa from a total of 73 considered). Some of these are also Austral (i.e., southern Southern Hemi-

sphere), a category that may have been under-represented in the analysis, because taxa well represented in Asia were placed in that category even when they extended to Austral regions. The second most common affinity was that of taxa restricted or nearly restricted to Malesia (25). A considerable number (10) of the lowland and hill-forest Cyperaceae are pantropical, and even the lower montane forest taxa include some pantropical members (4). Austral species were fewest in the analysis (9), but 13 taxa considered Asian in affinity also extend to Austral regions. Only two species of the Cyperaceae were regarded as endemic or subendemic. It is well to keep in mind that the statement about endemism made by Stapf (1894) over 100 years ago still rings true, *i.e.*, "To speak of the endemism of a district so little known and forming part of a likewise imperfectly explored flora is a very difficult task, ..." Another consideration is that with a poorly known flora the smaller the area the more difficult it is to be certain that so-called endemics are truly endemic. Thus, species limited to Borneo are more readily designated than are those limited to Kinabalu, and still more assurance is possible concerning species endemic to Southeast Asia rather than Borneo.

Wide disjunctions are most prominent among the upper montane/summit area Cyperaceae. A pattern repeated in several taxa is from Mount Kinabalu to southwest Sulawesi (particularly Mt. Latimodjong, c. 3,460 m) to various high mountains in New Guinea. Species with this distribution may also occur in high mountains of the Philippines and extend on to Australia and New Zealand. The low number of Kinabalu endemics in the Cyperaceae is characteristic of all the non-orchid monocotyledons (some 490 taxa), of which 48 were thought to be endemic, subendemic or with restricted, disjunct occurrences, and only 17 taxa were indicated as known only from



Mount Kinabalu, a mere four percent of the non-orchid monocotyledons.

Because dicotyledons in the families Magnoliaceae to Winteraceae (in alphabetical order) have been recently studied for the enumeration, it seemed useful to have data from them in addition to the Cyperaceae for purposes of this symposium. For the dicotyledons the Magnoliaceae (Nooteboom 1988), Rosaceae (Kalkman 1993) and Symplocaceae (Nooteboom 1977) are among families already published in *Flora Malesiana* and provide suitable examples of geographical distribution. Together they constitute 70 taxa, about equal to the number of Cyperaceae previously analyzed. For purposes of this analysis subspecies and varieties were regarded as equivalent to species. Hybrids were not included. Taxa occurring in the lowlands, hill forest and lower montane forest were considered to be lower elevation taxa, and those occurring in upper montane forest and the summit area were counted as high-elevation taxa. Twenty taxa occur at both lower and higher elevations, extending from lower montane forest or below into upper montane forest. The geographical divisions of Malesia used in the analysis follow Johns (1995), in which the category of Central Malesia (the Philippines, Sulawesi, Moluccas and Lesser Sunda Islands) is recognized in addition to the usual distinction of West Malesia and East Malesia. In Appendix 1 the column for Kinabalu endemics is placed at the centre, with Borneo, non-Bornean West Malesia and East and Southeast Asia extending to the left and Central Malesia, East Malesia, Australia and the Pacific Islands extending to the right (at progressively greater distances from Kinabalu), similar to the organization used by Stapf (1894). With one notable exception incompletely determined taxa (*i.e.*, those with the qualifiers *aff.* and *cf.* were not included in the analysis. The exception was *Eriobotrya aff. bengalensis*, a very distinctive plant known only

from a single collection on extreme ultramafic substrate, which probably represents an undescribed species.

The predominant geographical affinity of the flora, based on these dicotyledons, is with Borneo (47 taxa), as shown in Appendix 1. The next strongest relationship is with West Malesia (excluding Borneo), with 35 taxa. The third highest affinity is with Central Malesia with 26 taxa, followed by East and Southeast Asia with 21 taxa. East Malesia is next with 16 taxa, and only three taxa extend to Australia and the Pacific islands. From this analysis it can be seen that the families Magnoliaceae, Rosaceae and Symplocaceae (possibly representative of all dicotyledons) are more localized around Kinabalu than is the case with the Cyperaceae. In contrast to the latter family, none of the dicots had a pantropical distribution. Furthermore, the dicots had a higher level of endemism, 16 of 70 taxa (23%), compared to the Cyperaceae, in which only two of the 73 taxa (2.7%) were considered endemic.

The occurrence of endemic and disjunct dicotyledons is to some extent correlated with higher elevations, but not to the extent as with the Cyperaceae. More of the endemic dicots (seven) occur only at high elevations, while four occur at both lower and higher elevations, and five are known only from low elevations. Among disjunct taxa four occur at high elevations, four at low elevations, and one at both low and high elevations. Smith (1986) made a compelling case for long-distance dispersal in the origin of Australasian alpine floras. A number of species in the high-elevation Kinabalu flora are likely to have been the result of dispersal events, but this problem is still in need of thorough investigation. The problems of autochthonous vs. allochthonous taxa alluded to by van Steenis therefore remain, and will be most effectively investigated through detailed phylogenetic studies.

The widely distributed dicots are relatively

numerous, with 19 occurring in four or more regions (in addition to Mount Kinabalu). Twelve of these are relatively low-elevation taxa (*i.e.*, lowlands, hill forest and lower montane forest), while seven occur at low and high elevations, *i.e.*, extending up to upper montane forest, but none is strictly high-elevation in occurrence. Fifteen taxa are restricted to only one region beyond Kinabalu, with nine occurring at low elevations, two at high elevations only, and four at both the lower and higher elevations. Twenty-two taxa are intermediate in distribution between widely distributed and localized (*i.e.*, in two to three regions beyond Kinabalu). Eleven of these are from lower elevations, seven from lower and upper elevations, and four from upper elevations only.

Seventeen of the dicots were classified as Asian-Malesian in distribution, 30 as strictly Malesian, and 16 as endemic. One taxon (*Rubus moluccanus* var. *discolor*) is Malesian-Austral, and two (*Rubus moluccanus* var. *moluccanus* and *R. rosifolius*) are widely distributed, *i.e.*, occurring in all seven areas included in the analysis. Six taxa are disjunct with extensions beyond Borneo, three of which occur at low and three at high elevations. The preceding discussion illustrates that the Kinabalu flora is

not only diverse but that the geographical distribution patterns also exemplify considerable complexity.

### Inventory of the flora

Collections upon which the Kinabalu botanical inventory are based have been obtained over a century and a half from 1851, when Hugh Low made the first collections, to the most recent in the last year or two. Collectors may be placed into five groups: (1) Mary Strong and Joseph Clemens, (2) Sabah Forestry Department collectors, (3) members of the Royal Society expeditions of 1961 and 1964, (4) the *Projek Etnobotani Kinabalu (PEK)* collectors, and (5) all other collectors. An analysis of the collections by these five groups is provided in Table 1.

