BERICHTE UND MITTEILUNGEN

ALTITUDINAL ZONATION OF CLIMATE AND VEGETATION IN A GLOBAL MEGADIVERSITY CENTRE, MOUNT KINABALU (NORTH BORNEO)

With 5 figures, 3 tables and 3 photos

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Herrn Prof. Dr. Wilhelm Barthlott zum 60. Geburtstag

Zusammenfassung: Höhenstufen des Klimas und der Vegetation in einem globalen Megadiversitätszentrum, Mount Kinabalu (Nord Borneo)

Im Rahmen des Langzeitvorhabens „Biodiversität im Wandel” der Akademie der Wissenschaften und der Literatur, Mainz, fand Anfang Oktober 2005 eine Erkundungsreise nach Sabah (Borneo) statt. Ziel dieser Reise war es, die Möglichkeiten zur Etablierung eines Forschungsprojektes zur Verbreitung und Ökologie der epiphytischen Blütenpflanzen in den Primärwäldern eines globalen Megadiversitätszentrums, Mount Kinabalu, zu sondieren. Topoklimatische Studien zur hygrothermischen Höhenstufung des Mount Kinabalu sollen als Grundlage der vegetationsökologischen Untersuchungen das Vorhaben begleiten. Da die Tieflandregenwälder am Mount Kinabalu bereits weitgehend anthropogen verändert und Kulturland gewichen sind, wurden drei naturnahe Waldreservate (Sepilok bei Sandakan, Danum Valley bei Lahad Datu und die Crocker Range bei Kota Kinabalu) in der weiteren Umgebung des Mount Kinabalu besucht, um auch einen Eindruck von den für Borneo typischen Dipterocarpaceen-Tieflandregenwäldern zu gewinnen. Mit dem Besuch einiger kleinerer Inseln an der West- (Tungku Abdul Rahman Nationalpark) und Ostseite von Sabah (Turtle Island) wurde beabsichtigt, die Möglichkeiten eines Vergleiches des Epiphyten-Besatzes der Wälder des Festlandes mit denen der dem Festland vorgelagerten Inseln zu erkunden. Beobachtungen zur Höhenstufung der Vegetation und Messungen der Bodentemperatur ermöglichten die Einordnung der Vegetationszonen in ein Schema der hygrothermischen Höhenstufung des Kinabalu-Massivs. Die Bergregenwälder am Mount Kinabalu sind epiphytenreich, die Tieflandregenwälder des Festlandes und der Inseln vor Sabah hingegen stellten sich als relativ epiphytenarm dar. Ursache für die Epiphytenarmut der Tieflandregenwälder könnte das regelmäßige Auftreten der El Niño-Ereignisse sein, die in Südostasien für den Einschub der Blühperiode und den Fruchtansatz der Bäume in den Wäldern, aber auch für die immense Artenvielfalt am Mount Kinabalu verantwortlich gemacht werden.

Summary: In the context of the long term project “Changing Biodiversity” („Biodiversität im Wandel”) of the Academy of Sciences and Literature (Mainz) a study trip to Sabah (North Borneo) was conducted. The aim of the trip was to explore the possibilities of establishing a research project on the distribution and ecology of epiphytic angiosperm plants in the primary forests surrounding Mount Kinabalu. Topo-climatic studies on the hygrothermal altitudinal zonation of Mount Kinabalu should be included in the project. Because the lowland rain forest of the foothills of Mount Kinabalu have to a large degree been degraded and converted to agricultural lands, three well-preserved forest reserves (Sepilok near Sandakan, Danum Valley near Lahad Datu and the Crocker Range near Kota Kinabalu) were selected in order to gain some insight into the Dipterocarpaceae-dominated lowland rain forests of Borneo. Additionally, certain islands off the western and eastern coasts of Sabah (Tungku Abdul Rahman National Park and Turtle Island respectively) were visited in order to assess the possibilities of comparing the epiphyte vegetation of the mainland forests with that of the outlying islands. Observations concerning the altitudinal zonation of the vegetation and measurements of the soil temperature allowed an integration of the vegetational zones into the hygrothermal altitudinal zonation of the Kinabalu Mountain massive. In contrast to montane forests, the lowland forests on the Sabah mainland are relatively poor in epiphytes. A possible reason could be the regular occurrence of ENSO events which in South-East Asia have been identified as one of the main causes of changes in the flowering phenology of forest trees and even for the immense species richness of the Mount Kinabalu.

1 Introduction

Mount Kinabalu (4,101 m a.s.l.) is situated between 06°00’–06°25’ north and 116°25’–116°35’ east (Fig. 1). This relatively young massif consists of plutonic rocks which rose only 100,000 B.P. (late Pliocene-Pleistocene) (Jenkins 1971; Beaman 2005). Its central section, i.e. today’s summit area is made up by granite containing hornblende. In the mid-altitudes of the massif, especially of the southerly quadrants, ultrabasic and serpentine rocks form “pearl rows” that were lifted up together with the plutonic granite. The varied geologic basis gave rise to different types of soil. This and the hypsometric differentiation of the climate and the relief, is the basis for a high diversity of habitats and an impressive biodiversity at Mount Kinabalu.

