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Dick Johansson

Ecology of vascular epiphytes in West African rain forest

Résumé:
Ecologie des épiphytes vasculaires dans la forêt dense humide d'Afrique occidentale

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ECOLOGY OF VASCULAR EPIPHYTES IN WEST AFRICAN RAIN FOREST

Ecologie des épiphytes vasculaires dans la forêt dense humide d'Afrique occidentale (French summary)

Doctoral dissertation to be publicly discussed in the Botanical auditorium, Uppsala University, on May 2, 1974, at 10 a.m., for the degree of Doctor of Philosophy (according to Royal proclamation No. 327, 1969)

Abstract The ecology of 153 species of vascular epiphytes (101 orchids, 39 pteridophytes and 13 others) in the Nimba Mts in Liberia is described. 29 species are recorded in Liberia for the first time including one new species, *Rhipidoglossum paucifolium,* Orchidaceae. Field characteristics, flowering periods and some pollinators of the orchids are also given.

In high forest with the canopy 30 m or more above the ground, 50.4 % of the trees (phorophytes) 10 m or higher carried epiphytes, compared to 14.8 % for the phorophytes in regenerating forest. The ratio between fern and orchid species was 1:3 at 500-700 m alt. and 1:1 at 1000-1300 m. Most of the epiphytic species occupy a ± restricted part of the phorophyte, as judged by their occurrence in the five sectors in which the phorophytes were subdivided.

Ten different epiphyte communities are recognized. Their floral composition and development are also described. Certain species of phorophytes, e.g. *Heritiera utilis, Lophira alata* and *Parinari excelsa* generally carry an abundance of epiphytes, while others, e.g. *Anthocleista nobilis, Fagara tessmannii* and *Terminalia invorensis* are mostly devoid of epiphytes.

Colonization by epiphytes begins late in the life of the phorophyte, which is indicated by the higher frequency of epiphytes on the larger specimens. The effect of the epiphytes on their phorophytes is reviewed and observations from Nimba and East Africa provided. The environmental influences on the occurrence of the epiphytes on the phorophytes are discussed. In addition, field observations and experiments concerning water economy microclimate, substrate properties and light intensities are presented.

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Content

Preface

My first contact with a tropical rain forest dates back to August 1964 when I commenced employment for Lamco J.V. Op. Co. in Liberia. As a high school teacher at the International school in Yekepa I used my spare time during the following six years to explore the rain forest. In the vicinity of the newly constructed Yekepa community, at 500 m altitude, virgin rain forest covered the slopes of the Nimba range up to the peaks at 1300 m altitude. The rain forest was very poor in species in the field layer. On the trees, however, vascular epiphytes were abundant and soon caught my particular interest. While trying to learn about the ecology of the epiphytes it soon became evident that the literature on this subject was very scanty. Although the vascular epiphytes are a very characteristic floristic element in the rain forest inaccessible growing sites have resulted in few and often superficial reports on their ecology.

After an introductory period in which to become acquainted with the tropical flora a preliminary plan for the future investigation was outlined in cooperation with Prof. Hugo Sjörs at the Institute of Ecological Botany in Uppsala.

After returning to Sweden in 1970 my work was continued at the newly started Afro-Botanical Dept. of the Institute of Systematic Botany in Uppsala under the guidance of Prof. Olov Hedberg.

During an excursion to Kenya and Tanzania in January 1971, under the leadership of Prof. Hedberg, I was able to study epiphytes in several environments different from those of the lowland tropical rain forest. As an indirect result of a three months ecological study the same year for Sweco in the Kidatu area in Tanzania, a knowledge of epiphytes in dry environments was gained.

Several persons have contributed to the completion of this study. Harvey Boettcher, Manuel Diaz and Franz Zimsek often accompanied my tours of the forest. Kurt Eriksson helped in the construction of the light-measuring equipment and Miss Anne Croné carried out some laboratory work in Liberia. Many other Lamco employees have in one way or another helped or simplified my field work.

Help and guidance in the determination of critical specimens have been received from Jean Bowden, F.N. Hepper, Frances Jarrett, M. Sands and P. Taylor of the Kew Herbarium, and from L. Garay of the Oakes Ames Herbarium, Harvard Univ., Cambridge, Mass. Prof. Sanford, Univ. of Ile Ife, Nigeria, provided an unpublished manuscript on the use of epiphytic orchids in general ecology work.

The determinations of the insects were performed by M.A. Grogan, S.L. Shute and I.H.H. Yarrow of the Entomological Dept. of the British Museum (Natural History).

Aina Alm, Gertie Backlund, Margareta Hellman and Barbro Enander have typed the manuscript. Märta Ekdahl has prepared the large tables and Ulla-Britt Sahlström has copied the photographs. The map over the investigated area was drawn by Per Åke Söderman.

In the preparation of the manuscript valuable criticism has been provided by Doc. Örjan Nilsson. Dr Jerk Hellkvist at the Institute of Physiological Botany in Uppsala has commented on the section about the water economy of the epiphytes. The linguistic revision has been carried out by André Brochu and the French resumé was translated by Renée Perrette.

Gränges International Mining Division, Stockholm, has supplied a grant for the photographic illustrations.

Prof. Hedberg, my teacher and tutor, has through his never failing enthusiasm and encouragement actively contributed to the completion of this work.

Finally, Astrid did a considerable amount of work behind the scenes.

All persons and institutions mentioned above I want to sincerely thank for valuable cooperation.

Uppsala, January 1974

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I. Introduction

GENERAL NOTES ON VASCULAR EPIPHYTES

Distribution

Epiphytism, as defined by Barkman (1958:9), occurs in many plant orders. It has a very extensive geographical distribution among non-vascular plants such as algae, mosses, and lichens.

The vascular epiphytes, pteridophytes and phanerogams, are on the other hand more or less restricted to tropical regions. In tropical rain forests especially, they form a significant part of the flora, and their presence and abundance are often used as a characteristic of such forests (Schimper 1903:260, Richards 1964:8). Vascular epiphytes are rare in temperate climates. In humid climates, e.g. certain coastal and high mountain areas, a large number of plant species may occur for varying periods of time as epiphytes although lacking special adaptations to such a life (Sharp 1957). The somewhat confused terminology of the different types of epiphytes will be presented later in this chapter.

Occurrence in various families

In the tropical rain forest epiphytism among vascular plants occurs in a limited number of families, but in a large number of genera. Schimper (1888) mentioned 33 families and 232 genera. Naturally the number of known epiphytic genera has increased since then, but the number of families given by him is reasonably up to date (Richards 1964:112).

It is very difficult to estimate the total number of epiphytic species in the world. However, their presence in certain families is better known. The estimated total number of species in the families mentioned below, in parentheses, is taken from Willis (1966). The majority of the orchids (20 000) are epiphytes (cf. Hunt 1967, Summerhayes 1968). The bromeliads (1400) play an important part in the epiphyte flora of the New World and to a lesser extent this also applies to the Cactaceae (2000). The latter family also includes a pantropical genus, *Rhipsalis,* with numerous epiphyte species. Ericaceae (1350) has a considerable number of epiphytes especially in the Vaccinioideae. The families of Araceae (2000), Asclepiadaceae (2000), Gesneriaceae (2000), Melastomataceae (3000), and Rubiaceae (6000) are also rich in epiphytes.

A geographical pattern can be observed in the composition of the epiphyte flora. In Africa pteridophytes and orchids almost solely form the epiphyte flora, while in South America bromeliads and cactaceous plants also are important. In Asia and Australia species of Asclepiadaceae and Rubiaceae are well represented together with the pteridophytes and orchids.

Phylogeny

Schimper (1888) maintained that the tropical epiphytes have developed from terrestrial types that were growing in dark humid forests. Went (1895) claimed that the epiphytes have evolved from root climbers. Pittendrigh (1948) suggested that the epiphytic bromeliads originated from terrestrial ancestors that lived under semi-desert conditions. The same would probably apply to the epiphytic Cactaceae and maybe the majority of the epiphytic flowering plants.

Garay (1972:211) date the development of the epiphytic mode of life among the orchids back to the Pliopleistocene. He also rightly states that while the terms geophytic and epiphytic convey the meaning of ecological habitats, in reality they express distinct evolutionary adaptations through morphological modifications in the roots.

Properties

What are the properties that make a plant successful as an epiphyte? Two conditions must be fulfilled. (1) The plant or its diaspores must in one way or another be able to reach a position on the phorophyte. (2) It must possess the ability to survive drought after its establishment.

(1) The weight of the diaspores has been emphasized

by Schimper (1888) as a chief limiting factor for potential epiphytes. He pointed out that many of the numerous epiphytic bromeliads in South and Central America have particular adaptations in the seeds for wind dispersal.

The largest number of epiphytes occurs among the orchids and the pteridophytes which both have very minute diaspores. These are so small that they can easily be carried by the wind. 84 % of 50 true epiphytes in New Zealand exhibit minute spores or seeds (Oliver 1930:19). The weight of an orchid seed (*Dendrobium attenuatum*) was given as 6.5 µg by Ames (1922).

The role of animals in the dispersals of the diaspores of epiphytes has been stressed by several authors. Holtum (1960) reports dispersal by insects: "Ants may have an important function in several ways. They may carry seeds, especially small seeds which contain food useful to them. Some of these seeds, including seeds of orchids, are sought chiefly for oil drops in the outer tissues and the embryos may not be destroyed by ants; the seeds grow in ants' nests, which provide shelter and minerals for the seedlings." Numerous birds, bats, monkeys and squirrels, living in the trees may also contribute to the dispersal of the epiphytes. Fruits may be eaten and the seeds spread with the excreta. A somewhat stranger way of dispersal is reported for the epiphytic bromeliad, *Tillandsia usneoides*, 'spanish moss', that occurs in the South Eastern parts of USA (Fig. 1). This lichen-like plant is used by certain birds as building material for their nests. The plant survives the breeding period and continues to develop afterwards. The most common way of dissemination, however, occurs during violent gales, when pieces are broken off and carried by the wind to new phorophytes in the same manner as among certain lichens (Pennfound & Deiler 1947).

(2) Once located on the phorophyte the young plant must have an effective system of attachment to the substrate so as not to be washed down by the rainfall. The root systems are often very extensive, superficial or aerial, and in many cases specially developed only for anchoring purpose (certain bromeliads).

A common problem is the short time of water uptake due to the limited ability of the substrate to store water. The plants are often adapted to a rapid uptake and high storage capacity of water, replacing the storage in the substrate.

Fig. 1. *Tillandsia usneoides*, 'spanish moss' (Bromeliaceae). New Orleans, La.

Drought is the most serious threat to the life of the epiphytes. Drought resistance shows a wide range of variation, from the poorly adapted filmy ferns to the extremely resistant epiphytic cactaceae and bromeliads. It is reported that bromeliads survive in areas with about 400 mm/year in N. Argentina (Tixier 1966:22).

The greatest abundance of epiphytes is found where there is a yearly rainfall of 100 inches (≈ 2500 mm) or more and where no month has an average of less than 2 or 3 inches (Holtum 1960). In Indochina the epiphytes disappear when the rainfall is less than 1000 mm per year (Tixier 1966:121). The temperature seems also to limit the geographical distribution of certain epiphytes, as can be observed e.g. in the East African high mountains where the pteridophytes occur at much higher altitudes than the orchids.

The epiphytes show an interesting variety of both morphological and physiological adaptations for

withstanding unfavourable conditions. It would, however, take too far to discuss these adaptations here. A brief description of the major life-forms is given in chapter II.

Ecological subdivisions

Several authors have grouped the epiphytes into large units, based upon life-forms, life-cycles or their dependence on light, substrate and humidity. The divergent terminology for such groups makes comparisons between different investigations difficult. Barkman (1958:9-15) has given a valuable summary of the terminology concerning non-vascular epiphytic cryptogams.

Regarding non-vascular cryptogams the term obligate is often used for typical epiphytes sensu Oliver (Table 1). The rest of the epiphytes are called facultative (Barkman 1958:11). A subdivision of the facultative epiphytes into three categories, preferential, indifferent, and occasional has been used by Hilitzer (1925). Both vascular and non-vascular plants are included in the micro and macro-epiphytes of Tixier (1966:45) and in the Sonnen(licht), Schatten, and Epiphyllen vegetation of Knapp (1973).

Oliver (1930) presented a scheme that will be used here as a base for comparing the terminology of different authors (Table 1).

I. Typical epiphytes. Species which are habitually epiphytic.

II. Occasional epiphytes. Here are included those plants which are under ordinary circumstances terrestrial. Occasionally they are found on trees where they appear to thrive until maturity.

III. Hemi-epiphytes. These are trees which begin their existence on other trees or tree ferns, send down one or more taproots to the ground and eventually establish themselves as independent plants.

IV. Ephemeral epiphytes. These are accidental epiphytes. They are for the most part seedlings of trees which fail to gain maturity in their epiphytic position, and consequently die after attaining a size which demands more nutrients than the substrate can furnish.

The term 'ephemeral orchids' is used by Smith (1925) for plants that carry their flower only one day, e.g. *Dendrobium crumenatum*. In F.W.T.A. 1:1 (1954:220) the term 'sub-epiphyte' is used for a *Begonia* that is 'creeping over logs, etc'.

The typical epiphytes, have also been divided into a large number of units based on the habit or dependence of water, light, and substrate.

Growth habit

Schimper (1888) recognized three types: proto, nest or bracket, and tank epiphytes, based on the habit of the plant.

Water

The dependence on water is a common criterion for a subdivision. Oliver (1930) distinguishes between hydrophytes, mesophytes and xerophytes. Schnell (1952:282) recognizes the same units as Lebrun (1937) with one addition, 'les epiphytes hygro-mésophiles'. The units used by Schnell are thus:

I. Epiphytes hygrophiles de la base de troncs

II. Epiphytes hygromésophiles de la région moyenne des troncs

III. Epiphytes mésophiles des grosses branches et du sommet des troncs des grand arbres

IV. Epiphytes xérophiles des branches supérieures

Light

A division into shade-, sun-, and extreme xerophilous epiphytes, has been used by Davis & Richards (1933:380-381), and Richards (1939:31-32). Richards admits the difficulties in distinguishing the latter two groups.

Table 1. Classification of epiphytes by some authors.