The database presently contains 61,352 records (specimens) representing 218 families, 1,070 genera, and 5,128 species and infraspecific taxa. The ten largest families, based on number of species and infraspecific taxa, are listed in Table 2. Not surprisingly the Orchidaceae are the largest, with 127 genera and 856 species and infraspecific taxa. The Rubiaceae, a family on Kinabalu dominated by shrubs, is second largest, with 66 genera and 296 species

**Table 1.** Numbers of collections and taxa obtained from Mount Kinabalu by five major groups of collectors.

Group	No. of Collectors	No. of Specimens	No. of Collections	No. of Taxa
J. & M. S. Clemens	2	24,443	11,066	2,757
Sabah Forestry Department	~213	8,564	5,665	1,994
Royal Society	3 <sup>1</sup>	5,075	2,698	1,313
<i>PEK</i>	17	6,302	6,302 <sup>2</sup>	1,777
Additional collectors	~413	16,972	11,458	3,148
Total	648	61,356	37,189	— <sup>3</sup>

<sup>1</sup> Chew, Corner & Stainton in 1961; Chew & Corner in 1964.

<sup>2</sup> The number of specimens and collections is equal for the *PEK* material, because the count is based only on specimens in K. The first set of these collections is in the Sabah Parks Herbarium at Kinabalu Park headquarters and has not been examined for this project. Duplicate specimens have been distributed to several other herbaria, including K, where most of the determinations have been made.

<sup>3</sup> The column cannot be totalled, because the various collectors obtained many of the same taxa.



and infraspecific taxa. A ratio has been calculated based on the number of species vs. genera for each family. The highest ratio (22.5) is for the Moraceae, resulting primarily from the large number of *Ficus* species in the flora. High ratios are suggestive that active speciation has taken place in the family. Corner (1964a) noted that the evolution of subg. *Ficus* seems to have occurred where there has been relatively recent mountain-making, and to have employed regionally the section or series that happened to be on the spot. The ratio for the Ericaceae is also high; this family includes only five genera, but numerous species in *Diplycosia* and *Rhododendron* contribute to the high ratio. In contrast, the ratio is low for the Poaceae. The large number of genera and few species per genus may indicate that evolution in the Kinabalu grasses has been relatively static.

The Kinabalu flora is arguably the richest in the world on a per-unit-area basis. Now that the botanical inventory is completed, opportunities abound for more intensive investigations. While research for the inventory is finished, much of the flora is still not well understood. Names for over one-tenth of all taxa (686 names) have been designated with quali-

fiers. Thus 135 taxa are determined as "aff." some other species, 127 are qualified with "cf.", 211 are designated as "sp. 1", "sp. 2" etc., and 213 genera include specimens that have not been identified to species (*i.e.*, those indicated with "indet."). That so many taxa and specimens remain incompletely identified in itself presents challenges for further study of the flora.

Table 3 provides a list of the ten largest genera in the Kinabalu flora. The figure of 114 taxa for *Bulbophyllum* (Orchidaceae) is especially impressive. It is noteworthy that the Orchidaceae as the largest family in the Kinabalu flora (by a wide margin) also includes three of the largest genera, whereas the other large genera listed in Table 3 all belong to different families. Among the dicotyledons 21 genera have 20 or more species, of which *Ficus* with over 90 taxa is the second largest genus in the Kinabalu flora. Analyses in any of these and other relatively large genera that would reveal the number of neoendemics vs. paleoendemics and autochthonous vs. allochthonous taxa would be an especially rewarding extension into the origin and evolution of the Kinabalu flora but remains to be done.

**Table 2.** Ten largest families in the flora of Mount Kinabalu, with numbers of genera and species and ratios of species per genus.

Family	No. of genera	No. of species and infraspecific taxa	Ratio (species/genus) <sup>1</sup>
Orchidaceae	127	856	6.74
Rubiaceae	66	296	4.48
Euphorbiaceae	48	197	4.10
Moraceae	6	135	22.5
Fabaceae	42	133	3.17
Lauraceae	13	126	9.69
Melastomataceae	20	98	4.90
Ericaceae	5	97	19.4
Myrtaceae	11	97	8.82
Poaceae	52	91	1.75

<sup>1</sup> The ratio of species per genus is obtained by dividing the number of species by the number of genera in a particular family.

**Table 3.** Ten largest genera in the flora of Mount Kinabalu.

Genus	Number of species and infraspecific taxa
<i>Bulbophyllum</i> (Orchidaceae)	114
<i>Ficus</i> (Moraceae)	91
<i>Syzygium</i> (Myrtaceae)	76
<i>Dendrobium</i> (Orchidaceae)	73
<i>Eria</i> (Orchidaceae)	50
<i>Rhododendron</i> (Ericaceae)	44
<i>Ardisia</i> (Myrsinaceae)	42
<i>Asplenium</i> (Aspleniaceae)	37
<i>Lithocarpus</i> (Fagaceae)	37
<i>Litsea</i> (Lauraceae)	37

### Collectors and collections

Mary Strong and Joseph Clemens made more collections on Mount Kinabalu than any other collectors (Table 1). During their Kinabalu expeditions they obtained some 11,066 collections that we have been able to examine, represented by 24,443 specimens (Table 1). It is awesome to realize that they collected more than one-third of all Kinabalu specimens and more than half the total flora. An account of their lives and work is provided by Beaman *et al.* (2001).

The first Kinabalu specimen records of the British North Borneo (Sabah) Forestry Department are those of Foster and Puasa in 1931. Collectors from that department have been active ever since, especially since the 1950s; 8,564 specimens and 5,665 collections from the Forestry Department are included in the Kinabalu database.

The Royal Society expeditions of 1961 and 1964 focused on the Eastern Shoulder and the Pinosuk Plateau respectively and made collections at a wide diversity of elevations from about 500 m to the summit or near the summit of King George Peak (4,050 m). The Kinabalu database includes 5,075 specimens and 2,698 collections from these expeditions. The 1961 expedition was discussed in detail by Corner (1964a, b) and others, but an account of the

1964 expedition was not published. From this fieldwork Corner gained knowledge of the Kinabalu flora that was eloquently presented in *Kinabalu: Summit of Borneo* (Corner 1996).

A group of local people have served as collectors of the Kinabalu flora under a programme called *Projek Etnobotani Kinabalu (PEK)*. Over a period of about seven years 17 PEK collectors in nine communities made about 9,000 collections. Over 6,000 of these have been identified at Kew as part of the overall botanical inventory of Mount Kinabalu. A PEK collections database is maintained at Kinabalu Park headquarters.