The present rough and steep rugged surface structure of the mountain is probably due to the continuing uplift of the massif (approximately 5 mm per year) (Milsom 2001) and shows the traces of ice age glaciation in the shape of erosion and accumulation forms (glacial abrasion, sharpened ridges and moraine sediments) (Photo 1). The periphery of the massif consists of tertiary and cretaceous sandstone and shale of the so-called Crocker formation, which also constitutes the Crocker Range to the south (Jacobson 1970; Jenkins 1971).

Mount Kinabalu is the highest mountain of South-East Asia between the Himalayas in the west and Irian Jaya (New Guinea) in the east. It probably also is the South-East Asian mountain with the highest number of visitors (300,000 per year), not least because a ridge with a relatively comfortable inclination on the southern flank of the mountain makes the ascent to the summit comparatively easy.

The thermal climate of Mount Kinabalu is characterised by clear altitudinal zonation (see below) with the typical isothermal conditions of the inner tropics (Lauer 1995). In contrast, the hygric climate of the relatively small area in northern Borneo – with humid conditions all year round – is rather varied. Whereas the western part of Sabah receives a maximum of precipitation in the course of the monsoon in the summer and the autumn, the winter monsoon dominates the precipitation in the eastern part (Fig. 2). Relatively dry periods in the course of one year are also differently distributed on both sides of north Borneo. This disparity of the distribution of precipitation in space and time can be assumed to influence the phenology and ecology of the forests on both flanks of Mount Kinabalu, which should be noticeable in flowering period and fruiting of the angiosperms; this phenomenon still has to be studied.

Mount Kinabalu is extremely rich in plant species (5,000 plant species per 10,000 km^2) and is one of only five megadiversity centres worldwide (Barthlott et al. 2005) with a high degree of endemism (Beaman 2005). The fact that more than 5,000 species of plants are concentrated on an area of just 1,200 km^2 underlines the importance of this mountain for global biodiversity.

Its exceptional natural beauty and species richness led to early collections and studies of the species composition at Mount Kinabalu. The first botanical collector was the governor of the English colony in Labuan (Borneo), Sir Hugh Low in 1851 (Beaman 2005). The first description of the flora of Mount Kinabalu, however, was published much later (Stapf 1894). Van Steenis published a number of works on the origin of the flora and the plant geography of Mount Kinabalu. The "Flora of Mount Kinabalu", edited between 1992 and 2004 by Beaman and collaborators (Parris et al. 1992; Wood et al. 1993; Beaman a. Beaman 1998; Beaman et al. 2001; Beaman a. Anderson 2004) comprises almost all plant families.

The present report uses the known results on the flora and altitudinal distribution of the vegetation of Mount Kinabalu in the context of our own measurements of soil temperature and eco-climatic observa-

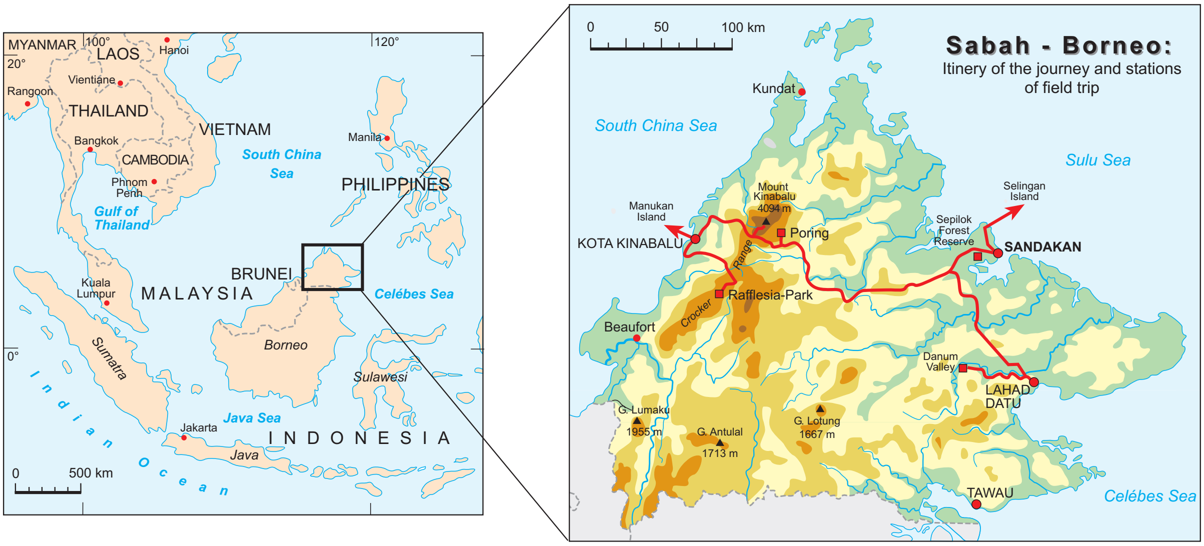

Fig. 1: Northern Borneo and Mount Kinabalu. Itinerary of the journey and stations of the field trip

Nord-Borneo und Mount Kinabalu. Verlauf der Studienreise und Stationen des Feldaufenthaltes tions for the development of a scheme of the hygrothermal altitudinal zonation of this mountain massif. Comparing two other equatorial high mountain regions – Mount Kenya and the Eastern Cordillera of Ecuador – with Mount Kinabalu will illustrate the problem of the altitudinal boundaries of the vegetation and climate in this mountain massif. Furthermore the question of the epiphytic vegetation of the lowland rain forests and the islands will be discussed.