Oliver 1930	Typical ep.	Occasional ep.	Hemi-ep.	Ephemeral ep.
Schimper 1888	Holo ep.		Hemi-ep.	
Went 1895	Wahre ep.		Hemi-ep.	
Pessin 1925	Eu-ep.	Pseudo ep.	Hemi-ep.	Pseudo ep.
Lebrun 1937	Ep. authentique	Ep. accidentel	Hemi-ep.	Ep. accidentel
Hosokawa 1968	Ep. typica	Ep. occasionalis	Hemi-ep.	Ep. ephemeralis
Schnell 1970	Ep. hygrophiles	Ep. accidentels	Lian-ep.	
	Ep. mesophiles			
	Ep. xerophiles			

Grubb et al. (1963:592) is also critical of this division. In his studies of mountain rain forests in Equador he remarks: "extreme xerophilous epiphytes, sensu Richards, are not markedly more distinct from each other in their biology than crown-base and bole-base skiophytes." Grubb et al., use the terms photophyte and skiophyte for epiphytes that live in well-lit and ill-lit habitats respectively.

Guillaumet (1967:60) distinguishes between a héliophile, a mésophile and a sciaphile group.

Hosokawa (1968) groups the epiphytes into four ecological types: (a) the sun-type growing in direct sunshine, (b) the stem and/or leaf succulent xerophilous type, (c) the shade-tolerant type growing in diffuse weak light, (d) the hygrophilous type.

Substrate

Went (1940) considers the demand on the substrate as a dividing line between epiphytes. He differentiates between two groups: bark epiphytes and those that need an accumulation of humus to be able to develop, so called humus epiphytes.

It is of course impossible to rank the importance of all the environmental factors without experimental proof. Which one of the many factors involved that is decisive can be very hard to determine since they are often interacting.

PREVIOUS STUDIES OF VASCULAR EPIPHYTE ECOLOGY

Research on epiphytic plants was started by Schimper. In a pioneering and comprehensive work 'Die Epiphytische Vegetation Amerikas' (1888) he focuses his attention on the anatomy, morphology and ecology of epiphytes.

Even though the epiphytes form a characteristic part of the rain forest they are usually mentioned only casually in ecological reports (see section Field work).

In Asia specialized studies have been carried out on Java by Van Oye (1921, 1924 a), and Went (1931, 1940), and in Micronesia and elsewhere by Hosokawa (1952 a, b, 1954 a, b, c, 1955, 1957, 1968). Hosokawa has also written numerous articles on the terminology of epiphyte communities and the life-forms of epiphytes. From Vietnam Tixier (1966) has presented a thorough study of epiphytes including bryophytes.

In Africa, Van Oye (1924 b) and Lebrun (1937) have studied epiphytes in the Belgian Congo. Sanford (1967, 1968 b, 1969, 1973) has presented a series of interesting papers concerning the distribution and ecology of epiphytic orchids in Nigeria and elsewhere. Several authors e.g. Piers (1968), Morris (1968, 1970), and Stewart (in Stewart & Campbell 1970) have revealed interesting facts about the ecology of orchids in East and Central Africa. In a penetrating study of the epiphytic fern genus *Platycerium* in the Ivory Coast, Boyer (1964) assembled an impressive amount of facts, useful for the understanding of the ecology, not only of the *Platycerium* ferns but also of epiphytes in general.

Regarding the New World surprisingly few publications are available (Dunn 1941). The bromeliads have naturally received interest from many directions. Picado (1913) published a report on the ecology of the bromeliads and their remarkable adaptations in the epiphytic life-forms. Their anatomy and importance as breeding sites for various insects have been studied by Pennfound & Deiler (1947) and Pittendrigh (1948).

SCOPE OF THE PRESENT STUDY

It is no exaggeration to say that the composition and geographical distribution of the vascular epiphytic flora both in Africa and elsewhere in the tropics are poorly known. Even less known are the presence and distribution of the various species in the great number of habitats that exist on the trees. This study has aimed at recording the growing sites of epiphytes in the rain forest and particularly the occurrence of epiphytes in the highest parts of the forest, since such information is extremely scarce.

This is partly a quantitative study of the spatial distribution, since whenever possible the actual number of epiphytes was counted according to a special system. However, the ecological requirements for the individual species were also investigated.

Special attention has thus been paid to the light and substrate and their possible effect on the presence and abundance of epiphytes. The often observed tendency of epiphytes to form some kind of community induced a detailed investigation of the abundance, floral composition and development of such communities.

Previous reports of a correlation between the epiphyte flora and species of 'host tree' offered another aspect that was investigated. The many adaptations that occur among the epiphytes induced studies into

their water economy. The use of epiphytes as indicators of microclimate and forest destruction was also investigated (cf. Sanford 1972).

A more specialized study regarding the phenology, pollinators and special field characteristics of the orchids was also included.

My study is restricted to the vascular epiphytes. However, the so-called filmy ferns, e.g. *Trichomanes* and *Hymenophyllum*, are in the main excluded, but the species observed are listed in chapter II (Table 7). In several ways these ferns resemble the non-vascular epiphytes. Their leaves are usually one cell layer thick and without stomata and can take up water in the same manner as mosses. The facultative (occasional, hemi- and ephemeral) epiphytes are also excluded but listed (Table 7) and referred to when of importance for the epiphyte flora.

FIELD WORK

My field work was carried out during 1964-1970, with the major part of the distribution recordings from the last two years of this period.

The scanty knowledge of the presence and the distribution on the trees of epiphytes in the tropics can be traced back to two different causes. The first is the very inaccessible growing sites of these plants. The second is the difficulties connected with the determination of the epiphytes. Several species are extremely similar in size and shape in their flowerless states (Fig. 33).

To overcome the first obstacle my research has been directed in three different ways: recording of the epiphyte flora, (1) on felled trees (close observation), (2) of standing trees (distance observation), (3) on a minor part of a tree by close or distance methods (occasional observation). The two first methods give a rather accurate picture of the distribution of epiphytes on the trees while the third is utilized for additional information.

To get acquainted with the epiphytes in various stages of their development I started from the very beginning to collect specimens and grow them in small wooden boxes in a specially constructed 'frame house'. The phenology of the various species could then easily be studied and minor characteristics observed. The investigation includes the examination of 220 felled trees and 236 trees examined according to the distance method on 47 species of phorophytes in the high forest. The so-called occasional recordings number more than three thousand observations from roughly 1500 trees, palms, ferns and lianas.

Outside the specially investigated area I have carried out surveys of the epiphyte flora in every county of Liberia. The neighbouring countries of Guinea and Ivory Coast have also been visited on several occasions enabling a comparison of the flora.

Epiphytes in environments, different from the rain forest types, have been studied in Kenya and Northern Tanzania (Jan. 1971), and in Southern Tanzania (April-June 1971). Brief visits in Zambia (July 1971) and in Cameroon (Mt Cameroon, July 1971) have supplied additional information.

Efforts have been made to get photographs from specimens growing in situ, but difficulties in obtaining good pictures of some of the phorophytes in the dense forest and of the epiphytes in the crowns, explains why some of them had to be photographed in rather unnatural environments. All pictures, except Fig. 31, are taken by the author.

TERMINOLOGY

Epiphyte is here used as defined by Barkman (1958:9). When nothing else is stated the term epiphyte refers to vascular epiphytes. The 'host tree' (shrub, palm etc.) of the epiphyte is referred to as the phorophyte following Ochsner 1928; (cf. Barkman 1958, Sjögren 1961, Tixier 1966, Skye 1968). This term is according to the definition by Ochsner (1928). The nomenclature of the phorophytes agrees with Voorhoeve (1965) and for species not treated by him the nomenclature in Hutchinson & Dalziel: Flora of West Tropical Africa (F.W.T.A.) 2nd ed., is followed.

The term high forest is applied to forests with a canopy at a height of 30 m or more regardless of the origin. Secondary or regenerating forest refers to forests in various stages of regrowth with the canopy below 30 m height.

The area of investigation

The area investigated, called the Nimba area, is situated in northern Liberia, near the border between Guinea and the Ivory Coast (Fig. 2) and includes parts of the Nimba Mts. The countries relevant to this investigation are shown in Fig. 3.

Large mountains are poorly represented in West Africa but within the so-called Guinea Highland,

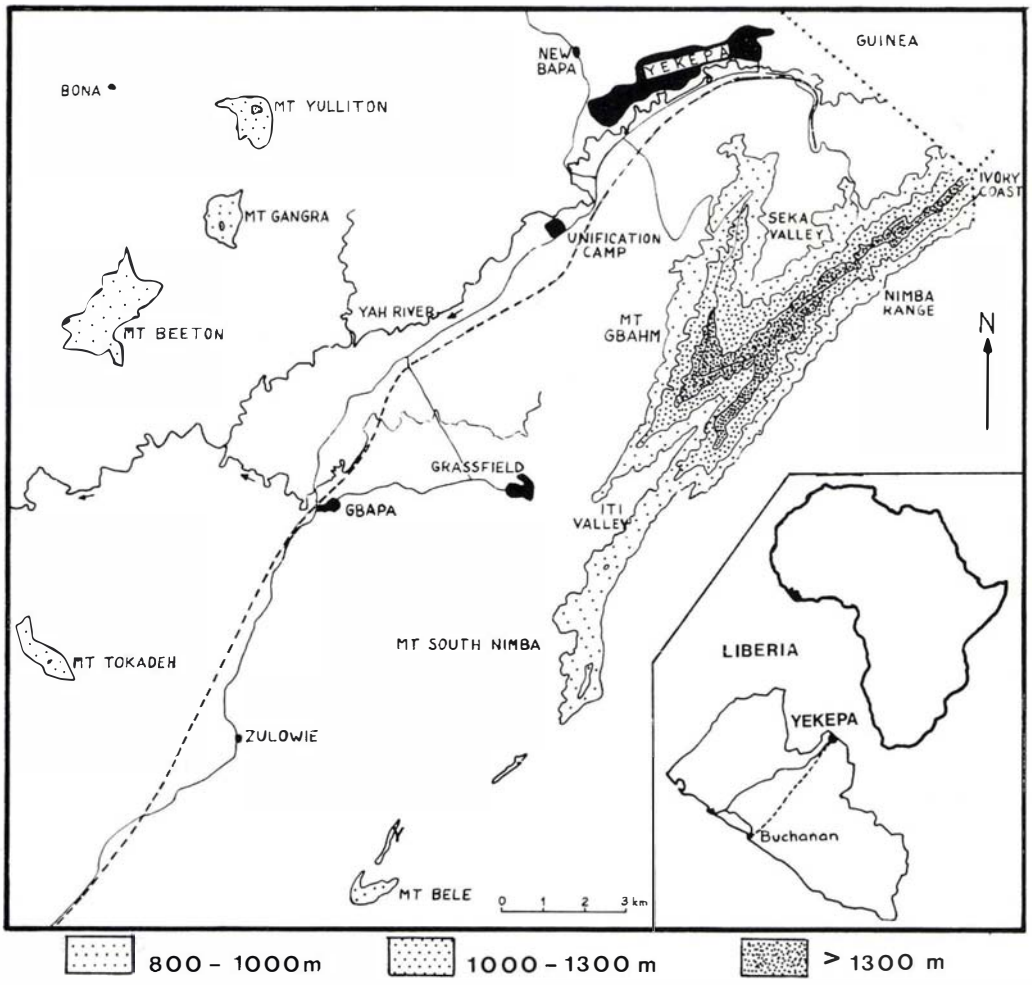


Fig. 2. Map of the investigated area and its location in Africa.

stretching from Fouta-Djallon in Guinea to the Dans massif in the Ivory Coast, a series of ridges and peaks rise to altitudes of more than 1000 m. In northern Sierra Leone, the Loma Mountains reach 1947 m at the Bintumane peak. In Guinea, Mount Bala in the Ziama massif is 1387 m high, but even more imposing are the Nimba Mountains with a number of high peaks (e.g. Mt Molard 1752 m). In the Ivory Coast the Dans massif contains the two high peaks of Mount Tonkoui, 1240 m, and Mt Dou 1340 m. The Nimba Mountains stretch from Guinea into Liberia, where the ridge has a NE-SW direction with the highest part slightly above 1300 m (Fig. 4). Here the range is rising abruptly from a tableland at around 500 m altitude. Its highest part is built up by a narrow ridge or crest with steep slopes on each side

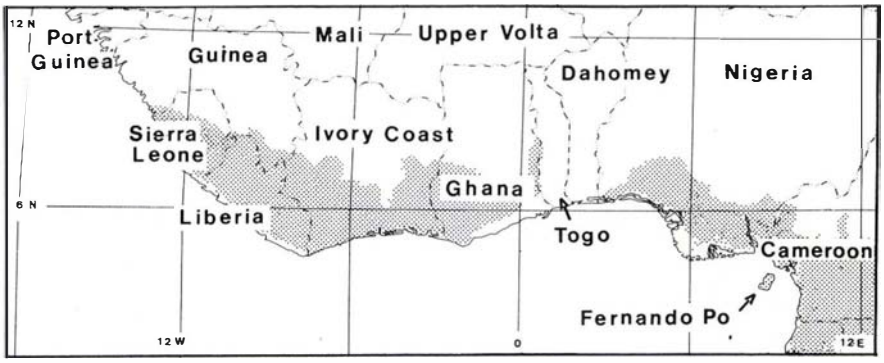


Fig. 3. Some West African countries of relevance to this investigation. The distribution of rain forest at low and medium altitudes is marked by dots.

(Fig. 11). The southernmost part ends in a steep mountain, Bele (Bilimu). East of the ridge the two peaks Mt Gangra and Mt Yulliton of more than 1000 m dominate the landscape. South of these peaks rises another ridge with the highest part at Mt Tokadeh at around 1000 m altitude. After the discovery of iron ore in the Liberian Nimba in 1955 and the start of mining operations in 1963, a large influx of people has taken place into this previously sparsely populated area. The early stages in the exploration and the new developments in this area are described in Gårdlund (1967).

CLIMATE

For Liberia as a whole the year can roughly be divided into a rainy season from March/April to October/November, and a dry season during the remaining months. These extreme weather types are created by the yearly movements of the Inter Tropical Front (I.T.F.). This front is formed between the relatively cool, moist air of the equatorial zone over the Atlantic Ocean, the Equatorial Maritime Air Mass, and the hot dry mass of air over the Sahara, the Tropical Continental Air Mass. During the dry season the movements of these air masses are, simply speaking, regulated by the high-pressure belt formed over the Sahara and the low-pressure belt over the area of South Africa. The wind blowing from the high-pressure belt to the low is deflected to the west owing to the earth's rotation. This wind will thus appear as a northeastern dry often hot and dust-laden wind, commonly known as the Harmattan. During the rainy season the wind is blowing from a high-pressure belt above the subcontinent of South Africa towards a low-pressure belt formed above North Africa. This wind is in West Africa known as the southwest monsoon.