In addition to the collectors and collections discussed above, a fifth group includes some 400 other individuals or teams, for which the Kinabalu database includes 16,972 specimens and 11,458 collections. The earliest collector and the first person to climb Mount Kinabalu was Hugh Low (later Sir Hugh), who collected there in 1851 and 1858. The most important botanical expedition to Kinabalu during the 19<sup>th</sup> century was that of George D. Haviland in 1892. Stapf's enumeration and analysis of the flora were largely based on the Haviland collections.

### Important collection localities

Table 4 provides an analysis of 24 localities from which the greatest number of collections has been obtained. The six numeric columns in this table indicate the number of collections by which each taxon is represented at a particular locality. For example, at Tenompok 610 taxa have been collected only once, while 84 taxa have been collected six or more times. In view of the predominance of collections by Mary Strong and Joseph Clemens it is not surprising that three localities (Tenompok, Penibukan, and Dallas), where their efforts were concentrated, are shown in the table as having especially large numbers of taxa. Other localities from which numerous taxa were gath-



**Table 4.** Twenty-four Kinabalu localities where large numbers of collections and taxa have been obtained.

Number of collections for each taxon <sup>1</sup>	1	2	3	4	5	6+
Locality						
Tenompok	610	252	127	75	50	84
Penibukan	502	219	124	73	49	60
Dallas	497	207	83	41	23	22
Park Headquarters	368	127	57	20	13	15
Eastern Shoulder	412	83	37	10	2	0
Marai Parai	336	107	36	28	13	13
Melangkap Tomis	354	102	39	13	8	6
Mesilau River	318	123	42	21	8	5
Gurulau Spur	370	100	32	7	2	1
Nalumad	321	59	10	2	0	1
Kemburongoh	220	80	37	17	6	30
Summit Trail	213	70	46	14	9	23
Sosopodon	207	78	31	20	14	20
Hempuen Hill	273	55	26	3	3	2
Kundasang	267	68	14	7	4	1
Pinosuk Plateau	251	49	10	2	1	1
Kiau	234	45	11	11	5	6
Bambangan River	242	53	9	6	0	0
Marai Parai Spur	221	54	18	4	6	4
Bundu Tuhan	220	33	9	6	4	1
Poring	196	45	17	7	3	2
Takutan	195	38	18	7	3	4
Mesilau Cave	172	54	23	9	3	4
Tahubang River	219	26	7	2	0	1

<sup>1</sup> The numbers in columns headed 1–6+ indicate for each locality the number of collections by which all taxa known from that locality are represented.

ered by the Clemenses are Marai Parai, the Gurulau Spur, and the Tahubang River. Many collectors have worked along the Mesilau River, especially the East Mesilau River, but the Royal Society expedition of 1964 collected extensively in that locality. The Eastern Shoulder and Bambangan River are also prominent localities because of Royal Society collections. Mesilau Cave (actually a nearby landslide with ultramafic substrate) was a major site for Royal Society collections.

### Number of collections by which taxa are known

In spite of the relatively intensive collecting activity that has been devoted to parts of Mount Kinabalu, its flora still cannot be considered well known; 1,184 taxa are represented by a single collection (Fig. 1) and only 708 taxa are represented by more than 15 collections (not shown in Fig. 1). Thanks to the work of the Clemenses, the Sabah Forestry Department, the Royal Society expeditions and other collectors, the southern half of the mountain is now reasonably well collected. That is not the

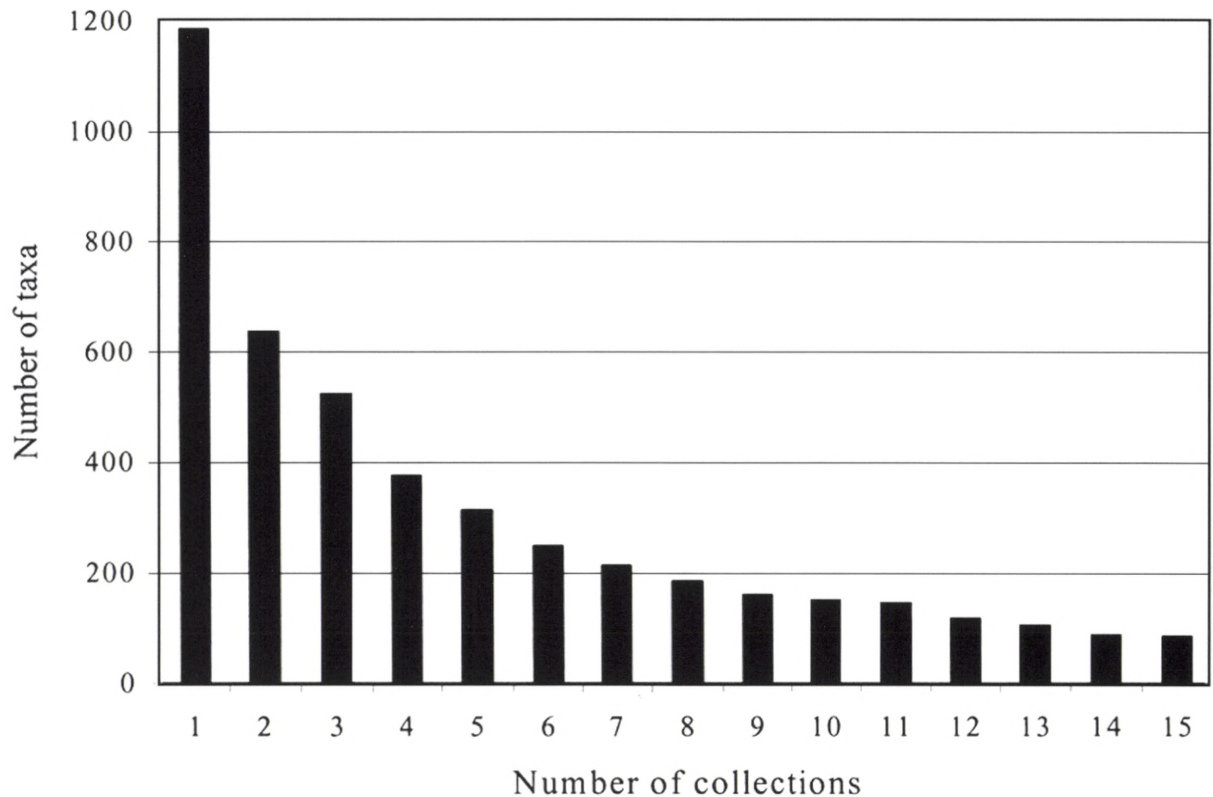


Fig. 1. Number of collections by which each taxon in the Kinabalu flora is represented.

case, however, for the northern section, which remains incompletely explored because of its rugged topography and because no climbing route to the summit is located there.