2 *Altitudinal zonation of Mount Kinabalu*

2.1 *Altitudinal belts of the vegetation*

The zonation of vegetation at Mount Kinabalu into altitudinal belts has been the subject of quite a number of publications. The most recent studies are those of Kitayama (1991, 1992) who used a transect for the differentiation of the vegetation into six altitudinal zones.

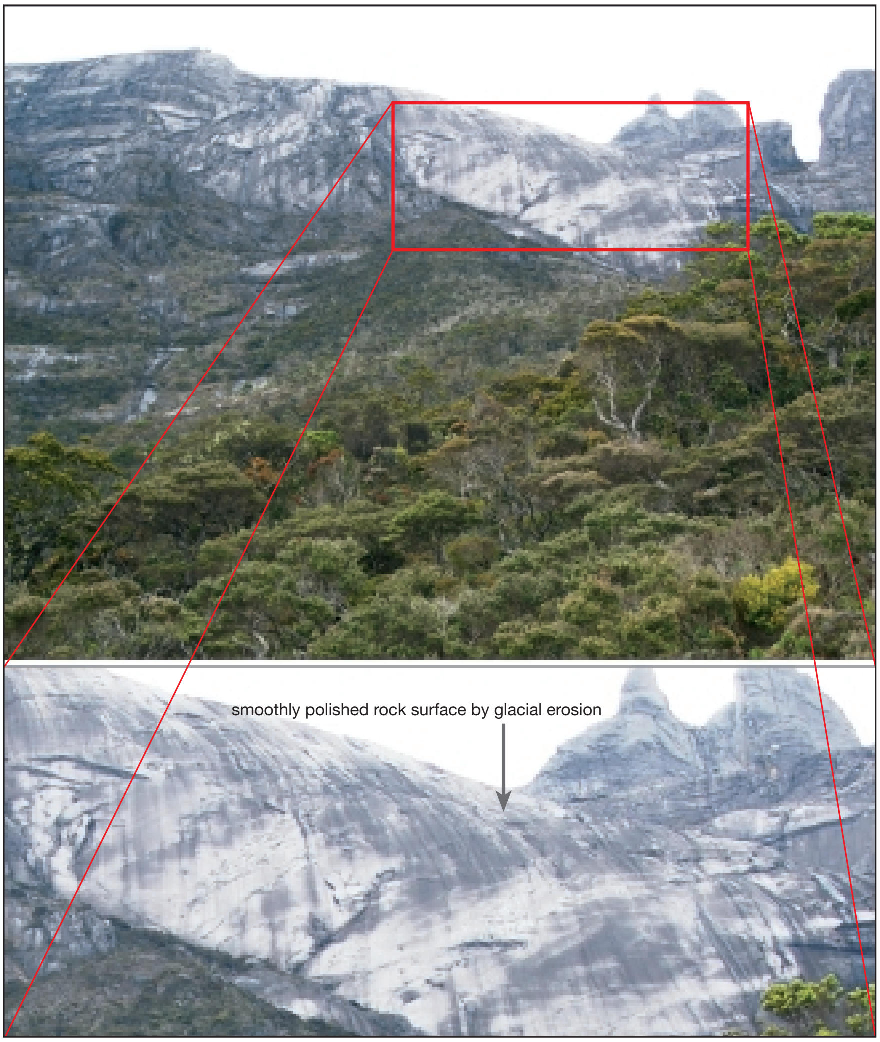

Photo 1: The pluton massive of Mount Kinabalu with abraded and smoothly polished rocks by glacial erosion in the almost vegetation-free alpine zone. In the foreground the sub-alpine shrub belt with *Rhododendron ericoides*, *Leptospermum recurvum* (trees of medium height with light and twisted stems) and *Dacrydium gibsiae* (light green shrub on the right corner below) (Photo: Rafiqpoor, October 2005)

Das Pluton-Massiv des Mount Kinabalu mit Gletscherschliffflächen in der nahezu vegetationslosen alpinen Stufe. Im Vordergrund die subalpine Gebüschstufe mit *Rhododendron ericoides*, *Leptospermum recurvum* (mittel hohe Bäumchen mit hellen, gewundenen Stämmen) und *Dacrydium gibsiae* (hellgrün, rechts unten) (Photo: Rafiqpoor, Oktober 2005)