When the moist SW-monsoon reaches the Liberian coast heavy rains start to fall. The rainfall in the coastal strip is very high, generally more than 4000 mm a year. Towards the interior precipitation decreases, and in the northern part the precipitation is less than half of the amount of the coast.

In the southeast of the country, a short dry period, 'the middle dry', often appears in July-August, which in certain years is even felt in Nimba (Fig. 5).

In periods of varying length the macroclimate at Yekepa (510 m) has been measured, in a traditional way, with the instruments in a meteorological box, 1.5 m above the ground. The rainfall has been measured with a standard rain gauge also at 1.5 m above the ground. The maximum and minimum temperatures were taken at seven o'clock for each 24 hours period. The relative humidity was recorded with a hygrograph, which was calibrated to a psychrometer (dry and wet bulb thermometer). At the peak of the ridge, the mining company, Lamco J.V.Op.Co., has since 1957 performed regular meteorological observations. Unfortunately the observation site has been moved twice, and the data after January 1967 only include rainfall and cloudiness.

The microclimatical effects on the distribution of the epiphytic plants within the trees are more conspicuous than macroclimatic effects. (However the difference between the epiphytic flora at the crest of the ridge and that in the surrounding lowland is no

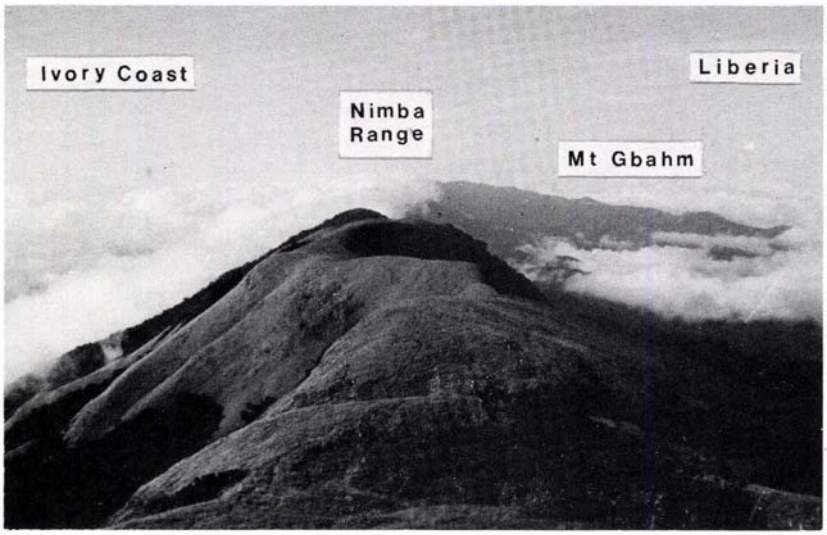
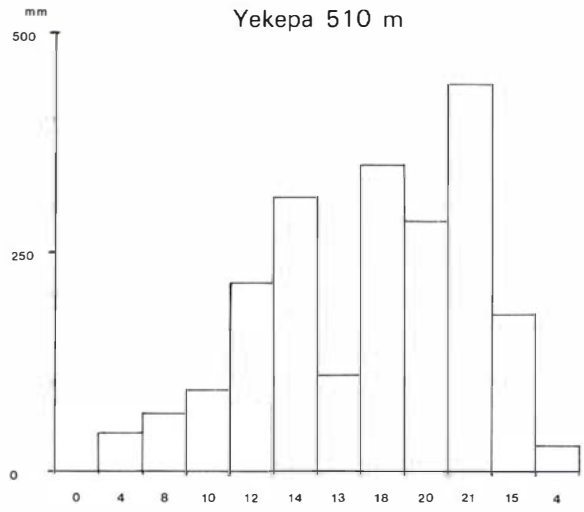


Fig. 4. The Nimba Range seen from Mt Molard (1752 m) in Guinea in a SW direction. Note the absence of clouds on the west side of the Range and on Mt Gbahm. March 1965.



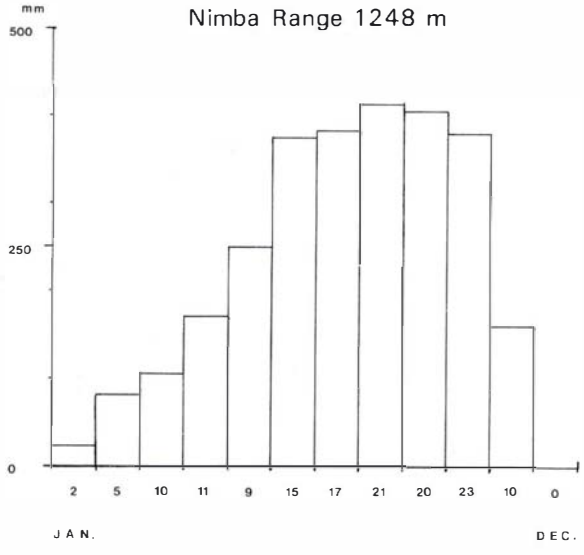


Fig. 5. Monthly rainfall at Yekepa 510 m and at Nimba Range 1248 m, 1969. The number of days with rainfall is given below each month.

doubt regulated by the macroclimate.) Unfortunately, microclimatical investigations in the treetops and along branches, 30-40 meters above the ground, have been impossible to perform. The microclimate in a rain forest, discussed later in chapter V, has been investigated in Nigeria by Evans (1939) and in the Ivory Coast by Cachan (1963), and Cachan & Duval (1963).

Temperature

In Yekepa the daily maximum temperature during the rainy season is close to 30°C and the minimum

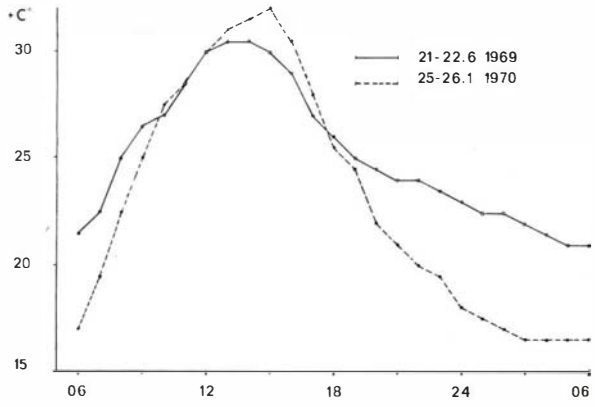


Fig. 6. Temperature variations during a day in the wet and a day in the dry season. Yekepa 510 m.

temperature around 22°C. The daily variation of the temperature in the rainy and dry seasons is shown in Fig. 6.

A shower of rain will of course alter this daily pattern. The temperature may then drop 4-5°C in a few minutes. In the dry season the difference between maximum and minimum temperatures is much wider than in the rainy season. This can, somewhat simplified, be correlated to the low frequency or total absence of clouds during that period. This results in an increased influx of radiation during the day, but also a larger outflow at night.

With the arrival of the Harmattan winds from the north a few days often show very low night temperatures. The lowest temperature recorded is from February 1, 1970 when a reading of 12.5°C was registered during the night. The following day the maximum temperature reached 32.5°C which gives a difference of 20.0°C (Fig. 8). The daily variation of the temperature at the higher parts of the ridge is unknown but there is a five year (1963-1967) series of maximum and minimum temperature recordings from the Geologist's Camp Nimba. The figures from 1966 are given in Table 2. The differences between the mean maximum and minimum temperatures are small. The largest differences occur in the dry season.

In a high forest, at ground level, the daily variation in temperature, as one would expect, is smaller than outside the forest (Table 3). Kunkel (1966), who has carried out occasional temperature recordings from various places in Liberia, estimates the temperature in an open area to be around 5°C higher than inside the forest.

Table 2. Maximum and minimum temperatures (mean) at Nimba Range 1340 m, 1966. (Source: Lamco J.V.Op. Co.)

Period	Temperature °C Max.	Min.	Mean
January	22.8	19.2	21.0
February	22.4	19.0	20.7
March	21.7	18.7	20.2
April	21.0	18.3	19.6
May	20.4	17.9	19.1
June	20.2	18.3	19.2
July	18.8	16.7	17.7
August	19.5	17.7	18.6
September	19.1	17.4	18.2
October	20.6	18.4	19.5
November	22.7	20.3	21.5
December	20.9	18.3	19.6

Table 3. Temperature one meter above the ground, in a high forest and in the open, during a day in the wet and a day in the dry season. Seka Valley 600 m.

	Date	Season	Temperature °C Max.	Min.	Diff.
High forest	23.6 1969	wet	25.5	23.5	2.0
	22.1 1970	dry	26.0	22.0	4.0
Open area	26.6 1969	wet	29.0	22.0	7.0
	22.1 1970	dry	31.0	17.5	13.5

Rainfall

In an area with differences in altitude of 500-600 m within a few kilometers distance, local effects in the distribution of the rainfall will of course be pronounced. From the highest part of the ridge, at two different sites, records of the rainfall are available. The first series of observations are from the Geologist's Camp Nimba, 7°31′N, 8°31′W, at an altitude of 1340 m, and include the years 1957-1966. The second observation point was at the Mine Office, 7°38′N, 8°29′W, at an altitude of 1248 m, from the years 1968-1970. The average rainfall for the four years 1963-1966 at Geologist's Camp Nimba was 3106 mm compared to 2487 mm for the three-year-series at Mine Office. During 1962, the rainfall in Yekepa was only 54.0 % of that at Geol. Camp. (Adam 1971:15).

The distribution of the rainfall in one month reveals some interesting details. Even in a month during the rainy season, June 1969, with a total of 316 mm, 14 days had no rainfall, and at the middle of the month it only rained 10 mm during a 12-day-period (Fig. 7). These 'dry periods' of shorter duration probably influence the distribution pattern of epiphytes on the phorophytes.

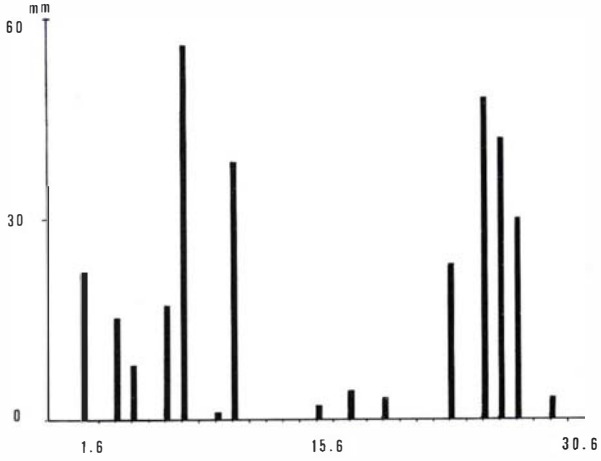


Fig. 7. Daily rainfall (in mm) during June 1969. Yekepa 510 m.

In the beginning of the rainy season, May-July, the rain often falls as a drizzle. In June, particularly, it may rain more or less continuously for half a day, which is rare any other time of the year. This is the time when the surface front of the I.T.F. has passed. At the end of the rainy season, Sept.-Nov. the mornings are often clear but in the afternoons heavy thunder-showers are usual. These rainfalls are of a convective nature, e.g. the humid air which is warmed by the sun rises and condensation occurs. In the afternoon huge clouds have built up and large amounts of water are released. These rainshowers are of a short duration.

The number of days per month with rainfall varies from year to year. The figures for 1969, at 1248 m and 510 m are shown in Fig. 5. The period August-October has the largest number of rainy days.

In Yekepa, no rain was recorded during the period December 12, 1969 - February 8, 1970 (58 days of drought), and at the Mine Office, 1248 m, no rain was recorded during the period November 16, 1969 - February 16, 1970 (92 days of drought).

Humidity

At nighttime, the relative humidity is 100 % or thereabouts during the whole year. The absolute content of water in the air varies naturally with the seasons. Even in the dry season the air is on the verge of saturation during the nights, a fact which the low night temperatures can account for. From the saturated level at nighttime the humidity level is

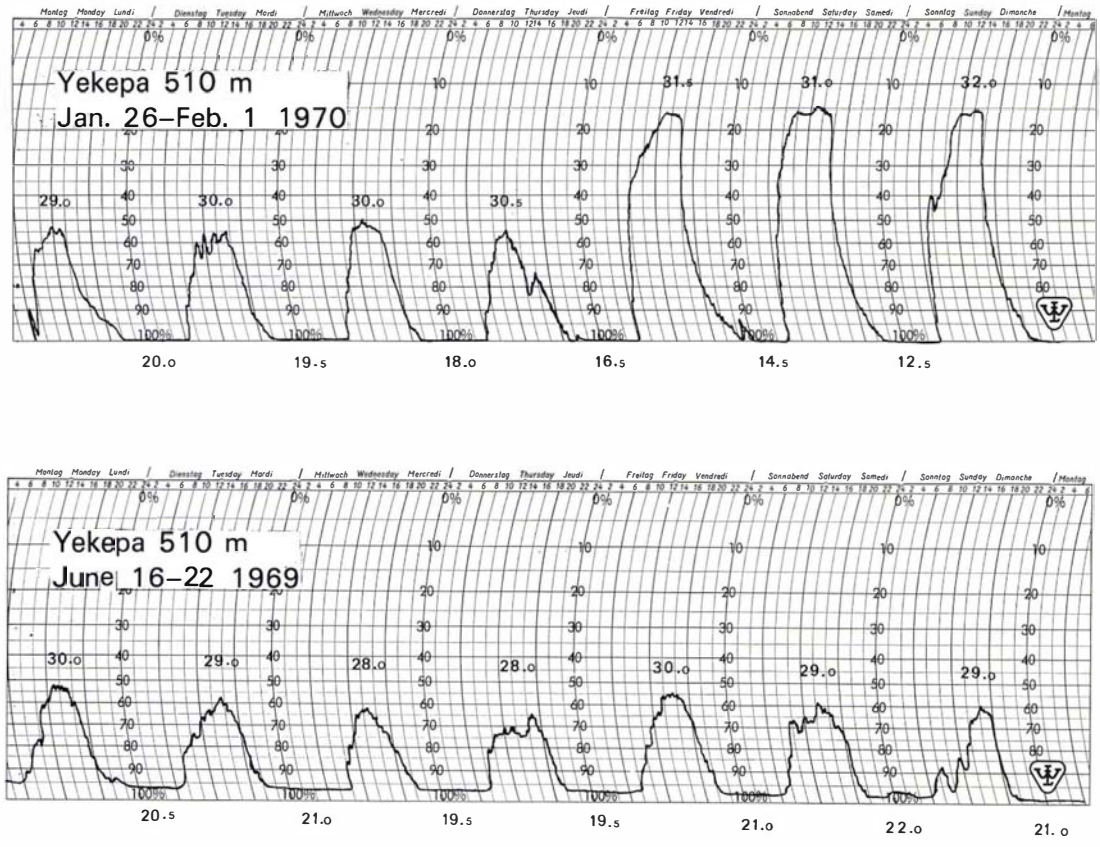


Fig. 8. Relative humidity during a week in the wet and a week in the dry season. Yekepa 510 m. Figures for maximum and minimum temperature (°C) are given for each 24 hr period.

lowered during the day as the temperature rises. The absolute minimum relative humidity (Table 4), although only lasting for a short period in the afternoon, can be used to illustrate the yearly variation in the desiccation effect on the plants.