An examination of which taxa are most extensively collected on Mount Kinabalu illustrates why certain species tend to be frequently gathered. Table 5 provides a list of the ten most-collected species, all of which are herbs, shrubs or small trees. They all have a wide elevational range, and most are especially evident in upper montane forest along the Summit Trail. These plants are easy to collect and conspicuous at eye-level, common in vegetation types with limited species diversity, and have long flowering and/or fruiting periods. Four species on the list do not occur above 3,000 m,

while the others mostly extend well above that elevation, in the case of *Phyllocladus hypophyllus* up to the summit area. *Ficus oleifolia* subsp. *intermedia*, found at up to 3,200 m, is the highest occurring fig on Mount Kinabalu.

### Causes of high species diversity

The extremely high species diversity of Mount Kinabalu apparently has resulted from a combination of factors, among which the most important are: (1) great altitudinal and climatic range from the hot humid lowlands near sea level to freezing alpine conditions at the summit; (2) precipitous topography causing effective geographic and reproductive isolation of species over short distances; (3) geolog-



**Table 5.** Ten most-collected taxa in the flora of Mount Kinabalu.

Taxon	No. of collections	Habit	Elevation range (m)
<i>Symplocos adenophylla</i> var. <i>adenophylla</i>	85	Shrub or small tree	900-2,600
<i>Elatostema lineare</i>	76	Erect herb	900-3,000
<i>Ilex havilandii</i>	75	Shrub or small tree	1,200-3,500
<i>Rhododendron rugosum</i> var. <i>rugosum</i>	73	Shrub or small tree	1,000-3,400
<i>Elatostema penibukanense</i>	65	Herbaceous root-climber	800-3,200
<i>Ficus uniglandulosa</i>	65	Shrub, climber or small tree	400-2,300
<i>Smilax lanceifolia</i>	64	Slender woody climber	700-2,700
<i>Ficus oleifolia</i> subsp. <i>intermedia</i>	63	Shrub	500-3,200
<i>Dysoxylon cyrtobotryum</i>	61	Small to medium-sized tree	600-1,800
<i>Phyllocladus hypophyllus</i>	61	Shrub or small to large tree	1,200-4,000

ical history of the Malay Archipelago involving movement of several tectonic plates; (4) many localized edaphic conditions, particularly the ultramafic or serpentine substrates; (5) frequent climatic oscillations resulting in droughts influenced by El Niño events; and (6) additional environmental instability such as landslides, river flooding and glaciation.

The role of climatic fluctuations in increasing floristic diversity has been noted in areas such as in the West African mountains (Morton 1972) and alpine regions of Australasia (Barker 1986). Morton referred to these processes as an "evolutionary pump." Beaman & Beaman (1990) suggested that the model of edaphic endemism and catastrophic selection in speciation, as outlined by Lewis (1962) and Raven (1964) could be relevant to the high diversity of the Kinabalu flora. Raven noted that this mode of origin of new species is most likely to have been of particular importance in areas characterized by extreme climatic fluctuations. Catastrophic selection on Kinabalu could have been driven by the frequent El Niño droughts. Various reports have been made of dead plants at the higher elevations after droughts, *e.g.*, Beaman *et al.* (1986), Kitayama *et al.* (1999), Lee & Lowry (1980), Lowry *et al.* (1973) and Smith (1979). Numerous ultramafic outcrops offer the unusual

edaphic conditions that the catastrophic selection hypothesis requires. Raven & Axelrod (1978) suggested that the process may be most important in annuals of mediterranean climates, but the concept merits examination with respect to the woody species, especially the many shrubby species, of Mount Kinabalu.

In the short time during which Mount Kinabalu has been elevated numerous new habitats have been created that could be occupied by newly evolved plants. Some of the rarest and most interesting species occur on old landslides, *i.e.*, geologically recent habitats. Landslides are a prominent feature of the Kinabalu landscape. New ones occur frequently and provide open habitats for plant colonization. Corner (1964a) noted that these were often recognizable because of the abundance of the pioneer theaceous tree *Adinandra*. The upper slopes, far distant from other similar habitats, simulate a new oceanic island system such as Hawaii. The terrain presents many situations where immigrant populations can be effectively isolated from donor populations. Rapid adaptive radiation could be facilitated under these conditions. The environments on Kinabalu are so diverse and so localized as to virtually enforce occurrence of highly localized populations, particularly on the many small and widely scattered ultramafic outcrops at dif-

ferent elevations. The physiognomy of numerous sharp ridges and profound valleys results in circumstances that severely limit movement of both pollinators and seed-dispersers. The possibility of a role also for genetic drift in the small populations on Mount Kinabalu is intriguing. The processes of catastrophic selection and genetic drift may be acting jointly, a possibility suggested by Grant (1981).

Hybridization likewise may have played a role in increasing diversity in the high-elevation Kinabalu flora, as has been noted in papers by Barkman (2001), Cannon (2001) and Conant and Stein (2001). *Rhododendron* on Kinabalu, with 33 taxa (excluding hybrids) currently recognized (Beaman *et al.* 2001), includes seven named hybrids and seven more instances in which interspecific hybrids occur. Most of these are found at high elevations, especially on ultramafic substrates. It appears likely that habitat disturbance could have been a major factor in promoting hybridization. Cannon (2001) noted that introgressive hybridization in the diverse genus *Lithocarpus* may have served as a mechanism facilitating survival of refugial populations during changing environmental conditions.

### Similarities (or lack thereof) to other mountains

Mount Kinabalu is in a class by itself relative to other mountains in Southeast Asia. Except for New Guinea, where a range of high mountains extends almost the length of the island, most of the mountains of the rest of Malesia are lower by 1000 m or more. Furthermore, the high mountains of Sumatra, Java and the Philippines are volcanic rather than sedimentary or granitic and ultramafic. The second highest mountain in Sabah is Mount Trusmadi at 2,649 m. Various expeditions have been made to Trusmadi, but to our knowledge no enumeration or database is available for its flora. If considered separate from Mount Kina-

balu, Mount Tembuyuken at 2,579 m would be the third highest mountain in Sabah, but its proximity and geology are so close to Kinabalu that it has been considered integral for purposes of the Kinabalu inventory.