Tabelle 1: Comparison of altitudinal belts of vegetation at Mount Kinabalu, after various authors (Data from KITAYAMA *1992)*

Vergleich der Höhenstufen der Vegetation am Mount Kinabalu nach verschiedenen Autoren (Daten aus KITAYAMA 1992)

Elevation m a.s.l.	COCKBURN (1978)	HOTTA (1974)	MENZEL (1988)	KITAYAMA (1992)
4,100 m				
		alpine		
4,000 m		4,000 m	unforested summit	alpine
		ericoid surub		
	summit	3,800 m		
				3,700 m
		conifer forest	3,500 m	upper sub-alpine
				3,400 m
		3,200 m		
	3,150 m	edaphic variation	ultrabasic montane	lower sub-alpine
3,000 m				
	ultrabasic	2,800 m		2,800 m
			2,600 m	
	2,550 m	upper montane oak forest		upper montane
				2,180 m
		2,100 m		
2,000 m	montane	lower montane oak forest	montane	lower montane
				1,200 m
1,000 m		1,000 m		
	900 m	hill rainforest	900 m	
		600 m		lowland
	lowland dipterocarp	lowland rainforest	lowland	
0,000 m				

Table 1 shows the altitudinal belts of vegetation after different authors for this massif. Figure 3 expresses the altitudinal zonation of vegetation at Mount Kinabalu, based on the detailed floristic studies of BEAMAN (2005) and our own observations. In the following this scheme will be discussed against the backdrop of the existing literature on the subject.

In the planar zone (up to 600/700 m a.s.l.) around Mount Kinabalu today large tracts of the original dipterocarp lowland rainforest have been transformed into cultivated areas or secondary forests respectively, and is dominated by the intensive cultivation of fruit and vegetables through small farmers. Dipterocarp lowland rainforests, however, have up to 240 tree species per ha and thus are considered to belong to the most alpha-diverse forests worldwide (KARTAWINATA et al. 1981; ASHTON 1989). In these forests the canopy reaches a height of 30–40 m and is mainly composed of trees of the genera *Hopea* and *Vatica* (both Dipterocarpaceae), together with species from the Burseraceae and Sapotaceae (MACKINNON et al. 1996). Some emergent trees, e.g. from the genera *Dipterocarpus, Dryobalanops, Shorea* (Dipterocarpaceae) rise to a height of up to 65 m (see WHITMORE 1984). Below the closed canopy – i.e. at the third layer of the forest vegetation, tree species from the families Euphorbiaceae, Rubiaceae, Annonaceae, Lauraceae and Myristicaceae are common. Apart from the Dipterocarpaceae, Euphorbiaceae are the most important tree family in the lowland rain forests of Borneo (see NEWBERRY et al. 1992). A characteristic of the third forest layer is the frequent phenomenon of cauliflory, e.g. in the case of the kura-kura durian tree (*Durio testudinarum*, Bombacaceae), which could be observed flowering in the forest of Danum valley in October 2005. On the forest floor the huge flowers of *Rafflesia* (Rafflesiaceae), which develop the largest single flowers of the plant kingdom and are endemic to south-east Asia, can be found. In the

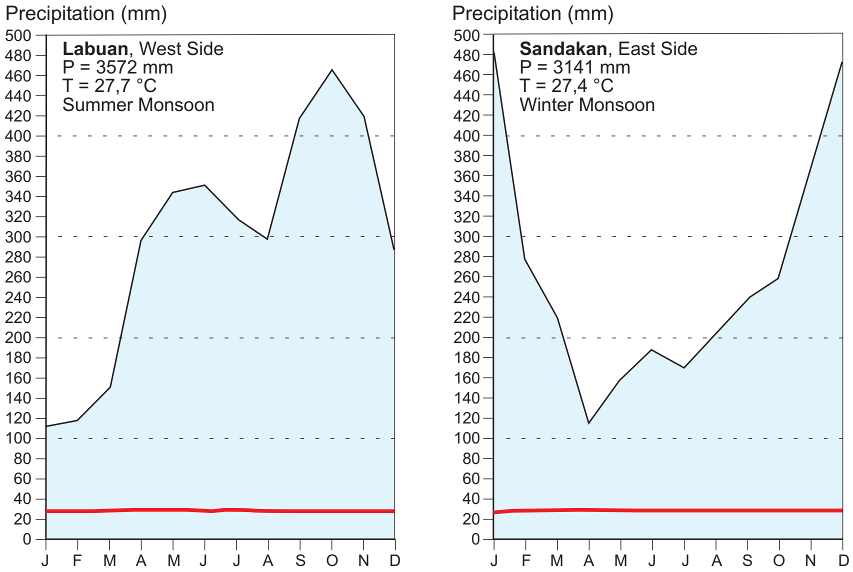

Fig. 2: Annual cycle of precipitation and temperature on the west and east side of Northern Borneo
Jahresgang des Niederschlags und der Temperatur auf der West- und Ostseite von Nord-Borneo