Naturally large variations are found in the daily changes in the relative humidity. This applies to variations between individual days of the same season as well as between whole periods in different seasons. The daily variation of the relative humidity during a week in the rainy season (July 22-27, 1969) and the dry season (February 2-8, 1970) illustrates this (Fig. 8). The impact of the dry Harmattan winds is clearly visible in the graph from the dry season. During the period 31.1-5.2 1970 the mean absolute minimum relative humidity was only 23.2 %.

At higher levels, e.g. at Mt Gbahm 1300 m, where mist and rainfall particularly from June to August keep the air saturated, the daily variation is very small (Fig. 9). The weekly average of the absolute minimum relative humidity is as high as 84 %.

Table 4. Absolute minimum relative humidity. Mean for the periods. Yekepa 510 m.

Period		Absolute minimum relative humidity (%)
16.6-23.6	1969	58.8
22.7-27.7	1969	68.0
11.8-17.8	1969	73.1
22.9-28.9	1969	55.7
4.11-9.11	1969	48.0
8.12-14.12	1969	46.4
12.1-18.1	1970	47.4
2.2-8.2	1970	35.7
2.3-8.3	1970	37.3
6.4-14.4	1970	46.6
27.4-3.5	1970	48.6

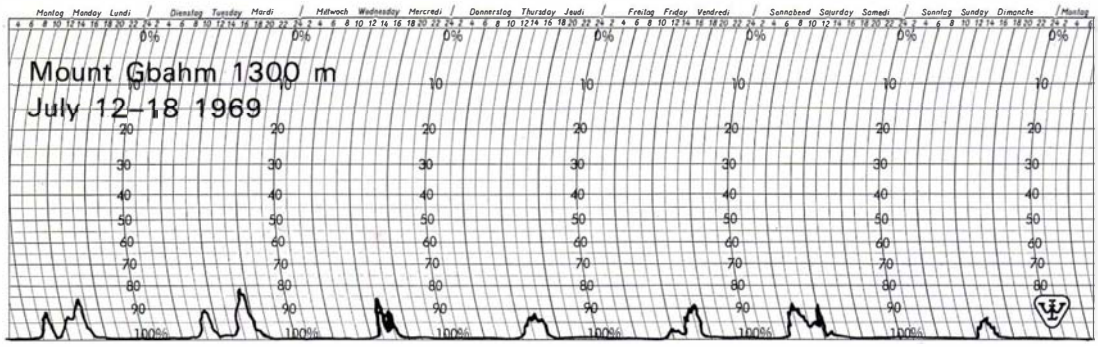


Fig. 9. Relative humidity during a week in the wet season. Mt Gbahm 1300 m.

Cloudiness

The cloudiness has been recorded at the Geologist's Camp Nimba and Mine Office at 1248 m. The day was divided into two recording periods, 06^{00}-12^{00} and 12^{00}-18^{00} (Fig. 10). The ratio between cloudy and sunny days in 1969 reveals that June, July and August were the cloudiest months, although the period September to October had the same mean rainfall as the three earlier months. January 1970 showed only five mornings with more than 50 % cloud cover and all the afternoons were cloudless.

During the period January 12 to February 6, 1970 no clouds whatsoever were reported at any period of the day. The local cloud or mist system that frequently can be observed around the highest parts of the ridge during the dry season seems to be correlated with the NE-winds (Fig. 11).

Wind

In general wind velocities are low. Thunderstorms are accompanied or rather preceeded by strong winds that usually last for only a few minutes. Kunkel (1966:59) reports that, at the end of February 1962, a very strong thunderstorm passed John-Davis Town (Putu district) in eastern Liberia. The wind had a hurricane-like strength and created an almost 100 m gap in the forest east of the settlement. Only around 20 % of the trees were still standing after the storm had passed. In the Nimba area no such storms of signs of earlier ones have been observed.

For certain short periods the dry Harmattan winds are strongly felt in the Nimba area. The wind is weak, merely as a breeze, but is characterized by its dust-filled, very dry air. The visibility is low (a few

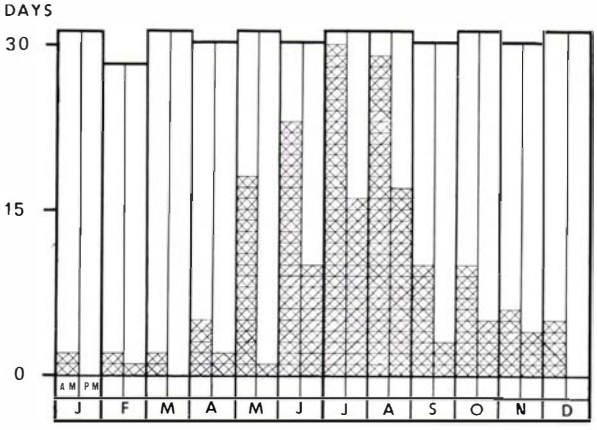


Fig. 10. Annual distribution of cloudiness (hatched) and sun at Nimba Range 1248 m, 1969. The days are divided into two parts, AM and PM, and cloudiness means that more than 50 % of the sky was covered with clouds. (Source: Lamco J.V. Op. Co.).

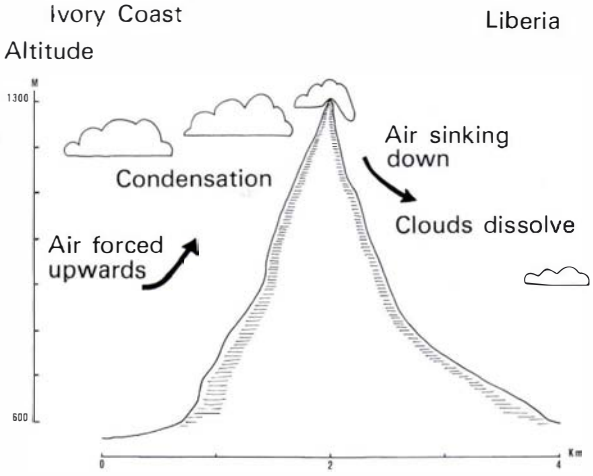


Fig. 11. Cloud formation over the crest of the Nimba Range under easterly winds during the dry season. (Schematic cross-section of the Range 1.1 km SW of the Three Border Point, in a NW-SW direction.)

kilometers only). The sun disappears as a red-glowing ball in the afternoon, and the relative humidity reaches its absolute yearly minimum.

VEGETATION

Earlier botanical exploration

The Nimba Mts in what today is part of Guinea and the Ivory Coast were during the French administration subject to a series of studies covering several aspects of natural history (e.g. Lamotte et al. 1955). A remarkable work on the vegetation of the Nimba Mountains was presented by Schnell (1952).

From the Liberian part of the Nimba Mountains botanical collections have been performed by W. Harley at and around Mt Bilumi (Mt Bele). Under the sponsorship of the Nimba Research Committee, headed by K. Curry-Lindahl, botanical collections were carried out by P. Adams (1964) and J. Adam (1964-1965 and 1970). Based upon his extensive collections from all parts of the ridge, Adam (1971) published a work entitled 'Flore descriptive des Monts Nimba'. During his study of Liberian high forest trees, Voorhoeve (1965) visited the Nimba Mts and made collections there.

Primary and secondary forest

Generally speaking the rain forests can be divided into two main groups, primary and secondary. The primary forest does not bear any sign of human influence (Fig. 12), while the secondary has been affected in one way or the other by human activities (Figs. 13 and 14). There are diverging opinions as to the presence of true primary forest in West Africa and Liberia. The term 'high forest' is often used (Voorhoeve 1965:19) to describe a forest without stating an opinion of its origin. In French literature the term 'forêt dense' (Aubreville 1938) is often used. It includes the evergreen rain forest as well as the mixed deciduous forest. 'Closed forest' (Richards 1964) is equivalent to the 'forêt dense' of modern French writers, and includes all types of lowland forest in which the trees form a closed canopy and the ground is not covered with grass. The rain forest is often divided into mixed and single dominant communities. The greater part of the primary forest in the Nimba area consists of mixed forest composed of a very large number of species.

The secondary forest (or degraded forest) is characterized by its physiognomy and the abundance of trees from the lower strata of the primary forest. It is in many cases extremely difficult to distinguish a mature secondary forest, e.g. a secondary forest of some hundred years age, from a primary one.

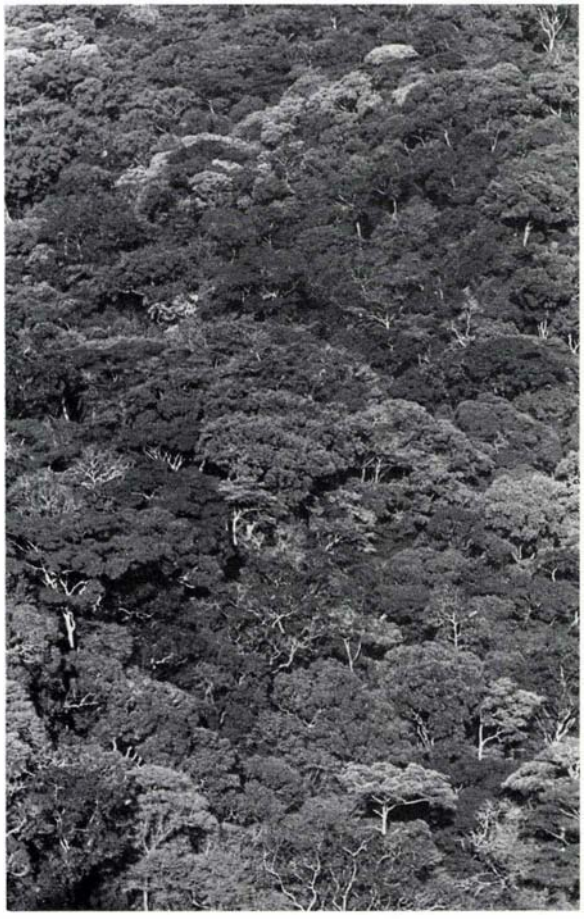


Fig. 12. The canopy of the high forest. Mt Gbahm 800 m. 1969.

It has been estimated that it takes 80 years for a moist forest species of tree to reach maturity (Cole 1968) and that the cycle towards a mature high forest lasts 300 to 400 years (Voorhoeve 1965:20).

It is very hard to characterize the plant communities in tropical forests because they are very rich in species when compared to temperate forest stands of equivalent sizes (cf. Richards et al. 1940). Some ecologists name a closed forest using the emergents in the A-stratum (the canopy), but these emergents are generally few and far between and dominance by a few species is the exception rather than the rule. Even in the forest as a whole the majority of tree species are rare or occasional. Aubreville (1938) does not consider any true associations in the mixed rain forest of West Africa. The whole mix-

Fig. 13. 'Farmland' in high forest. The forest is cut and burned. Rice, and cassawa (manioc) are cultivated in the clearing for a few years after which the farmland is abandoned. Mt Yullition 700 m. 1966.

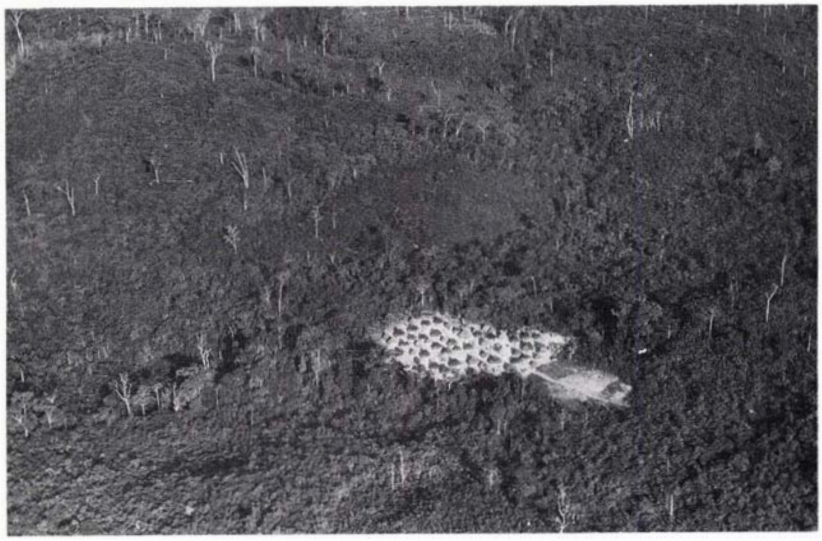


Fig. 14. 'Farmland' in various stages of regrowth near a native village. West of Bona, 1966.

ed forest in this case could be regarded as a single association of fluctuating composition. Richards (1964:262) states: "The failure of any one species to gain the upper hand in the mixture may be due, as Aubreville suggests, to all the species having very similar ecological requirements and responding in a very similar way to slight variations in the environment. As would be expected on grounds of probability, under these conditions the composition of these mixed communities will fluctuate in space and probably in time as well."

The Liberian rain forest

Through human interference only 35 % of Liberia is at present covered by high forest (Voorhoeve 1965:19), although climatic and edaphic conditions would be favourable for it throughout most of the country.