The highest mountain in Sarawak is Mount Murud (2,424 m), for which an inventory of the summit flora was published by Beaman & Anderson (1997). They enumerated 260 fully determined taxa, and concluded that its most salient phytogeographic relationship appears to be with Kinabalu. Indeed, they found that the similarity of the Murud and Kinabalu floras was stronger than to floras of Murud's geographically closer neighbours in Sarawak. Among the Murud pteridophytes, 24 (77%), and Murud orchids, 31 (74%), also occur on Mount Kinabalu. During specimen examinations for the Kinabalu enumeration Kongkemul in East Kalimantan was often noted to have species in common with Kinabalu, but we have no data for it. Species in common with Mounts Halcon and Apo in the Philippines likewise have been noted but quantitative comparisons cannot be made in light of available data.

Johns (2001) made a comparison of floristic aspects of Mount Kinabalu and Mount Jaya in Papua (west New Guinea). At 4,860 m Mount Jaya is the highest mountain between the Himalayas and the Andes and the only mountain in Southeast Asia with glaciers. It has a limestone geology, which differs dramatically from that of Kinabalu. Johns noted that the number of alpine and subalpine vascular plants on Mount Kinabalu is *c.* 120 species, a significantly lower number than the *c.* 500 species recorded for Mount Jaya. Higher diversity of the high-elevation flora on Mount Jaya probably is a consequence of the long backbone (2,300 km) of high mountains in New Guinea, which must have provided a local and rich source of propagules for high-elevation colonization. Families such as the Asteraceae



are much more diverse on Mount Jaya, with genera like *Gnaphalium*, *Olearia*, *Senecio* and *Tetramolopium* not occurring in the sub-alpine/alpine flora of Mount Kinabalu, but represented by 3, 6, 3 and 14 species, respectively, on Mount Jaya. These species tend to be very closely related to one another. Even where genera of Asteraceae occur on both mountains the diversity on Mount Jaya seems significantly greater. *Keysseria* with one species on Mount Kinabalu and six species on Mount Jaya is a good example. Unfortunately, comparisons between the entire floras of Kinabalu and Jaya cannot be made, because the flora at lower elevations on Mount Jaya has not yet been enumerated. Johns suggests that the flora of the Mount Jaya area may include *c.* 8,000 to 8,500 vascular plant species, which would make it an even hotter spot for plant diversity than is Mount Kinabalu. However, it must be realized that Kinabalu is isolated and very young while Jaya is part of an extensive chain, perhaps not quite so geologically young, and much of it botanically totally unexplored.

### Geographic information system

A geographic information system (GIS) is being used in the taxonomic, biogeographic, phylogenetic, and ethnobotanical studies. It has had an especially important application in the production of a location map of Mount Kinabalu. The map has been completed recently and will be printed at 1:50,000 scale, with 200-m contour intervals, and shows over 500 localities, many of which were derived from a database of place names in the Dusun language (Beaman *et al.* 1996). The map, a Landsat TM image, and an introduction to the map with gazetteer will be published together as a single product. An example of a GIS application is provided in Fig. 2, a drape of the satellite image over a digital elevation model prepared from topographic map data. This image

shows the upper part of the northwest side of Mount Kinabalu, and has been used to localize Wusser Falls, an important collecting locality recorded by Joseph and Mary Strong Clemens ("Wusser" probably was how they understood *wasai*, the Dusun word for waterfalls).

GIS coverages from satellite imagery and topographic maps have been prepared for the topography, hydrography, vegetation, Park boundary, geographic locations, geology, and land use. Geodetic control of these coverages has been enhanced through linkage with a database of global positioning system (GPS) points provided by the Sabah Department of Lands and Surveys and many additional points obtained by Reed Beaman and myself. The geo-referenced locality records in the specimen database can be mapped to associate diversity at various taxonomic and altitudinal levels with environmental parameters.

The greatest diversity in the Kinabalu flora, as shown in Fig. 3, occurs at around 1,500 m, where 661 genera and 1,925 species and infra-specific taxa are recorded. These data have been summarized from elevations recorded on specimen labels. Elevation data lower than 200 m have not been recorded, because the base of the mountain is at about 200-300 m. The small number of genera and species recorded at lower elevations is partly artifactual. Much of the original vegetation already had been destroyed before collecting began in 1851. The ethnobotanical collections, most of which are from around the base of the mountain, lack elevation data, so do not contribute to knowledge of the elevation of taxa. Grytnes & Vetaas (2002) have noted that different aspects of sampling seriously affect observed species richness patterns at varying elevations. At the extremes of altitudinal sampling only the species that have actually been recorded are counted, but for intermediate elevations interpolated species not observed at an actual level but included in a range are counted. A further





**Fig. 2.** Drape of part of a Landsat image of Mount Kinabalu over a digital elevation model. The figure shows the upper elevations of the northwest side of the mountain, with a particularly prominent feature, Low's Gully, at the head of the Penataran River. This image has been used to localize an important collecting locality, the "Wusser" River of Joseph and Mary Strong Clemens, which is circled on the image. The thin red lines in the background at the upper right are roads on the Pinosuk Plateau. This is a false-colour image in which the light colours at the summit of the mountain represent nearly bare granitic substrates and the reddish colours just below show subalpine scrub vegetation.

factor likely to influence the elevational hump in Fig. 3 is that the mid-elevations on Kinabalu (and many other tropical mountains) provide the most pleasant working conditions for botanists and therefore are most intensively collected. It is noteworthy that a graph by Hemp (2002, fig. 7) for species number and constancy of pteridophytes in relation to altitude on Mount Kilimanjaro in Africa corresponds remarkably closely with the elevational distribution of the Kinabalu flora. Hemp's data were derived from plot sampling, whereas the Kinabalu data are based on herbarium records.

### Phylogenetic analyses

My research role in the Kinabalu inventory has been primarily that of data gathering and enumerating the flora. A number of collaborators, however, have concentrated on selected genera and applied cladistic analysis to their taxa. In a symposium held at the 16<sup>th</sup> International Botanical Congress in 1999, four of them discussed evolutionary relationships of the species in four genera in unrelated families. Some of their conclusions were remarkably similar, especially that various high-elevation endemic species are probably of recent origin and are