4,101 m a.s.l 3,700	8,5 - 6,5 °C	frost debris belt with herbs and grasses
2,900	10,0 - 8,5 °C	subalpine "ceja-shrub" with *Dacrycarpus kinabaluensis, Rhododendron ericoides*, *Darcrydium gibbsiae*
2,600	12,5 - 10,0 °C	high montane „ceja forest“ with *Dacrycarpus, Leptospermum, Eugenia* and other gymnosperms (e.g. *Dacrydium gibbsiae)* and angiosperms
2,200	16,0 - 12,5 °C	montane elfin forest with *Eugenia, Olea, Ilex* and epiphytic and ground orchids as well as numerous ferns, mosses and lichens
1,400	20,0 - 16,0 °C	submontane cloud forest of the families *Fagaceae, Lauraceae, Myrtaceae, Cyathea, etc.*
600	24,0 - 20,0 °C	Dipterocarp hill forest with *Lithocarpus, Shorea, Shima, Castanopsis, Darcrycarpus, Quercus, etc.*
0	27,0 - 24,0 °C	Dipterocarps lowland forest with ca. 240 tree species per 1 ha area (today secondary forest and/or agricultural land)

Fig. 3: Vertical arrangement of vegetation zones at Mount Kinabalu. The zone of maximum species density is marked in grey.
Höhenstufen der Vegetation am Mount Kinabalu. Die Höhenstufe größter Artmächtigkeit ist grau markiert.

Crocker Range we found *Rafflesia pricei*, a parasite on *Tetrastigma lanceolarum* (Vitaceae) (Photo 2).

At the hill (collin) zone of Mount Kinabalu (600–1,400 m a.s.l.) dipterocarps also dominate the forest, showing their conspicuous buttress roots and large umbrella-shaped crowns. On the forest floor, e.g. at Poring (eastern slopes of Mount Kinabalu, 600 m a.s.l.), a small *Amorphophallus* species together with *Impatiens* (Balsaminaceae) and *Begonia* (Begoniaceae) occurs. Occasionally, we find ferns of the genus *Asplenium*, growing epiphytically on the otherwise epiphyte-free trees.

Along the so-called "summit trail" at Mount Kinabalu (Fig. 4) we first pass the submontane cloud forests (1,400–2,200 m a.s.l.). In Sabah, these forests are still

Fig. 4: Schematic representation of the "summit trail" at Mount Kinabalu (varied from a flyer of Kinabalu national park 2004). In this scheme the sites for some species of *Nepentes* found by the authors are indicated.

Schematische Darstellung der Aufstiegsroute zum Gipfel des Mount Kinabalu (geändert nach einem Werbeprospekt des Nationalparks 2004). Darin sind die Fundorte einiger von uns gefundenen *Nepentes*-Arten angegeben.

Tabelle 2: The ten largest angiosperm families in the flora of Mount Kinabalu (Data after BEAMAN *2005)*

Die zehn größten Blütenpflanzenfamilien in der Flora von Mount Kinabalu (nach Angaben von BEAMAN 2005)

Families	Genera	Species
Orchidaceae	127	888
Rubiaceae	66	296
Euphorbiaceae	48	197
Moraceae	6	135
Fabaceae	42	133
Lauraceae	13	126
Melastomataceae	20	98
Ericaceae	5	97
Myrtaceae	11	97
Poaceae	52	91

preserved in their natural state and they belong to the most species-rich forests of Borneo. The highest regional diversity of the flora of Kinabalu is reached at this altitudinal belt, comprising about 1925 species out of 661 genera (BEAMAN 2005). Tree ferns (genus *Cyathea*) can be found here. Fagaceae, Lauraceae, Myrtaceae and Rubiaceae trees form a 20–30 m high canopy. A few specimens, however, rise above the canopy up to a height of 40–50 m. More than one quarter of all the orchids of Malaysia occur in this national park, most of them are epiphytes in the submontane forest. Comprising 856 species from 127 genera (BEAMAN 2005), they represent the largest plant family at Mount Kinabalu (Tab. 2).

In the montane elfin forests (2,200–2,900 m a.s.l.) the Dipterocarpaceae lose importance and are substituted by members of the Fagaceae (*Quercus, Lithocarpus, Castanopsis*), Myrtaceae, Theaceae and conifers (especially *Dacrycarpus* and *Phyllocladus*, Podocarpaceae). At this altitudinal belt epiphytic angiosperms (mainly orchids) are indeed present, but they increasingly give way to epiphytic mosses and lichens that occur in high abundance and frequency (see FRAHM et al. 1996). Ferns, among them primarily the genus *Asplenium*, constitute a considerable part of the epiphytic vegetation.