The Liberian rain forest is part of a rain forest belt that stretches from Ghana to Sierra Leone, and which is a western extension of the huge lowland rain forest of the Congo basin (Fig. 15). A region with dry climate from Western Nigeria to Eastern Ghana separates the two forested areas from each other. This break is commonly known as the 'Togo-Dahomey gap'. The high forests of Liberia exhibit several features typical of tropical rain forests such as a large number of species which are mostly woody plants, e.g. many tree species (Cooper & Record 1931, Kunkel 1965, Voorhoeve 1965). The undergrowth is also mainly composed of woody plants. The herbaceous plants are mainly represented

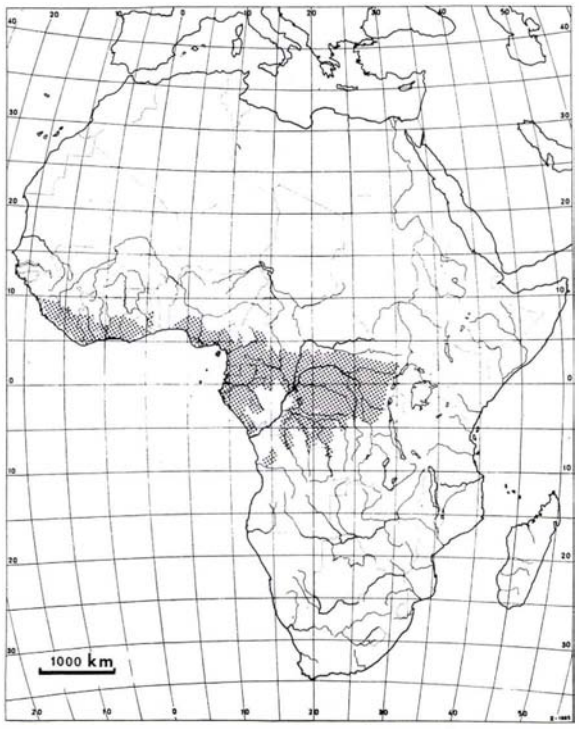


Fig. 15. Distribution of rain forests at low and medium altitudes. (From Keay 1959.)

by epiphytes. A striking abundance of climbers, both herbaceous and woody (lianas) is also observed. Voorhoeve (1965) divides the Liberian rain forest into three categories: primary forest, old secondary forest that has reached climax, and old secondary forest which has not yet reached the climax. Concerning the distribution he remarks (1965:19): "The first group appears to be extremely rare in Liberia, it is restricted to remote and limited localities of which only the gorges in the Nimba Mountains are known to me. Steep slopes prevented all agriculture there and the belief in numerous spirits made the people afraid to penetrate the area."

In neighbouring Sierra Leone human activity started to take its toll in the forest very early. It is interesting to note that Adam Afzelius, in his Sierra Leone Journal (ed. by A.P. Kup, Uppsala 1967), already observed this. In his notes from May 28 1795 he states: "Fleming complained that there was now not to be found any timber on the Company ground, complaint which I have long expected, and from the manner of treating the wood, I am sure they won't 10 years hence have any timber in Sierra Leone, but in the highest and inaccessible mountains."

Concerning the development of the Liberian forest interesting speculations have been presented: "It is possible that as recently as 300 years ago there was considerably less high forest area in Liberia than is found today. The subsequent sharp decline in population, as heavy tribal warfare and slaving activities exerted their drain, possibly coupled with the ravages of new diseases, would have permitted many cleared areas to complete their reversion to high forest. Over a period of several centuries, stands such as now occur throughout much of Liberia would probably develop. Their composition would differ notably from original stands in the same general area, but their density would be very similar. Only by such an hypothesis can the writer explain the over-all compositional inferiority of Liberian high forests as compared with those considered typical of the Ivory Coast and the Gold Coast." (Mayer 1951:25.)

A similar view is reflected in a report of the German Forestry Mission to Liberia, which express the opinion that all the forests of Liberia were once destroyed by shifting cultivation since remnants of villages have been found even in the most distant places of the forest.

The human influence on the fauna may indirectly affect species' composition of the rain forest. The elephants that nowadays are almost extinct are said to promote the reproduction and distribution of *Sacoglottis* and *Parinari* trees. They eat the trees' fruits, and after passing through the alimentary canal the seed germinates extraordinarily well and at the same time is transported over a considerable distance.

The high forest in the Nimba area that previously was sparsely populated is nowadays subject to a rapid deterioration (Adam 1966, 1970; Coe & Curry-Lindahl 1965). However, precautions recommended by I.U.C.N. are being taken by the Liberian government to spare certain areas from the devastating effects of shifting cultivation (Curry-Lindahl 1969).

Classification of the forest in the Nimba area

Schnell (1952:444) divided the high forests into four groups:

(1) Climax mésophile, caractérisé par *Triplochiton scleroxylon* et *Chrysophyllum perpulchrum*

(2) Climax ombrophile à *Lophira procera*

(3) Climax ombrophile à *Tarrietia utilis (Heritiera utilis)*

(4) Climax montagnard à *Parinari excelsa*

Table 5. The number of trees, 40 cm or larger in diameter, in a forest at 525 m altitude east of Grassfield. Total area investigated, 4 ha. (From Adam 1969.)

Piptadeniastrum	33	Ongokea	1
Parinari excelsa	17	Terminalia	1
Lophira	12	Erythroxylum	1
Tarrietia (Heritiera)	10	Newtonia duparquetiana	1
Calpocalyx	7	Funtumia	1
Chlorophora	4	Nauclea	1
Parkia	4	Lovoa	1
Amphimas	2	Anthonotha fragrans	1
Uapaca guineensis	2	Newtonia aubrevillei	1
Anopyxis	1		
Klainedoxa	1	Total	103

Adam (1969:384) recognizes two alliances in the rain forest in the lowlands surrounding the Nimba Mountains. On drained soils on peaks and slopes, *Piptadeniastrum* + *Parinari excelsa* + *Parkia.* In valleys and levelled areas an alliance with *Lophira* + *Tarrietia* + *Uapaca* + *Erythroxylum* + *Newtonia.*

Forest at altitudes below 800 m

The species' composition of a forest east of the Grassfield Airstrip at 525 m has been investigated by Adam (1969:380–385). The canopy of this forest lies at approximately 40–45 m height above the ground (Table 5).

Remarkable is the dominance by the family Leguminosae. It is represented by seven genera, eight species and 49 individuals in the inventory. The species of this family constitute nearly 48 % of the total number of trees. Four families, Leguminosae, Rosaceae, Ochnaceae and Sterculiaceae together represent 85 % of the trees in the inventory. Adam (1969) also emphasizes the large differences in the flora composition between the Kitoma and the Nimba forests. The Kitoma forest is located 30 km south of the Nimba Mts. In Kitoma 177 individuals of *Calpocalyx aubrevillei* were found in an area of 15.2 ha, which gives 11.6 trees per ha. In Nimba 7 individuals were found which gives 1.7 trees per ha. The figures for the *Piptadeniastrum africanum* are 0.9 trees per ha in Kitoma, and 8.2 trees per ha in Nimba.

An inventory of the East Nimba National Forest and adjacent parts has been undertaken under the leadership of T.A. Gorgla (1969). This study included 15 species of trees that could be of commercial interest (Table 6). Although the study excludes the very common *Parinari excelsa* and several other species, it gives valuable information of the proportions between the enumerated species.

Table 6. The number of 15 different timber trees, 45 cm or larger in diameter in East Nimba National Forest. Total area investigated, 565.2 acres. (Source: Lamco J.V. Op. Co.)

Genera or species	Trade names	Number
Piptadeniastrum	Dahoma	703
Chlorophora	Iroko	289
Lophira alata	Azobe	281
Fagara	Bahe	178
Tarrietia (Heritiera)	Whismore	169
Terminalia ivorensis	Frimare	117
Parkia	Parkia	117
Erythrophleum	Tali	101
Nauclea	Bilinga	48
Entandrophragma	Mahogany	30
Canarium	White mahogany	29
Terminalia superba	Limba	21
Khaya	Mahogany	15
Guarea	Mahogany	6
Lovoa	Mahogany	5

Farming activities in the high forest favour the development of many small and middle sized trees typical of the secondary forest, e.g. *Musanga cecropioides* (Moraceae), (Coombe & Hadfield 1962), *Anthocleista nobilis* (Loganiaceae), *Harungana madagascariensis* (Guttiferae). Among the taller species easily observed in older secondary forests, *Ceiba pentandra, Pycnanthus angolensis* and *Elaeis guineensis* may be mentioned.

Forest at altitudes above 1000 m

In the higher parts of the Nimba Range a distinct change is noticed in the physiognomy and floral composition of the forest. These parts, which are very small and mainly consist of the narrow ridges, are covered by a low single dominant *Parinari excelsa* forest, reaching a height of 10–20 m. The smaller trees have their ramifications close to the ground, and the field layer is usually built up by herbs. At 1200–1300 m altitude the *Aframomum* herbs are typical. The single dominant *Parinari* forest is by no means something specific for the Nimba Mts but can be found at similar altitudes at e.g. Mount Wutivi in western Liberia (Kunkel 1962 b), Mt Tonkoui in the Ivory Coast and Fouta Djallon in Guinea. From Uganda a rain forest community occurring between 4500 and 5000 feet in which *Parinari excelsa* forms about 80 % of the canopy is reported by Eggeling (1947).

The canopy is not closed except in very minor sections. The light intensity in the lower parts of the forest and at the ground is therefore considerably higher than in the forest at the base of the mountains. Schnell (1952:338) remarks: "On retrouve dans les forêts à *Parinari excelsa* du Nimba et des massifs voisins, un certain nombre de caractères déjà signalés dans les forêts montagnardes, par J. Lebrun, H. Scaëtta (1973), Schluter, Eidmann: faible hauteur des arbres, tronc ramifié à quelques mètres du sol, réduction du nombre des espèces, réduction du nombre des lianes, abondance des épiphytes (surtout Cryptogames), feuillage généralement persistant."

On the crests at 1200–1300 m altitude the *Parinari excelsa* forest is in total dominance, but a little lower down at 1000–1100 m trees of a rather large number of species can be found (Adam 1970:204–207).

Seasonal changes in the forest

In the Nimba forest, not much seasonal changes in leaf-fall are noticed. The evergreen trees at the various strata appear luxuriant at all times of the year because progressive leaf-fall occurs, while the few deciduous trees appear dormant only for a rather short time. These deciduous trees are so few and scattered that their presence does not alter the face of the forest. Bernhard-Reversat et al. (1972:218) reveal that the maximum leaf-fall of various species in the Ivory Coast do no coincide, and there is no correlation with the precipitation, but rather with the incident radiation—a view that earlier had been stressed by Hopkins (1970) in a study of the seasonal growth in S Nigeria. Furthermore, the interspecific variation of the start and the length of the leaf-fall period at the same locality also tend to obscure the presence of these trees. Some of the more common deciduous trees in the forest are *Bombax buonopozense, Chlorophora regia, Ceiba pentandra, Daniellia ogea, Entandrophragma utile, Piptadeniastrum africanum, Rhodoghaphalon brevicuspe, Terminalia ivorensis,* and *Triplochiton scleroxylon.* In a phenological study of *Chlorophora regia* at Njala, Sierra Leone, Cole (1968:76) found not only an interspecific variation in leaf shedding time between trees growing within a radius of 100 yards, but also a difference in the length of the leafless period between male and female trees.

The phorophytes (the host trees)

As stated earlier the rain forest is very rich in tree species. When a doubt in the determination of species has arisen, the epiphyte flora has simply been recorded without correlation to a specific phorophyte. The list of phorophytes that briefly will be presented is dominated by medium to large sized trees. For each phorophyte a few properties that might be of importance for the epiphyte flora have been added. The majority of these phorophytes are included in the excellent study of the Liberian rain forest by Voorhoeve (1965).

The properties of the phorophytes refer to tall specimens and it must be emphasized that many of these properties are rather vague and dependent on environmental influence. The roughness of the bark refers to the basal parts of large branches, and the terms low, medium and tall refer to the classes 10–20, 21–35, 36 m or more, respectively. The phorophytes are presented in alphabetical order without regard to family.

Phorophytes in high forest

Albizia glaberrima (Schum. & Thonn.) Benth. (Leguminosae)
Large. Bark smooth. Crown open, spreading. Deciduous.

Albizia zygia (DC.) MacBride (Leguminosae)
Medium. Bark rather smooth. Crown open, spreading. Deciduous.

Alstonia boonei De Wild. (Apocynaceae)
Large. Bark rather smooth, soft. Crown fairly open, heavily branched. Evergreen.

Amphimas pterocarpoides Harms (Leguminosae)
Medium-large. Bark scaly. Crown dense. Deciduous. (Fig. 16).

Anthocleista nobilis G. Don (Loganiaceae)
Small. Bark with thorns. Crown open. Evergreen.

Anthonotha fragrans (Bak.f.) Exell & Hillcoat (Leguminosae)
Medium-large. Bark scaly. Crown dense. Deciduous.

Antiaris toxicaria (Rumph. ex Pers.) Lesch. var. *welwitschii* (Engl.) Corner (Moraceae)
Large. Bark smooth, thick. Crown fairly open. Briefly deciduous.

Berlinia confusa Hoyle (Leguminosae)
Medium-large. Bark smooth or scaly. Crown rather dense. Evergreen.

Bombax buonopozense Beauv. (Bombacaceae)
Medium. Rather smooth bark. Crown heavily branched. Deciduous.

Bussea occidentalis Hutch. & Dalziel (Leguminosae)
Medium. Bark smooth. Crown dense. Evergreen.

Calpocalyx aubrevillei Pellegr. (Leguminosae)
Medium. Bark smooth. Crown small. Evergreen.