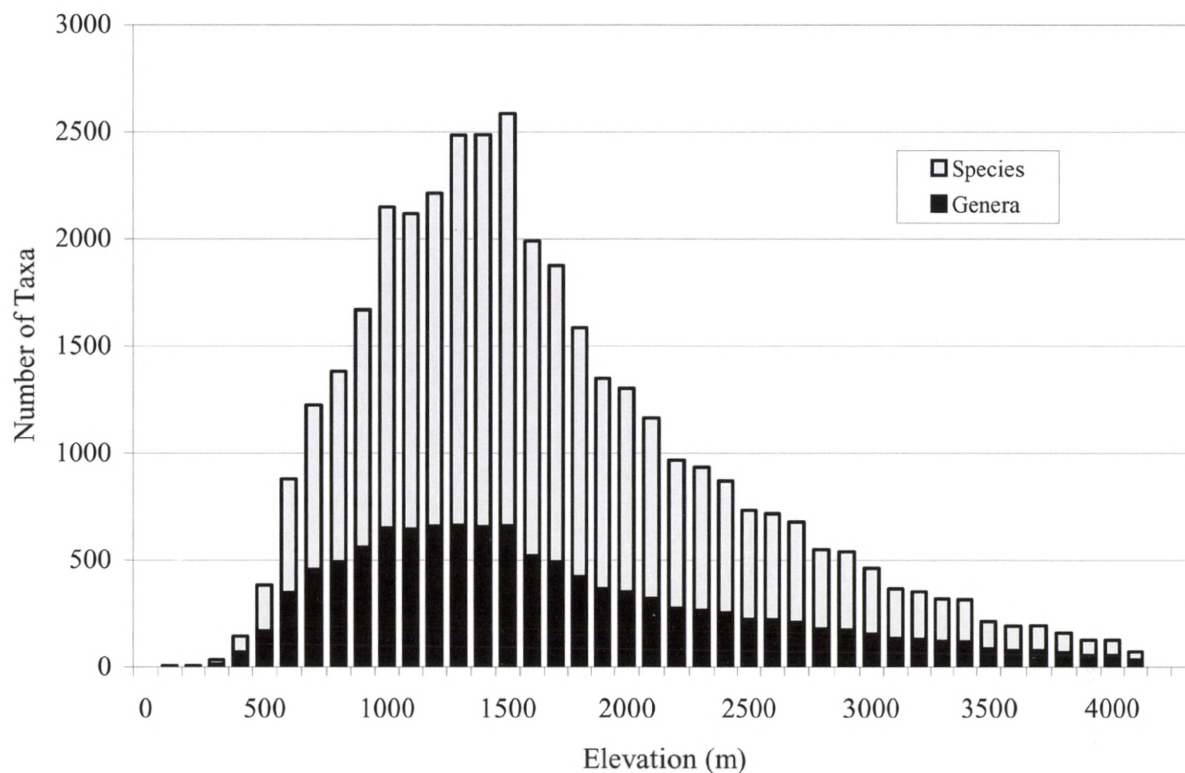


Fig. 3. Elevational distribution of genera and species in the flora of Mount Kinabalu.

most closely related to species of lower elevations on Mount Kinabalu rather than to preadapted high-elevation species from distant regions.

Barkman (2001) considered the *in situ* and probably recent speciation of high-elevation orchids in the SE Asian genus *Dendrochilum*, noting that five independent high-elevation *Dendrochilum* lineages arose from lower elevation Bornean ancestors. He was able to reject the hypothesis that they came from preadapted ancestors in the Philippines or Sumatra. He reported that reduced leaf surface area, increased leaf sclerophylly, and greater leaf thickness may have been key innovations allowing these plants to colonize successively higher habitats.

Conant and Stein (2001) discussed tree-fern

diversity and relationships in the family Cyatheaceae on Kinabalu and on a broader geographical basis. Their morphological and molecular data suggest the possibility that one of the serpentine-endemic Kinabalu tree-fern species (*Alsophila havilandii*) may share a common ancestry with another species (*A. oosora*) whose distribution is nearly restricted to Kinabalu.

Cannon (2001) examined diversity in the stone-oak genus *Lithocarpus* in the Kinabalu area, where this group attains maximum diversity. An enclosed-receptacle (ER) fruit occurs in at least two sections of the genus, suggesting convergent evolution of this unusual feature. Evolution of the ER fruit appears to have been rapid, with little corresponding molecular change. The ER fruit type is particularly com-

mon at higher elevations. Cannon noted the possible importance of Kinabalu as a refugial area for long-lived tree species such as *Lithocarpus*.

R.S. Beaman (2001) used cladistic and GIS techniques to analyze evolutionary and phylogeographic relationships of *Elatostema* (Urticaceae), a genus with many localized endemics on Kinabalu. His results indicate that recent speciation has occurred primarily in taxa occurring in mid- and high-elevation habitats. Species of *Elatostema* in low-elevation habitats, both ultramafic and otherwise, are phylogenetically basal (at least for the Kinabalu species). His approach of defining areas in cladistic biogeography using satellite-image analysis has not been carried out previously.

### Ethnobotanical research

In July 1992, researchers and staff from Sabah Parks, Universiti Malaysia Sarawak and the WWF-UNESCO-Kew People and Plants Initiative created the *Projek Etnobotani Kinabalu (PEK)*. The *PEK* has had four primary objectives: (1) ethnobotanical research, focused on building a team of local Dusun people, Park personnel, and visiting researchers who study patterns of Dusun classification, management, and use of plants; (2) conservation of pristine areas, by developing the ability of Park personnel to assess the ecological, cultural and economic importance of locally-used botanical resources and by strengthening links between the Park research staff and Dusun communities; (3) environmental education, by providing research and training opportunities for students from Malaysia and other Asian countries and by enriching interpretive programs and exhibits for the more than 300,000 people who visit the Park every year; (4) community development, through improving the management of unprotected forests in buffer zones around Kinabalu Park and promoting the viability of

Dusun ecological knowledge. In 1994 The John D. and Catherine T. MacArthur Foundation made a first grant to Sabah Parks for the *PEK* and in 1997 a second grant became effective.

In the course of the *PEK*, Dusun villagers from nine communities around Kinabalu Park made over 9,000 collections. Comparative analysis of non-*PEK* collections and ethnobotanical collections from the *PEK* indicate that the community-based collectors increased recorded palm taxa by 67%, and monocotyledons in general by 28% (Beaman & Beaman 1998; Martin *et al.* 2001). A new database, "*DusunPEK*," being developed by Gary Martin, will allow elucidation of the general structure of Dusun botanical classification according to general principles of ethnobiological classification (Berlin 1992) and standard methods set out in the *Ethnobotany Methods Manual* (Martin 1995). The total number of Dusun generic and specific botanical categories, and their affiliation with various Dusun life-forms (including *kayu* "tree", *wakau* "vine", *saket* "grasses and herbs", and *tuai* "rattans") will be ascertained by documenting the patterns of correspondence between the scientific name, plant family, Dusun name and Dusun life-form. These characterizations will be useful also for a projected *Dusun Ethnoflora*.