In the upper montane (oreal) "Ceja forest"[1] between 2,900–3,400 m a.s.l. the maximum canopy height is significantly lower, only 10 to 20 m. *Gymnostema, Leptospermum, Tristaniopsis* and conifers are the dominant tree species. Tree ferns are also common. The conifer *Dacrydium gibbsiae* ("Southern Pine", endemic for Kinabalu massif) can be found here and continues (though decreasing in maximum height) into the subalpine "Ceja-shrub" zone. Other shrubs are *Rhododendron* and *Vaccinium*. Like the montane cloud forest, the "Ceja forest" is characterised by the highly abundant mosses and lichens on the branches and twigs of trees – a consequence of the frequency of fogs (which is, however, less common than further below). Although there are conspicuous physiognomic differences in stem diameter, foliage and species composition between this type of forest and the montane cloud forest they have been group together as "upper montane forests" by KITAYAMA (1992). The significant taxonomic difference between these two forests is (among others) the occurrence of *Dacrydium gibbsiae*, which is not present in the montane cloud forest (see Fig. 3). There are, however, epiphytic orchids and ferns. Other orchids grow on the forest floor, together with *Selaginella* and carnivorous *Nepenthes* (Photo 3), mosses, lichens and ferns, of which there are more than 608 species in the Kinabalu National Park (BEAMAN 1996).

In the subalpine Ceja-shrub zone (3,400–3,700 m a.s.l.) *Dacrycarpus, Dacrydium, Leptospermum* and *Rhododendron ericoides* are very abundant. The majority of *Rhododendron* species (total: 24, of which four are endemic for the area) at Mount Kinabalu occur in the upper cloud forest and the subalpine zone (see WONG a. CHAN 1997). The canopy height of the Ceja-shrub is considerably lower (3–5 m); the treelets are similar in species composition, but their trunks are gnarled and twisted. Larger specimens of *Leptospermum recurvum* are covered with beard lichens, due to the lingering influence of fog at this altitude. Terrestrial orchids and some carnivorous *Nepenthes* (*N. villosa, N. lowii*) together with numerous ferns and mosses make up the undergrowth.

The alpine zone (3,700–4,101 m a.s.l.) is almost devoid of vegetations, due to the inhospitability and abruptness of the pluton massif with its impressive glacial abrasion forms (see Photo 1) and lack of soil formation. Only in crevices and patches where fine material has accumulated do some alpine brushes (among others *Rubus*), herbs (*Gentiana, Potentilla, Ranunculus*) and grasses occur.

2.2 Hygrothermal zonation of Mount Kinabalu

The soil temperature, measured at a fixed depth (usually between 30 and 50 cm) is considered as a valuable measure of heat quantity for the characterisation

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[1] "Ceja forest" is the forest formation above the montane elfin forest which is relatively species rich and in the South American Andes is called "ceja de la montaña" (literally "eyebrow of the forest"). VARESCHI (1980) uses in this context the term "Chirivitales". The forest trees of this formation are lower and have a smaller breast height diameter (BHD) compared to the trees of the montane elfin forest. This formation contains elements which at lower levels are not present, like many gymnosperm species, partly endemic to the Kinabalu massif.

Photo 2: *Rafflesia* the largest flower of the world. Here *Rafflesia pricei* (Rafflesiaceae), with a diameter of approximately 50 cm (as a scale a Malaysian 50 cent coin) in the rainforest of the Crocker Range (Photo: RAFIQPOOR, October 2005)

Rafflesia, die größte Blüte der Welt. Hier *Rafflesia pricei* (Rafflesiaceae) mit ca. 50 cm Durchmesser (als Maßstab eine malaysische 50-Cent-Münze) in den Regenwäldern des Crocker Range (Foto: RAFIQPOOR, Oktober 2005)

Photo 3: The carnivorous plant *Nepenthes villosa* close to the summit trail at 2,800 m a.s.l. (Photo: RAFIQPOOR, October 2005)

Die karnivore *Nepenthes villosa* nahe "Summit Trail" in 2.800 m NN (Photo: RAFIQPOOR, Oktober 2005) of the thermal structure of a tropical landscape (Winiger 1981; Lauer 1982; Dronia 1983; Lauer et al. 2001; Bendix a. Rafiqpoor 2001; Richter 2003; Rafiqpoor 2004). It was measured at 15 cm depth in intervals of 100 m altitude while climbing the southern flank of Mount Kinabalu (see Fig. 4), using a "testo 600" instrument. Permission to use "heavy gear" (drill, spade) to do the measurements at 50 cm depth could unfortunately not be obtained. However, the measurements in 15 cm depth do show a characteristic picture of the thermal zonation (Körner a. Paulsen 2004) and can be considered representative for the mountain massif in the before mentioned altitudinal range.

Fig. 5 shows a scheme of the hygrothermal altitudinal zonation, using as a basis our measurements of the soil temperature along the "summit trail" (1,800–3,000 m a.s.l.) and integrating the altitudinal zonation of the vegetation. The humidity along the measurement profile was estimated using the so-called phytoindication, in the case of Mount Kinabalu the abundance and frequency of epiphytes.