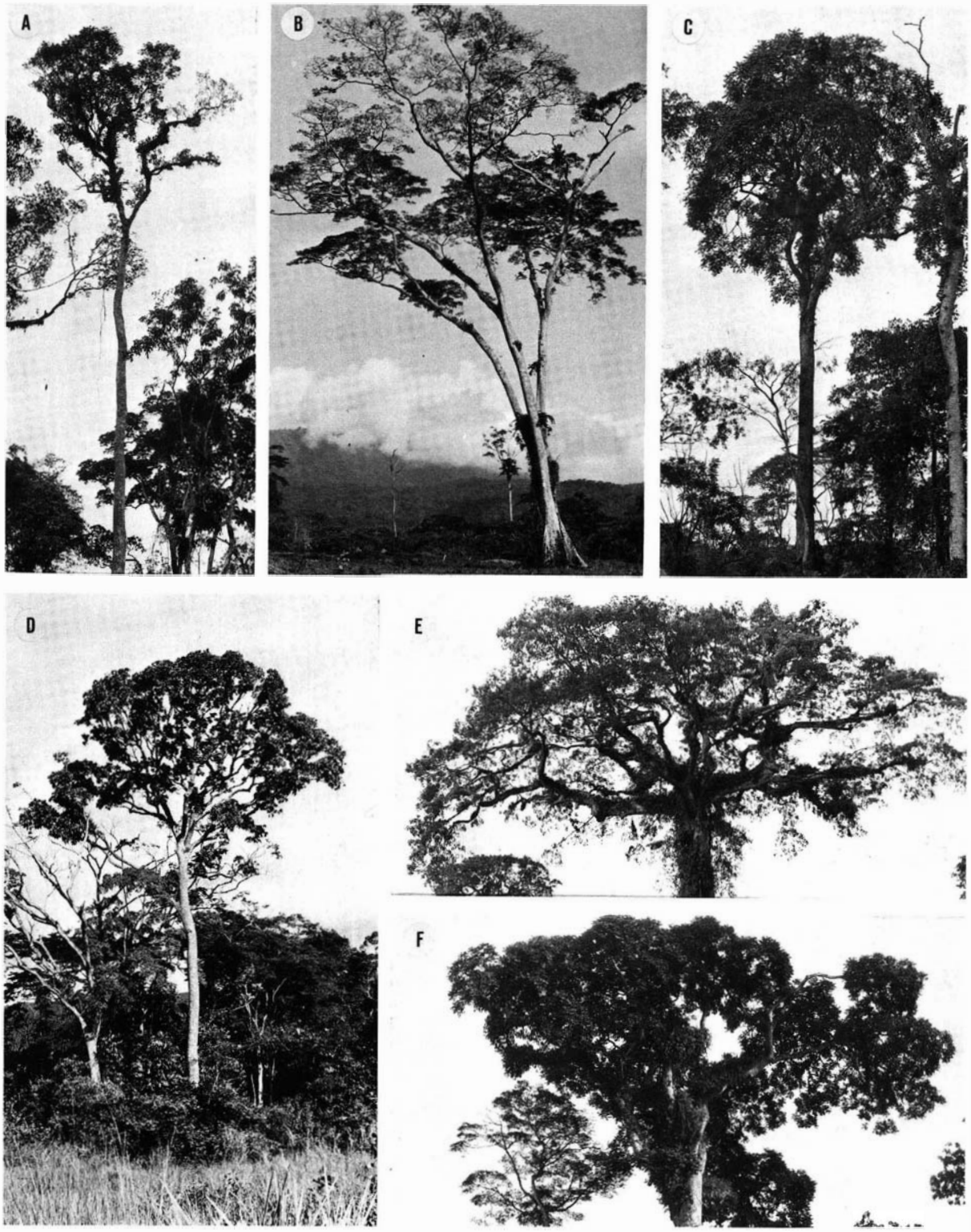


Fig. 16. Trees common in the Nimba area. (A) *Heritiera utilis*, (B) *Piptadeniastrum africanum*, (C) *Amphimas pterocarpoides*, (D) *Lophira alata*, (E) *Ceiba pentandra*, (F) *Entandrophragma utile*.

Canarium schweinfurthii Engl. (Burseraceae)
Large, often emergent. Crown rather open. Bark smooth. Briefly deciduous.

Ceiba pentandra (L.) Gaertn. (Bombacaceae)
Large to emergent. Bark smooth. Crown rather open. Deciduous. (Fig. 16).

Chidlowia sanguinea Hoyle (Leguminosae)
Small-medium. Bark smooth. Crown small, rather dense. Evergreen.

Chlorophora regia A. Chev. (Moraceae)
Large. Bark thick and rough. Crown dense. Briefly deciduous.

Chrysophyllum perpulchrum Mildbr. ex Hutch. & Dalziel (Sapotaceae)
Medium. Bark smooth. Crown dense. Evergreen.

Combretodendron macrocarpum (P. Beauv.) Keay (Lecythidaceae)
Large. Bark thick, deeply grooved. Crown fairly dense. Briefly deciduous.

Coula edulis Baill. (Olacaceae)
Medium. Bark rough and scaly. Crown dense. Evergreen.

Cryptosepalum tetraphyllum (Hook. f.) Benth. (Leguminosae)
Medium. Bark smooth, superficially cracked. Crown open. Briefly deciduous.

Daniellia ogea (Harms) Rolfe ex. Holl. (Leguminosae)
Large to emergent. Bark smooth. Crown small, fairly open. Deciduous.

Distemonanthus benthamianus Bail. (Leguminosae)
Medium-large. Bark smooth, defoliating. Crown fairly open. Deciduous.

Entandrophragma utile (Dawe & Sprauge) Sprauge (Meliaceae)
Large-emergent. Bark grooved, thick. Crown dense. Briefly deciduous. (Fig. 16).

Erythrophleum ivorense A. Chev. (Leguminosae)
Large. Bark rough. Crown very dense. Evergreen.

Fagara tessmannii Engl. (Rutaceae)
Medium. Bark rough, with thorns. Crown open, translucent. Evergreen. (Fig. 17).

Guarea cedrata (A. Chev.) Pellgr. (Meliaceae)
Medium-large. Bark smooth, scaly. Crown fairly open. Evergreen.

Heritiera utilis (Sprauge) Sprauge (Sterculiaceae)
Medium. Bark thin, peeling. Crown dense. Evergreen. (Fig. 16).

Khaya anthotheca (Welw.) C. DC. (Meliaceae)
Large-emergent. Bark smooth, sometimes peeling. Crown rather dense. Deciduous.

Lophira alata Banks ex Gaertn. f. (Ochnaceae)
Large-emergent. Bark scaly or grooved. Crown fairly open. Briefly deciduous. (Fig. 16).

Lovoa trichilioides Harms (Meliaceae)
Large. Bark scaly. Crown fairly open. Evergreen.

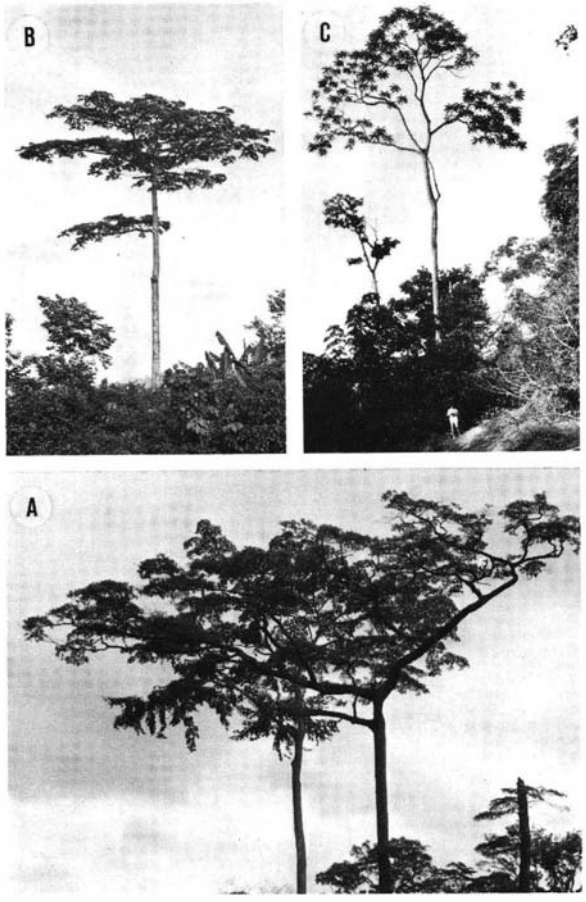


Fig. 17. Some trees that seldom carry epiphytes. (A) *Terminalia ivorensis,* (B) *Terminalia superba,* (C) *Fagara tessmannii.*

Mammea africana Sabine (Guttiferae)
Large. Bark rather rough, scaly. Crown small, dense. Evergreen.

Mitragyna ciliata Aubrev. & Pellegr. (Rubiaceae)
Medium-large. Bark thin, scaly. Crown rather dense. Evergreen.

Nauclea diderrichii (De Wild) Merrill (Rubiaceae)
Large. Bark rather smooth, or somewhat scaly. Crown small. Evergreen.

Parinari aubrevillei Pellegr. (Rosaceae)
Medium. Bark smooth or somewhat scaly. Crown dense. Evergreen.

Parinari excelsa Sabine (Rosaceae)
Medium-large. Bark scaly. Crown fairly open. Evergreen. (Fig. 18).

Parinari glabra Oliv. (Rosaceae)
Large. Bark smooth, scaly. Crown rather open. Evergreen.

Parkia bicolor A. Chev. (Leguminosae)
Large. Bark thinly scaly. Crown fairly open. Deciduous.

Pentaclethra macrophylla Benth. (Leguminosae)
Medium-large. Bark irregularly scaly. Crown dense. Evergreen.

Fig. 18. *Parinari excelsa.* Grassfield 550 m.

Pentadesma butyracea Sabine (Guttiferae)
Medium. Bark rough. Crown rather dense. Evergreen.

Piptadeniastrum africanum (Hook. f.) Brenan (Leguminosae)
Large-emergent. Bark smooth. Crown open and spreading. Briefly deciduous. (Fig. 16).

Pycnanthus angolensis (Welw.) Warb. (Myristicaceae)
Medium. Bark fissured or scaly. Crown open. Evergreen.

Rhodognaphalon brevicuspe (Sprauge) Roberty (Bombacacae)
Large-emergent. Bark scaly, soft. Crown rather dense. Deciduous.

Sacoglottis gabonensis (Baill.) Urb. (Humiriaceae)
Large. Bark scaly, untidy. Crown very large, open, spreading. Evergreen.

Terminalia ivorensis A. Chev. (Combretaceae)
Large. Bark deeply grooved. Crown rather open. Deciduous. (Fig. 17).

Terminalia superba Engl. & Diels (Combretaceae)
Large. Bark grooved and scaly. Crown open. Deciduous. (Fig. 17).

Triplochiton scleroxylon K. Schum. (Sterculiaceae)
Large-emergent. Bark rather smooth, more seldom scaly. Crown dense. Deciduous. (Fig. 77).

Uapaca guineensis Müll. Arg. (Euphorbiaceae)
Medium. Bark rough, cracked, scaly or flaky. Crown dense. Evergreen. (Fig. 76).

Vitex micrantha Gürke (Verbenaceae)
Small-medium. Bark grooved. Crown rather dense. Evergreen.

Phorophytes around villages and in farmlands

This group includes cultivated trees of various origins as well as trees of the young secondary forest and grasslands. The very common oil palm is also listed here because of its importance for epiphytic ferns.

Coffea sp. (Rubiaceae)
The coffee trees in cultivation are of heterogeneous origins.
C. liberica Bull ex Hiern. and *C. canephora* Pierre ex Froehner. Low. Bark smooth or somewhat rough. Crown open. Evergreen.

Cola nitida (Vent.) Schott & Endl. (Sterculiaceae)
The common cola tree, cultivated around the villages for its edible coffein-rich seeds. Low-medium. Bark fissured, soft. Crown dense. Evergreen.

Cussonia barteri Seemann (Araliaceae)
Low savanna tree. Bark deeply furrowed. Crown open, spreading. Deciduous.

Delonix regia (Boj. ex Hook.) Raf. (Leguminosae)
This tree is grown as an ornamental ("Flame of the forest" or "Flamboyant"). Low-medium. Bark smooth. Crown open, spreading. Foliage translucent. Deciduous.

Elaeis guineensis Jacq. (Palmae)
The oil palm. Low-medium.

Hevea brasiliensis (A. Juss.) Müll. Arg. (Euphorbiaceae)
The rubber tree. It is estimated (Kunkel 1965:12) that this covers 1 % of the total land surface of Liberia. However, there are only minor rubber plantations within the Nimba area.

Mangifera indica L. (Anacardiaceae)
The well-known Mango tree (locally called Plum tree). Medium. Bark rough. Crown dense. Evergreen.

Musanga cecropioides R. Br. (Moraceae)
The common umbrella tree that rapidly colonizes old farmlands etc. Low-medium. Bark smooth. Crown rather open. Evergreen.

Terminalia catappa L. (Combretaceae)
Cultivated for their edible seeds ("Almond tree") or as an ornamental. Low-medium. Bark fissured. Crown spreading, open. Deciduous.

Theobroma cacao L. (Sterculiaceae)
The cacao tree. Low. Bark smooth. Crown dense. Evergreen.

II. The epiphytic flora

Composition and geographical distribution

The flora of Africa is generally considered to be poorer in species than those of other tropical regions. The orchids, of which the majority are epiphytes, have been estimated to comprise two to three thousand species in Africa south of the Sahara, including the island of the Malagasy republic (Madagascar), and the islands of the Seychelles, Comoro, and the Mascarene groups (Stewart & Campbell 1970). This figure may be compared to the more than three thousand species of orchids recorded in the South American republic of Colombia alone. Another example from the orchid family may illustrate the relative poverty of species. In the Zaire (former Belgian Congo) there are a total of 414 species (Nihoul et al. 1964), compared with an estimated 5000 in Malaysia alone (Van Steenis 1938). The general poverty of the African rain forest has been suggested to be a result of past climatic changes (Mildbraed 1922). Stewart (Stewart & Campbell 1970:11) explains the relative low number of orchid species in Africa: "Vast tracts of the land mass are unsuitable as orchid habitats."

However, the poverty of epiphytic plants in the African rain forest is by no means an exception. From Sarawak, Borneo, Richards (1936:15-16) remarks: "One of the most striking features of the Sarawak rain forest, especially when compared with that of tropical South America, is the poverty of the epiphytic vegetation both in species and individuals."

The vascular epiphytic flora of the investigated area includes a total of 153 species (the facultative epiphytes excluded). The epiphytes may be divided into three major groups: (1) the Pteridophytes with

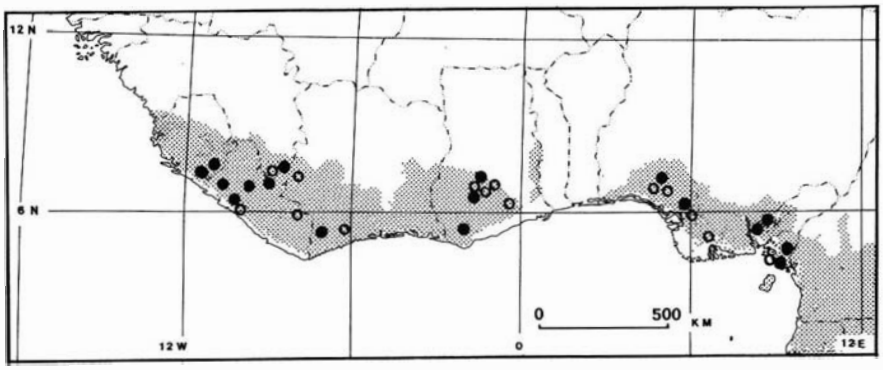


Fig. 19. Records of *Angraecum birrimense* (○) and *Cyrtorchis monteiroae* (●).