Dusun classification of the landscape provides key ecological categories used to describe the successional stage of the vegetation where plant resources are harvested. Their ecological classification includes seven essential categories: *timbaan* (primary forest with large trees), *puru* or *talun* (primary forest); *temulek* (secondary forest or earlier successional stages that originate from fallowed cultivated fields); *geuten* (dense, relatively impenetrable secondary vegetation best characterized as thicket); *butur* (grassy areas, in pasture or near a household); *tume* (cultivated fields, sometimes with trees); *nataad* or *liwan* (home gar-



den). The *DusunPEK* database has a field that identifies the Dusun vegetation category for the majority of the 9,000 *PEK* collections. Agnes Lee Agama has recently completed a Ph. D. thesis at the University of Kent at Canterbury in which comparative ethnographic work at the village of Kiau was used to gain a detailed understanding of the Dusun system of vegetation classification. Her research has focused on how knowledge of dominant or key plant resources varies according to an individual's age, gender, geographical location, level of acculturation, and other characteristics.

In the ethnobotanical research, patterns of plant distribution around Mount Kinabalu in both geographical and vegetational terms are being determined by drawing upon the locality information for collections in the taxonomic database. This should provide baseline data for a future analysis of Dusun community access to key plant resources and of Dusun preference for various habitats where plant resources are typically harvested. These data also should allow a broader biogeographic analysis for the Kinabalu flora and ethnoflora, following the cladistic methodology employed by Barkman *et al.* (1998) to elucidate orchid distributions and the GIS technology used by Beaman & Beaman (1997) to understand distribution and diversity patterns of pteridophytes. The resulting data could be used to create, through the Kinabalu GIS, distribution maps for the *Dusun Ethnoflora*. Such maps would show in precise detail where specimens have been obtained by the *PEK* collectors.

### Conservation of the flora and threats to Kinabalu Park

Mount Kinabalu has long been regarded as a sacred mountain by the Dusun people of the surrounding foothills region. With settlements now established on all sides, the mountain has

become a biological island, partly protected by the Park boundaries. The Kinabalu flora as it is being enumerated extends well beyond the Park boundaries and that outside part is much more subject to destructive forces. The Park has five main focus areas: (1) Conserving the biological and physical resources; (2) spearheading scientific research and enhancing educational values; (3) increasing recreational and tourist activities; (4) preserving cultural and historical values; and (5) instituting management procedures to support other strategic thrusts.

Potential threats to the integrity of the Kinabalu flora and Kinabalu Park are the following: (1) Native rights: claims of several areas in the Park by adjacent villagers as "native customary rights," *e.g.*, burial grounds. (2) Agriculture: cultivation of rice and fruit trees. (Agricultural activities by villagers inside the Park may cause management concerns in the future.) (3) Climate change: droughts resulting from El Niño events. (Forest fires during recent droughts destroyed nine locations in Kinabalu Park that covered an area of 2,500 hectares.) (4) Recreational use: visitor activities. These are concentrated in three main locations in the Park, representing approximately 5 percent of the total Park area. (In 1998 Kinabalu Park had more than 300,000 visitors, most of whom contributed to the local economy. Erosion, noise, and litter problems are largely under control.) (5) Mining. A copper mine that operated for 30 years has now been closed, but other areas on the mountain may contain valuable mineral resources for which there will be pressure for exploitation. (6) Logging. Illegal logging has happened in the past, partly because the loggers claimed that they could not recognize the Park boundary. The entire boundary has now been conspicuously marked, but pressure may be exerted for boundary changes that would permit access to timber resources.



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**Appendix 1.** Geographical affinity of taxa in the families Magnoliaceae, Rosaceae, and Symplocaceae in the flora of Mount Kinabalu.

Taxon	Habitat & elevation range in m (when known)	Ultramafic <sup>2</sup> or granitic substrate	East & South-east Asia	West Malasia	Borneo	Endemic or sub-endemic to Kinabalu	Central Malasia	East Malasia	Austr. & Pacific Islands	Comments
Magnoliaceae										
<i>Elmerrillia tsiampacca</i> subsp. <i>mollis</i>	HF			+ <sup>3</sup>	+		+	+		
<i>Magnolia candollii</i> var. <i>candollii</i>	LL, HF, LM 500-2100		+	+	+		+	+		
<i>M. candollii</i> var. <i>obovata</i>	HF, LM, UM 900-2700	+	+	+	+					
<i>M. candollii</i> var. <i>singaporensis</i>	LL, HF, LM	+		+	+					
<i>M. carsonii</i> var. <i>carsonii</i>	HF, LM 1200-1800	+			+					
<i>M. carsonii</i> var. <i>drymifolia</i>	HF, LM, UM 1400-2900	+			+					
<i>M. maingayi</i>	HF			+	+					
<i>M. persuaveolens</i> subsp. <i>persuaveolens</i>	LM 1500	+				+				
<i>M. persuaveolens</i> subsp. <i>rigida</i> var. <i>pubescens</i>	LM 1200-2300	+				+				
<i>M. persuaveolens</i> subsp. <i>rigida</i> var. <i>rigida</i>	LM, UM 1500-3400	+				+				
<i>M. sarawakensis</i>	HF 800	+			+					
<i>M. uvariifolia</i>	HF, LM 1200-1800	+			+					
<i>Manglietia dolichogyna</i>	HF, LM 500-1700			+	+					
<i>M. sabahensis</i>	HF, LM 1100-2100	+				+				
<i>Michelia montana</i>	HF 800-1200	+		+	+					

Taxon	Habitat <sup>1</sup> & elevation range in m (when known)	Ultramafic <sup>2</sup> or granitic substrate	East & South-east Asia	West Malaysia	Borneo	Endemic or sub-endemic to Kinabalu	Central Malaysia	East Malaysia	Austr. & Pacific Islands	Comments
Rosaceae										
<i>Eriobotrya aff. bengalensis</i>	UM 2000-2300	+				+				
<i>Photinia davidiana</i>	UM, SA 2700-4000	+	+	+		+ <sup>4</sup>				In Borneo only on Mt. Kinabalu
<i>P. prunifolia</i>	LM 1400-1700		+	+		+ <sup>4</sup>				In Borneo only on Mt. Kinabalu
<i>Potentilla borneensis</i>	UM, SA 3400-4100	+		+		+ <sup>4</sup>				Only N Sumatra & Mt. Kinabalu
<i>P. parvula</i>	UM, SA 3200-3800	+				+ <sup>4</sup>	+	+		Also in the Philippines, Sulawesi, & New Guinea
<i>P. polyphylla</i> var. <i>kinabaluensis</i>	UM, SA 3000-4000	+				+				
<i>P. arborea</i> var. <i>alticola</i>	UM 2400-2700	+			+		+			
<i>Prunus arborea</i> var. <i>arborea</i>	HF, LM 1100-1600			+	+		+	+		
<i>P. arborea</i> var. <i>densa</i>	HF, LM, UM 900-2400	+	+	+	+					
<i>P. arborea</i> var. <i>stipulacea</i>	HF, LM 600-1700			+	+					
<i>P. glabrifolia</i>	UM ?2300-2800	+		+	+					
<i>P. grisea</i> var. <i>tomentosa</i>	HF, LM, UM 1400-2400	+	+	+	+		+			
<i>P. javanica</i>	LL, HF, LM 600-1600		+	+	+		+	+		
<i>P. kinabaluensis</i>	HF, LM 600-2100					+ <sup>4</sup>	+			Also in Luzon, but variant
<i>P. lamponga</i>	LM			+	+					