In the submontane cloud forest the soil temperature decreases continuously with the increase in altitude. At the lower fog boundary (condensation zone: ca. 2,200 m a.s.l.) the decrease in temperature slows down and even stays constant in sections in the dense fog cover zone up to approximately 2,600 m a.s.l. The reason is the release of latent heat at this altitudinal level, compensating the decrease of air temperature (Lauer et al. 2003). Above the zone of dense fog (from ca. 2,600 m a.s.l. upwards) the soil temperature drops again, because here absolute humidity has decreased and consequently the condensation ability of the air masses has gone down. From ca. 2,900 m a.s.l. the soil temperature rises again. The possible cause is the opening of the vegetation cover in the area of the Ceja forest, where the canopy is no longer continuous. Furthermore at this altitude the fog cover is no longer as dense as at the condensation zone proper in the elfin forest and the insolation is more intense. In consequence, more insolation energy is converted into heat energy and the forest ground heats up. This phenomenon is even more noticeable at the subalpine Ceja-shrub zone above 3,400 m a.s.l., because here the canopy is more open and the ground is subject to an even more intense insolation. The same phenomenon was proven for the eastern cordillera of Ecuador (Bendix a. Rafiqpoor 2001; Lauer et al. 2003). At 3,700 m a.s.l. the upper limit of the tree growth at Mount Kinabalu is reached.

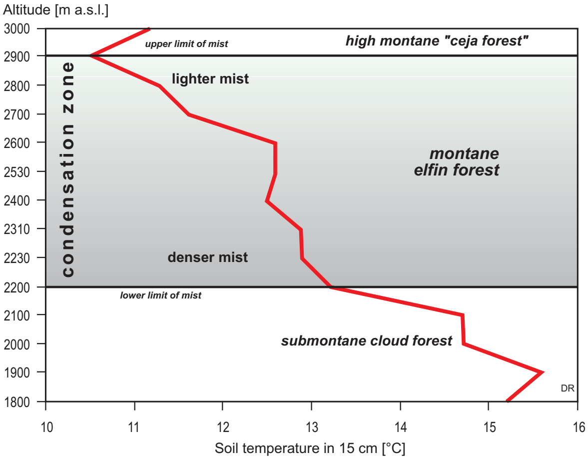

Fig. 5: Eco-climatic altitudinal zonation of Mount Kinabalu.
Ökoklimatische Höhenstufung des Mount Kinabalu.

A comparison of the altitudinal zones of the vegetation of three equatorial high mountain areas (Tab. 3) shows that the upper tree limit on Mount Kenya is 4,000 m a.s.l. (Niemelä a. Pellikka 2004) and in Ecuador it is 4,200 m a.s.l. (Bendix a. Rafiqpoor 2001; Lauer et al. 2003). In comparison, the tree limit at Mount Kinabalu is 300 m and 500 m lower, respectively. At Mount Kerinci (Sumatra) the upper tree limit is lower still (2,950 m a.s.l.), and the vegetation cover ends at 3,250 m a.s.l. (Oshawa et al. 1985). Assuming a gradient of decrease of 0.5°C/100 m the soil temperature of the frost debris zone of Mount Kinabalu should be between 8.5°C and 6°C. This zone thus should be potentially covered with trees, as at the upper limit (4,101 m a.s.l.) soil temperature in the root zone should be at least 6°C, which is recognised as the limit for the protein synthesis in the root system of tropical trees (Walter a. Medina 1969). The temperature interval of 5–6°C, together with seasonal variations are considered to be the limiting factor for tree growth at the upper tree line, according to Körner (1998) and Körner a. Paulsen (2004). Whereas at Mount Kerinci the recent volcanic activity is an impediment to plant growth (Oshawa et al. 1985), we suggest that at Mount Kinabalu the steepness of the granite rocks is the decisive factor for the depression of the upper tree limit – an explanation also proposed by Körner (pers. comm. 2006).

3 Why are the lowland forests of Borneo poor in epiphytes? A comparison between the mainland and outlying island

As explained above, the lowland forest around Mount Kinabalu has to a large degree been converted to agricultural land. In order to estimate the abundance and diversity of the epiphyte vegetation in the lowland forests of north Borneo, several nature reserves in

Tabelle 3: Comparison of vertical arrangement of vegetation zones of three equatorial high mountains. Our own scheme for Mount Kinabalu is compared with that of KITAYAMA *(1987/1991)*

Vergleich der Höhenstufen der Vegetation an drei äquatorialen Hochgebirgen. Eigene Höhenstufung für Mount Kinabalu ist der von KITAYAMA (1987/1991) gegenübergestellt