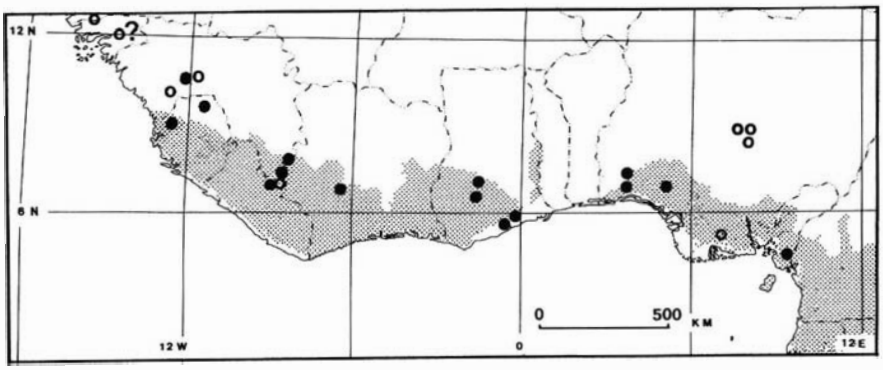


Fig. 20. Records of *Polystachya saccata* (○) and *Rangaëris rhipsalisocia* (●).

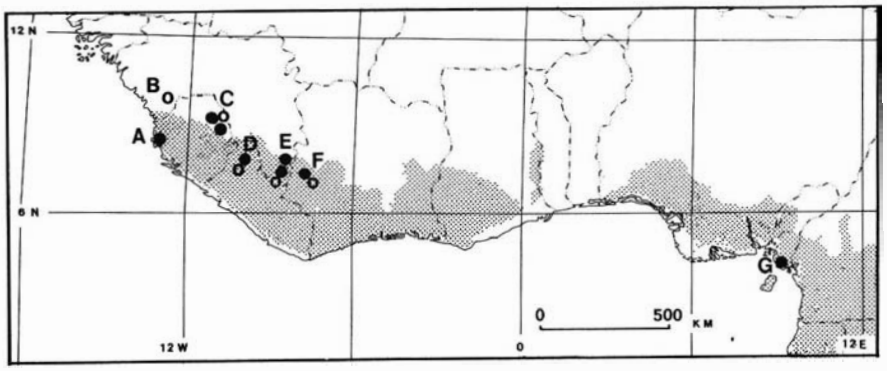


Fig. 21. Records of *Polystachya dalzielii* (○) and *P. leonensis* (●). (A) Picket Hill (B) Mt Kakouima (C) Loma Mts (D) Wologisi Range (E) Nimba Mts (F) Massif de Dans (G) Mt Cameroon

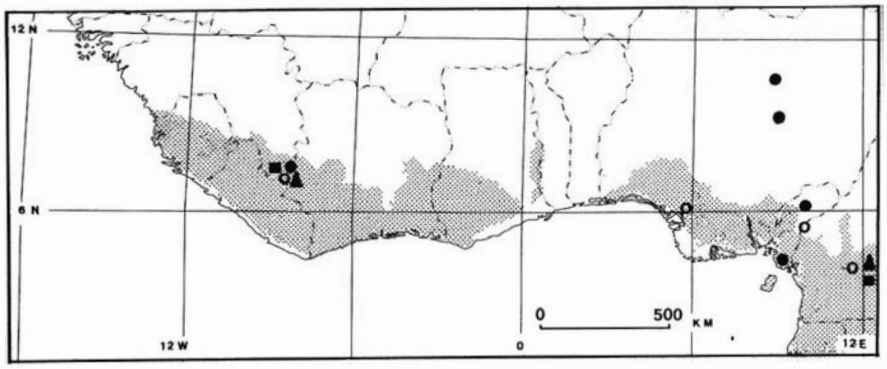


Fig. 22. Records of *Angraecum classensii* (■), *Angraecopsis elliptica* (●), *Diaphananthe densiflora* (▲) and *Stolzia repens* (○).

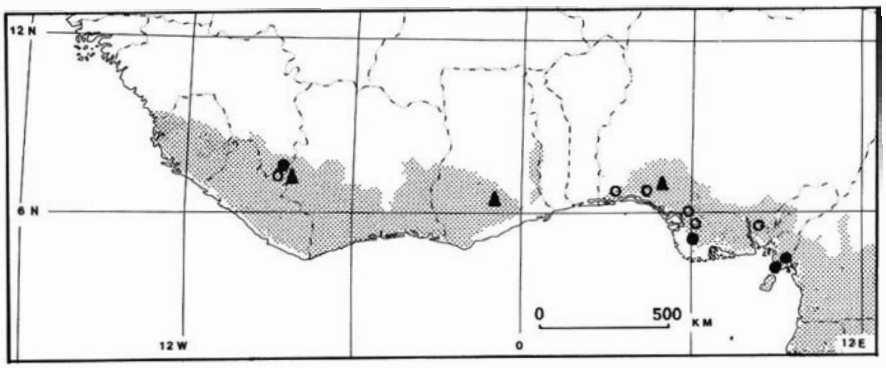


Fig. 23. Records of *Bulbophyllum magnibracteatum* (▲), *B. pavimentatum* (○) and *B. schimperanum* (●).

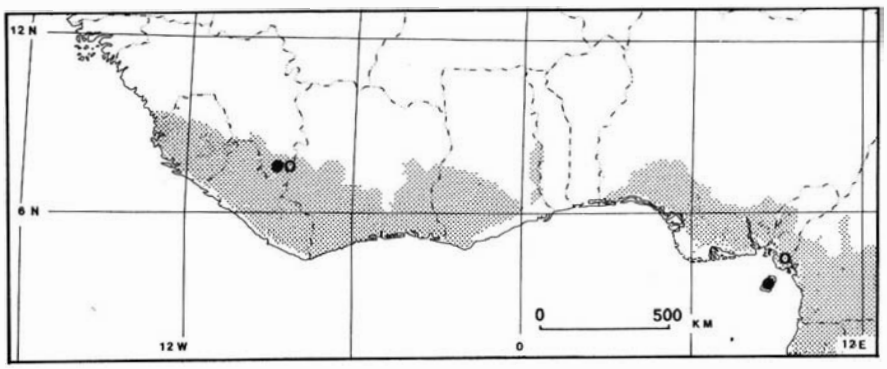


Fig. 24. Records of *Begonia rubro-marginata* (○) and *Elaphoglossum isabelense* (●).

39 spp., (2) the Orchids with 101 spp. and (3) the remaining species, called the Other vascular epiphytes, with 13 spp. This grouping is followed in the list and analyses.

The orchid flora seems to be composed of three different elements: (A) Species of the rain forest, e.g. *Angraecum birrimense* and *Cyrtorchis monteiroae,* (B) Species of the deciduous forest, e.g. *Ansellia africana* and *Rangaëris rhipsalisocia,* (C) and species restricted to high altitudes, e.g. *Polystachya dalzielii* and *Polystachya leonensis* (Figs. 19-21). A few species, e.g. *Bulbophyllum inflatum,* have only been reported from the Nimba Mountains in Liberia. However this endemic character may only result from insufficient knowledge (cf. Schnell 1952:407 and Curry-Lindahl 1969:23).

Some species with a ± wide distribution in tropical Africa, e.g. *Antrophyum immersum* and *Nephrangis filiformis* are in West Africa restricted to the Nimba region. Several other species have had their previously known area of distribution extended westwards, e.g. *Angraecum classensii, Angraecopsis elliptica, Begonia rubro-marginata, Bulbophyllum magnibracteatum, B. pavimentatum, B. schimperanum, Diaphananthe densiflora, Elaphoglossum isabelense,* and *Stolzia repens* (Figs. 22-24). A total of thirty-two species were recorded in Liberia for the first time.

List of species

The following list for the Nimba area includes for each species (1) their known geographical distribution in West Africa, (2) a brief autecologic description, and (3) (for the orchids) some field characteristics.

The notes on geographical distribution are based on F.W.T.A. 2nd ed. (1954, 1959, 1968) on Schnell 1952, Harley 1955, 1956, 1959, Alston 1959, Kunkel 1962 a, Aké Assi 1963, Guillaumet 1967, Adam 1971, and my own collections. The abbreviations of the countries follow F.W.T.A. 2nd ed. 1963, 2.

The autecological notes are based upon the quantitative studies (Tables 27-29) and general observations, and the terminology for light and substrate is in accordance with the one used during the field work. The abundance is given in three classes, subjectively estimated, common, rather common and rare. The flowering time is expressed in two months periods (when the most frequent flowering occurs).

A brief description of the plant is added for the orchids only. The particulars of the flowers are, due to their limited duration, mostly of minor importance in the field work. In most cases the determination has to be based on vegetative characteristics only. The inflorescences which often remain on the plant for several years have proved useful. (A field key to the epiphytic orchids of Ghana based on vegetative characteristics has been presented by Hall & Bowling 1969, and in a key to the orchids of Zaire, former Belgian Congo, Tournay (1955) used a similar technique.) Some species are difficult to determine even in a flowering state. The methods used to distinguish such species are discussed in connection with the presentation of the species. The size of the plants may vary widely due to environment.

In the following list the grouping previously presented is followed. Within each of the three groups the names of the genera and their species are given in alphabetical order. The first set of my collections (with few exceptions), is kept in the Herbarium of the Institute of Systematic Botany at the University of Uppsala (UPS). A second (almost complete) set has been given to the Kew Herbarium (K). For each species a voucher is quoted, e.g. D.J. 431 (UPS).

Pteridophytes

Antrophyum Kaulf.
A. mannianum Hook.
Guin., S.L., Lib., S.Nig., Cam.
A species of the high forest. Moss-covered trunks high above the ground or on the outer branches. "Occasionally on mossy boulders" (Harley 1955:91). Open shade, bark. Rare. D.J. 516 (K).

A. immersum (Bory ex Willd.) Mett.
Lib.
In West Africa only recorded from the Nimba area. In humid habitats, almost exclusively on the trunks of large trees. Heavy - open shade, bark - minor humus deposits. Rare. D.J. 554 (K), 582 (UPS).

Arthropteris J. Sm.
A. monocarpa (Cordem.) C. Chr.
Guin., S.L., Lib., Iv.C., Ghana, Cam.
Basal parts of trunks (particularly on the 'trunks' of the tree fern *Cyathea manniana*). Damp habitats in heavy shade, minor humus deposits. Rather common, similar to *A. orientalis,* which, however, occurs in better lit habitats. D.J. 481 (K, UPS).

A. palisoti (Desv.) Alston
Lib., Iv.C., Ghana, S.Nig., Cam.

Fig. 25. *Asplenium barteri.*

Harley (1955) reports three localities in Liberia. Middle part of branches of tall trees. Open shade, bark. Rare. D.J. 558 (K).

A. orientalis (Gmel.) Posth.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Basal parts of large branches. Open shade, humus deposits. Rather common. D.J. 806 (K, UPS).

Asplenium L.
A. aethiopicum (Burm.) Becherer
Guin., S.L., Lib., N.Nig., Cam.
Harley (1955:84) and Kunkel (1962:40) report it from various parts of Liberia. Trunks and branches. Open shade, humus deposits. Rare. D.J. 782 (K, UPS).

A. africanum Desv.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig.
Basal parts of large branches. Open shade, humus deposits. Rare. D.J. 852 (K), 834 (UPS). The roots hold humus in a fashion similar to *Microsorium punctatum,* which it resembles at a distance.

A. barteri Hook.
Guin., S.L., Lib., Iv.C., Ghana, Cam.
Basal parts of the trunks or moss-covered rocks. Humid habitat. Heavy shade, varying substrate. Common. D.J. 555 (K), 629 (UPS). Fig. 25.

A. dregeanum Kunze
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig., N.Nig., Cam.
On trunks in humid habitats. Heavy shade and humus deposits. Rather common at altitudes above 1000 m. D.J. 513 (K, UPS).

A. geppii Carruth.
Syn: A. anisophyllum Kunze
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Basal ramifications of tall trees. Open shade, large humus deposits. Rather common. D.J. 624 (K), 570 (UPS).

A. hemitomum Hieron.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
On trunks, often rather close to the ground. Open shade, humus deposits. Rare. D.J. 1060 (K, UPS).

Fig. 26. *Drynaria laurentii,* sterile and fertile leaves.

A. megalura Hieron. ex Brause
Guin., S.L., Lib., Iv.C., Ghana, Togo.
Middle - outer parts of large branches. Full sun, humus deposits. Common. D.J. 780 (K, UPS).

A. variable Hook. var. *paucijugum* (Ballard) Alston.
Guin., S.L., Lib., Iv.C., Ghana, Cam.
This taxon is often referred to as *Asplenium paucijugum* Ballard (Harley 1955:86, Kunkel 1962:43). Basal parts of trunks of tall trees or on moss-covered rocks. Wet and humid habitats. Heavy shade, humus deposits. Rather common. D.J. 589 K, 786 (UPS).

Davallia Sm.
D. chaerophylloides (Poir.) Steud.
Guin., S.L., Lib., Iv.C., Ghana, Togo, N.Nig., S.Nig., Cam.
Middle parts of large branches. Open shade — full sun, bark, - minor humus deposits. Rather common. D.J. 660 (K, UPS).

Drynaria (Bory) J.Sm.
D. laurentii (Christ.) Hieron.
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig.
Basal - middle parts of large branches. Open shade - full

sun. Colonizes bark surfaces. This is probably the most common epiphyte of the Nimba area. Several other epiphytes are associated to this fern in all types of forests. D.J. 431 (UPS). Fig. 26.

Elaphoglossum Schott
E. barteri (Bak.) C.Chr.
Guin., S.L., Lib., Iv.C., S.Nig., Cam.
Basal parts of trunks. Heavy - open shade, large humus deposits. Rare. D.J. 553 (K), 697 (UPS).

E. chevalieri Christ.
Guin., S.L., Lib., Iv.C.
Basal parts of moss-covered trunks. Heavy - open shade, humus deposits. Restricted to altitudes above 1100 m. Rare. D.J. 642 (K, UPS).

E. isabelense Brause
Lib. (new), F.Po.
Middle - basal parts of large branches of tall trees. Open shade - full sun, bark or minor humus deposits. Common. D.J. 495 (K, UPS).

E. kuhnii Hieron.
S.L., Lib., Cam.
Basal parts of tall trees, or rotten logs. Humid habitats. Heavy shade, humus deposits. Rare. D.J. 493 (K), 646 (UPS).

E. salicifolium (Willd. ex Kaulf.) Alston
Guin., Lib. (new), Cam.
Widely distributed over the phorophyte, mostly in the basal parts of the large branches. Full sun - open shade, bark. Common. D.J. 644 (K), 825 (K, UPS).

Lomariopsis Fée
L. guineensis (Underw.) Alston
Guin., S.L., Lib., Iv.C., Ghana, Togo, Dah., S.Nig., Cam.
Reported from various parts of Liberia (Harley 1955:87, Kunkel 1962:52). Basal parts of trunks. Heavy - open shade, bark. Rare. Rooted at the base of the phorophyte, which it climbs. Very tightly attached to the bark by short rootlets of the rhizome. After some time it normally loses contact with the ground. D.J. 777 (K), 482 (UPS). Fig. 116.