Taxon	Habitat <sup>1</sup> & elevation range in m (when known)	Ultramafic <sup>2</sup> or granitic substrate	East & South-east Asia	West Malaysia	Borneo	Endemic or sub-endemic to Kinabalu	Central Malaysia	East Malaysia	Austr. & Pacific Islands	Comments
<i>P. laxinervis</i>	HF, LM 1100-1800	+				+				
<i>P. mirabilis</i>	LM, UM 2000-3400	+				+				
<i>P. oocarpa</i>	HF, LM, UM 1200-3400	+			+					
<i>P. spicata</i>	HF, LM 1200-1500	+			+		+			
<i>Rhaphiolepis philippinensis</i>	LM 1500-1800	+				+ <sup>4</sup>	+			Also in the Philippines
<i>Rubus alpestris</i>	LM, UM 1600-2900	+	+	+	+		+			
<i>R. benguetensis</i>	LM, UM 1200-2900	+			+		+			
<i>R. elongatus</i>	LM 1400			+	+		+			
<i>R. fraxinifolius</i>	HF, LM, UM 900-3000	+	+	+	+		+	+		
<i>R. lineatus</i>	LM, UM 2100-3700	+	+	+	+					
<i>R. lowii</i>	UM, SA 2400-4000	+				+				
<i>R. moluccanus</i> var. <i>discolor</i>	LL, HF, LM, UM; 500-2900	+		+	+		+	+	+	
<i>R. moluccanus</i> var. <i>moluccanus</i>	LL, HF, LM ?-1800		+	+	+		+	+	+	
<i>R. moluccanus</i> var. <i>obtusangulus</i>	LL, HF, LM, UM; ?-1800	+	+	+	+		+	+		
<i>R. rosifolius</i>	LL, HF, LM 400-1800		+	+	+		+	+	+	
Symplocaceae										
<i>Symplocos adenophylla</i> var. <i>adenophylla</i>	HF, LM 900-2600	+	+	+	+		+			

Taxon	Habitat <sup>1</sup> & elevation range in m (when known)	Ultramafic <sup>2</sup> or granitic substrate	East & South-east Asia	West Malasia	Borneo	Endemic or sub-endemic to Kinabalu	Central Malasia	East Malasia	Austr. & Pacific Islands	Comments
<i>S. anomala</i>	HF, LM 800-2100	+	+	+	+					
<i>S. brachybotrys</i>	LM, UM 1500-2600	+			+					
<i>S. buxifolia</i>	UM, SA 2300-4000	+				+				
<i>S. celastrifolia</i>	HF		+	+			+	+		
<i>S. cerasifolia</i> var. <i>cerasifolia</i>	HF	+	+	+	+			+		An unusual disjunction
<i>S. cochinchinensis</i> subsp. <i>cochinchinensis</i>	HF, LM 1200-1700	+	+	+	+		+	+		
<i>S. colombonensis</i>	UM 2100-2900	+				+				
<i>S. crassipes</i> var. <i>ernae</i>	HF, LM 800-1500	+			+					
<i>S. deflexa</i>	UM 2300-3400	+				+				
<i>S. fasciculata</i>	LL, HF 500-1100		+	+	+		+	+		
<i>S. henschelii</i> subsp. <i>henschelii</i> var. <i>henschelii</i>	HF, LM, UM 1200-1600	+	+	+	+					
<i>S. johniana</i>	LM, UM 1200-2400	+			+	<sup>4</sup>				Also on Kongkemul, East Kalimantan
<i>S. laeteviridis</i> var. <i>alternifolia</i>	HF, LM 1100-1500	+				+				
<i>S. laeteviridis</i> var. <i>kinabaluensis</i>	HF, LM 1400-2700	+				+				
<i>S. laeteviridis</i> var. <i>laeteviridis</i>	HF, LM, UM 900-2400	+		+	+		+			
<i>S. laeteviridis</i> var. <i>mjoebergii</i>	HF, LM 1200-1700				+	<sup>4</sup>				Also on Mt. Murud, Sarawak



Taxon	Habitat <sup>1</sup> & elevation range in m (when known)	Ultramafic <sup>2</sup> or granitic substrate	East & South-east Asia	West Malaysia	Borneo	Endemic or sub-endemic to Kinabalu	Central Malaysia	East Malaysia	Austr. & Pacific Islands	Comments
<i>S. laeteviridis</i> var. <i>pauciflora</i>	UM; 2600	+			+	+ <sup>4</sup>				Also on Mt. Murud, Sarawak
<i>S. laeteviridis</i> var. <i>velutinoso</i>	HF, LM 900-1500	+			+	+ <sup>4</sup>				Also in the Kapit area, Sarawak
<i>S. odoratissima</i> var. <i>odoratissima</i>	LM; 1500			+	+		+	+		
<i>S. ophirensis</i> subsp. <i>cumingiana</i>	HF, LM, UM 1200-2700	+			+		+			
<i>S. pendula</i> var. <i>hirtistylis</i>	LM, UM 1300-3400	+	+	+	+		+	+		
<i>S. trichomarginalis</i>	LM, UM 1200-2400	+				+				
<i>S. tricoccata</i>	HF, LM 900-2100				+					
<i>S. zizyphoides</i>	UM 2700-3700	+				+				

<sup>1</sup> LL = lowlands, HF = hill forest, LM = lower montane forest, UM = upper montane forest, SA = summit area. Elevation ranges pertain only to the occurrence of these species on Mount Kinabalu.

<sup>2</sup> Some species occur on ultramafic and/or granitic substrates as well as other substrates. Thus, it should not be assumed that a species is restricted to a particular substrate. Above 3,000 m the substrate is mostly granitic, whereas below that elevation it is more generally ultramafic or sedimentary. The characterization of substrate pertains only to Mount Kinabalu, rather than to other areas in the range of a species.

<sup>3</sup> The + sign indicates that a particular species is common to Kinabalu and the region for which the sign is entered, or, in the case of substrates, that the species occurs on ultramafic or granitic substrates.

<sup>4</sup> Subendemic to Mount Kinabalu, or with otherwise interesting distribution noted in the Comments column.