Elevation m a.s.l.	Africa Mount Kenya NIEMELÄ a. PELLIKKA (2004)	South America Pappalacta/Ecuador LAUER et al. (2003)	Asia Mt. Kinabalu KITAYAMA (1987/1991)	Asia Mt. Kinabalu RAFIQPOOR a. NIEDER (2005)
4,100 m				
	Páramo			alpine frost debris belt
4,000 m	4,000 m	grass páramo with islands of forest	alpine	
	Ericaceous zone	3,700 m	3,700 m	3,700 m
		ceja transition forest	upper sub-alpine	sub-alpine “ceja shrub”
		3,550 m		
	3,500 m	elfin forest		
			3,400 m	3,400 m
	upper montane	3,100 m	lower sub-alpine	high montane “ceja forest”
3,000 m	3,000 m		3,000 m	
		evergreen montan forest		2,900 m
	Bamboo zone			montane elfin forest
			upper montane	
	2,200 m	2,200 m		2,200 m
2,000 m	lower montane			
	1,800 m		1,800 m	sub-montane cloud forest
		evergreen cloud forest	lower montane	
				1,400 m
			1,200 m	
1,000 m	agricultural land	1,000 m		hill rainforest
		hill rainforest		
		0,600 m	lowland	0,600 m
		lowland rainforest		agricultural land
0,000 m				

the wider vicinity were visited. These were the Sepilok Forest Reserve near Sandakan, the Danum Valley near Lahad Datu and the Crocer Range near Kota Kinabalu (see Fig. 1).

In general one can observe that the dipterocarp lowland rainforests of these forest reserves are relatively poor in epiphytes. The forests are dense and little light reaches the forest floor, the ultisols (USDA soil taxonomy) and/or acrisols (FAO classification) are extremely poor in mineral nutrients and covered with a thin layer of leaf litter and plant seeds which does not cover the naked soil completely. Only where the canopy is open do *Selaginella*, terrestrial orchids and tree seedlings occur. Lianas are abundant, epiphytes relatively rare in the understorey of the forest. Only a few trees host large specimens of *Asplenium nidus* (often in 40 m height) and orchids (beneath trees with epiphytes in the canopy fallen down specimens can often be found).

The epiphytism on islands off the coast of Sabah was studied by visiting some islands in west and east Sabah. In the Tungku Abdul Rahman National Park, which consists of a number of islands off Kota Kinabalu, no epiphytes could be found. Even the very common species *Asplenium nidus* did not occur. The islands east of Sabah (the Turtle Islands off Sandakan) showed similar results in this respect.

The islands of the Indo-Malayan archipelago are, of course, not totally devoid of epiphytes. One basic condition for their occurrence is, however, a sufficient hypsometric differentiation of habitat and a regular water supply. A varied topography facilitates a regular water supply in form of fog and/or rain, even during drier seasons, because daily convection and condensation processes provide for it. TAKEUCHI and WIAKABU (2001) and FOSTER (2001) found a high diversity of epiphytes in the montane zone (1,000–1,600 m a.s.l.) on New Britain and New Ireland (Bismarck Archipelago), where the lowland forests are also very poor in epiphytes. The same was found by WHISTLER (1995) on Samoa, where the forests of the lowland and the hill areas are almost free of epiphytes and the cloud forests between 1,000 and 1,680 m a.s.l., on the other hand, have a high abundance of epiphytes.

Why do the lowland forests of the mainland and the islands of North Borneo have such a scant epiphyte vegetation? A possible explanation could be El Niño (ENSO). Its influence on the SE Asian region is so marked that flowering and fruiting events of forest trees have been attributed to it. This was proven by long term observations of more than 50 species of Dipterocarpaceae in Kalimantan (Indonesia) (CURRAN et al. 1999; CURRAN et al. 2004; BLUNDELL 1999). BEAMAN (2005) considers the El Niño phenomenon one of the causes of the immense species richness at Mount Kinabalu.

In normal years there is an equatorial countercurrent in the Pacific Ocean (direction west-east, north of the equator). If the almost stationary subtropical high-pressure cell over south Pacific gets weaker, the Walker circulation above the central Pacific almost collapses. The equatorial westerly wind can push large amounts of warm surface waters from the warm ocean of the Indo-Malayan archipelago towards the eastern Pacific. During such an El Niño event there is a low pressure area over the eastern Pacific. Because a "tongue" of equatorial warm water reaches south across the equator, heavy rains occur on the western coast of South America, in Ecuador and the northern stretches of the Atacama desert of Peru (LAUER 1998; BENDIX et al. 2000). In the Indo-Malayan archipelago the consequence is the development of a stable high-pressure area, leading to an excessive, long-lasting drought (LAUER 1998). This in turn favours forest fires, as could be seen in large parts of Indonesia, Malaysia and Australia during the ENSO 1997/1998 (HÄNSLER 2002).

The almost regular occurrence of sometimes very intense and long-lasting dry periods (up to four months, June to September; CURRAN et al. 1999) during El Niño could be an explanation for the scarcity of epiphytes in the lowland rain forests. Because epiphytes do not have root contact with the soil, they are more dependent than other life forms on a continuous water supply in the form of precipitation. Lasting drought leads to severe water shortage for these plants and they die off. Therefore the epiphyte flora of the lowland dipterocarp rainforests of the mainland and the outlying islands is very limited. In contrast, in the montane forests of Mount Kinabalu and large mountainous tropical islands epiphytes are much more abundant, because the water supply is secure as a consequence of daily condensation processes.

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