Loxogramme (Blume) Presl
L. lanceolata (Sw.) Presl
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Mainly on the trunks. Open shade, minor humus deposits. Rare. D.J. 833 (K), 742 (UPS).

Lycopodium L.
L. mildbraedii Hert. Syn: *L. dacrydioides* Bak.
Guin., S.L., Lib. (new), Cam.
On moss-covered branches and trunks. Open shade, minor humus deposits. Common at altitudes above 1000 m. D.J. 503 (K, UPS).

L. warneckei (Hert.) Alston
Guin., S.L., Lib., Iv.C., Cam.
In the outer - middle parts of large branches. Full sun, humus deposits. Rather common. Often associated with *Drynaria laurentii*. D.J. 535 (K, UPS).

Fig. 27. *Nephrolepis biserrata.*

Micrograma Presl
M. owariensis (Desv.) Alston
Guin., S.L., Lib., Iv.C., Ghana, Togo, N.Nig., S.Nig., Cam.
On trunks and branches. Open shade, minor humus deposits. Common on trees and palms around villages, less frequent in the high forest. From Liberia a new form, f. *nana*, has been described (Kunkel 1962:37-38). D.J. 567 (K, UPS).

Microsorium Link
M. punctatum (L.) Copel.
Guin., S.L., Lib., Ghana, S.Nig., Cam.
Basal - middle parts of large branches. Open shade - full sun, minor humus deposits. Common. The debris held by the root system is often utilized by other epiphytes. D.J. 794 (UPS).

Nephrolepis Schott
N. biserrata (Sw.) Schott
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig.
Epiphytic or terrestrial, equally common in both habitats.

As epiphyte mainly at the basal part of the large branches. Open shade - full sun, large humus deposits. Common in secondary forests (particularly at the leaf bases of oil palms). Rare in the high forest. Used by the natives in treatment of snake bites and urinary complaints (Harley 1941). D.J. 765 (K). Fig. 27.

N. undulata (Afzel. ex Sw.) J.Sm.
Guin., S.L., Lib., Iv.C., Ghana, Togo, Dah., N.Nig., S.Nig., Cam.
Basal - middle parts of large branches. Open shade - full sun, minor - large humus deposits. Occurs in several epiphyte communities, particularly with *Platycerium* ferns. Common. D.J. 707 (K, UPS).

Oleandra Cav.
O. distenta Kunze
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig., Cam.
Around the basal ramifications of the tall trees. Open shade, humus deposits. Common in the high forest and on the trunks of the oil palm in farmlands. The humus held by this species is utilized by several other epiphytes. D.J. 805 (K), 427 (UPS). Fig. 80.

Phymatodes Presl
P. scolopendria (Burm.) Ching.
Guin., S.L., Lib., Iv.C., Ghana, Dah., Togo, N.Nig., S.Nig., Cam., F.Po.
Basal - middle parts of large branches in high forest. On trunks of trees and oil palms around villages. In high forest in open shade, bark - minor humus deposits. In secondary forests it is found in a wider range of habitats. Common. D.J. 532 (K), 831 (UPS).

Platycerium Desv.
P. angolense Welw. ex Hook.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig.
Middle parts of large branches of emergent trees or on the trunks of trees left in farmlands. Full sun, bark. Common on large *Triplochiton scleroxylon* trees in the Yekepa community. Rare in the high forest. In Iv.C. this species occurs mainly in the deciduous forests in the northern part of the country (Boyer 1964). D.J. 809 (UPS). Fig. 85.

P. stemaria (P. Beauv.) Desv.
Guin., S.L., Lib., Iv.C., Ghana, Dah., N.Nig., S.Nig., Cam.
In its ecology very similar to *P. angolense*. Rare in high forest, more common on tall trees in secondary forest. In Iv.C., this species occurs mainly in the secondary evergreen forest in the southern part of the country, and is ± absent in the primary rain forest (Boyer 1964). D.J. 791 (UPS). Fig. 84.

Pyrrosia Mirb.
P. mechowii (Hieron.) Alston
Guin., Lib. (new), N.Nig., Cam.
Middle parts of large branches. Open shade - full sun, minor humus deposits. Humid habitats, e.g. swamp forests. Almost exclusively on *Mitragyna ciliata*. Rare. D.J. 808 (K, UPS).

Tectaria Cav.
T. angelicifolia (Schum.) Copel.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
In the basal parts of tall trees (or on rocks). Frequently on the trunks of *Cyathea manniana*. Heavy shade, on various kinds of substrate. Common. D.J. 1059 (UPS).

T. fernandensis (Bak.) C.Chr.
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig., Cam.
Basal parts of large trees. Heavy shade, humus deposits. Only in very humid habitats. Rare. D.J. 795 (K).

Vittaria Sm.
V. guineensis Desv.
Guin., S.L., Lib., Iv.C., Ghana, Togo, S.Nig., Cam.
On all parts of the trees, but mainly in the basal and middle parts of large branches. Open shade, minor humus deposits. Often associated with *Microsorium punctatum*. Common. D.J. 762 (UPS).

Xiphopteris Kaulf.
X. oosora (Bak.) Alston
Guin., S.L., Lib. (new), Cam., F.Po.
Basal - central parts of large branches. Open shade, humus deposits. At altitudes above 1200 m. Rather common. D.J. 826 (K), 514 (UPS).

X. serrulata (Sw.) Kaulf.
S.L., Guin., Lib., Iv.C., F.Po.
Middle parts of large branches. Open shade, minor humus deposits. Rare. D.J. 592 a (UPS).

X. villosissima (Hook.) Alston
Guin., S.L., Lib., Iv.C., Cam., F.Po.
Basal and middle parts of large branches. Open shade, minor humus deposits. At altitudes above 1100 m. Rare. D.J. 518 (K), 827 (UPS).

Orchids

Aërangis Rchb.
A. biloba (Lindl.) Schltr.
Sen., Guin., S.L., Lib., Iv.C., Ghana, Togo, N.Nig., S.Nig., Cam.
Basal or middle parts of large branches. Full sun - open shade, bark - minor humus deposits. Common. Growing tips of roots orangish-pink (Piers 1959, Moir 1963, Sanford 1968). Stem short, woody. Leaves crowded at the apex of the stem, 8-18 cm, oblanceolate, curved and unequally bilobed, dark green. Inflorescence longer than the leaves, many flowered, somewhat pendulous. Flowers white, star-like. June-July. D.J. 562 (UPS). Fig. 28.

A. laurentii (De Wild.) Schltr.
Lib., Ghana.
Anywhere on the large branches. Full sun, bark. Rare. Erect, 10-15 cm. Stem short, woody. Leaves strap-shaped, arranged in a fan-shaped manner, acutely v-shaped in cross-section, rather thick and stiff. Inflorescence longer than the leaves, zigzag-shaped rachis. Flowers white, with a long spur. Jan.-Febr. The zigzag rachis distinguishes it from *Rangaëris muscicola*. *Plectrelminthus caudatus* has also a zigzag rachis, but leaves of a different shape. D.J. 449 (K), 411 (UPS).

Fig. 28. *Aërangis biloba.*

Ancistrochilus Rolfe

A. rothschildianus O'Brien

Guin., S.L., Lib., Iv.C., S.Nig., Cam.

Basal or central parts of large branches, occasionally on moss-covered trunks. Open shade, humus deposits. Rather common. Erect, 20-30 cm. Pseudobulbs crowded, conical - pyriform, 2-3 cm high, up to 5 cm in diameter, longitudinally sulcated, green. Leaf 15-30 cm, lanceolate - oblanceolate, thin, ribbed, dark green. Inflorescence long, curved. Flower large (8 cm in diam.). Oct.-Nov. D.J. 703 (UPS). Fig. 29.

Ancistrorhynchus Finet

A. capitatus (Lindl.) Summerh.

S.L., Lib., S.Nig.

Basal parts of large branches or on trunks. Open shade - full sun, bark - minor humus deposits. Common. Erect, 25-30 cm. Stem short, woody. Leaves crowded, curved, 20-50 x 1.5-3 cm, with a few teeth at apex. Inflorescences short, dense, on the stem below the leaves, long persistant. Flowers small, white. July-Aug. D.J. 531 (K, UPS).

A. cephalotes (Rchb.f.) Summerh.

Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig.

Trunks or the middle parts of large branches. Full sun, bark. Common. Erect or scrambling. Stem long, woody, twisted, covered with old leafbases and inflorescences. Leaves 8-20 cm, linear, apex bilobed. Inflorescences on the stem below the leaves, short, with a very large number of flowers. Flower white, small. June-July. D.J. 524 (K, UPS). Fig. 110.

A. clandestinus (Lindl.) Schltr.

S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.

Trunks or basal parts of larger branches. Full sun, bark. Rare. Erect, in the Nimba area a small to medium-sized plant, stem short, woody. Leaves 5-8 x 0.5-1.0 cm, stiff and fleshy, leathery, apical lobes of the leaf very acute and

Fig.29. *Ancistrochilus rothschildianus.*

unequal in length. (F.W.T.A. 2nd ed. 3:1, 1968:270 gives the length of the leaves up to 180 cm.) Inflorescence very short, dense, from the stem below the leaves. Flowers white, small. May-June. The leaves are similar to *Chamaeangis vesicata,* but the species is distinguished by the inflorescence. D.J. 804 (UPS).

A. recurvus Finet
Guin., Lib. (new), Ghana, S.Nig., Cam.
Occurs in the same habitats as *A. clandestinus*. Rare. Leaves 8-15 x 1.2-1.7 cm, not particularly stiff. Floral parts as *A. clandestinus*, but leaves of a different shape. D.J. 810 (UPS).

Angraecopsis Summerh.
A. elliptica Summerh.
Lib. (new), N.Nig., Cam.
Basal or central parts of large branches. Open shade, humus deposits. Rare. Erect, 6-10 cm. Stem very short. Leaves 4-10 x 1-2 cm, ligulate, curved. Inflorescence filiform, ± as long as the leaves. Flowers very small and tiny, yellow-green. Aug.-Sept. D.J. 611 (K, UPS).

Fig. 30. *Angraecum birrimense.*

Angraecum Bory
A. birrimense Rolfe
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Trunks, basal or middle parts of large branches. Open shade, humus deposits. Common. A climbing and pendulous plant, 1-2 m long. Stem woody. Leaves 6-12 cm, scattered, lanceolate - elliptical, bilobed, fleshy, light green. Inflorescence short. Flowers large. Tepals light green, lip white with a green centre. July-Aug. D.J. 436 (K), 568 (UPS). Fig. 30.

A. chevalieri Summerh.
Guin., Lib., Iv.C., Ghana, N.Nig., S.Nig.
Basal parts of large branches. Open shade - full sun, bark - minor humus deposits. Rare. Climbing, somewhat pendulous, stem woody. Leaves 3-7 cm, narrowly strap-shaped, fleshy, leathery. Inflorescence short. Flowers yellowish, small. June-July. D.J. 1055 (UPS).

A. classensii De Wild.
Lib. (new), Nig.
Trunks and branches of small trees, close to the ground. Full sun - open shade, bark. Rare. Ascending, 10-30 cm long. Stem woody. Leaves 6-10 x 1.5-3 cm, oblong - obovate, bilobed at apex. Inflorescences erect, 5-25 cm, usually much longer than the leaves. Flower ochra-coloured. May-June. D.J. 512 (K, UPS).

A. distichum Lindl.
Guin., S.L., Lib., Iv.C., Ghana, Dah., N.Nig., S.Nig., Cam.
Trunks or basal parts of large branches. Full sun - open shade, bark - minor humus deposits. Common. A dense tuft of branching stems, ± erect, 8-20 cm. Leaves 1.0 x 0.7 cm, fleshy, triangular, distichuous. Flower sessile, white, small. May-June. D.J. 525 (UPS). Fig. 59.

A. podochiloides Schltr.
Lib., Iv.C., S.Nig., Cam.
Trunks of tall trees. Open shade - full sun, bark. Rare. Pendulous, 20-60 cm. Leaves crowded, 1-2 cm, narrowly lanceolate - oblong, fleshy, hard. Flower small, sessile, white. June-July. D.J. 610 (UPS). Fig. 59.

A. subulatum Lindl.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Basal or middle parts of large branches. Open shade, minor humus deposits. Rare. Erect - pendulous. Leaves 3-8 x 0.1-0.3 cm, subulate - terete, falcate. Flowers small, sessile, white. June-July. Two other species with terete leaves are *Nephrangis filiformis* and *Tridactyle tridentata.* They are distinguished by a marked pendulous growth. D.J. 557 (K), 766 (UPS).

Ansellia Lindl.
A. africana Lindl.
Lib., Iv.C., Ghana, S.Nig., F.Po.
Basal or middle part of large branches. Full sun, large humus deposits. Erect 50 - 80 cm. Pseudobulb 30-50 cm. Leaves lanceolate, from the upper part of the pseudobulb. Flower yellow with large chocolate brown spots. Feb.-March. Numerous erect aerial roots occur at the base of the plant (cf. *Graphorchis lurida*). D.J. 790 (UPS). Figs. 31 and 62.

Fig. 31. *Ansellia africana*.Photo: Harvey Boettcher.

Bolusiella Schltr.
B. talbotii (Rendle) Summerh.
S.L., Lib., Iv.C., Ghana, S.Nig.
Outer parts of large branches. Full sun, bark. Rather common. Erect, 5-8 cm. Stem very short, woody. Leaves 2-4 cm, arranged in a fan-like manner, narrowly lanceolate, distinctly narrowed in the upper half, compressed, fleshy. Inflorescence thin, considerably longer than the leaves. Flowers scattered, minute, white. June-July. D.J. 438 (K), 1054 (UPS). Fig. 118.

Brachycorythis Lindl.
B. kalbreyeri Rchb. f.
Guin., S.L., Lib., Cam.
Basal parts of the trunks. Open shade, large humus deposits. Rare. Erect, up to 40 cm. Stem slender, spotted purple. Leaves evenly distributed along the stem, 6-9 cm, lanceolate, thin in texture. Flower large, up to 5 cm in diam, lilac-lavender. June-July. In the dry season the epigeal parts of the plant wilt and then it is difficult to trace but occasionally one finds the tubers in the humus. D.J. 497 (UPS). Fig. 32.

Bulbophyllum Thou. (Fig. 33)
B. barbigerum Lindl.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Middle parts of large branches. Open shade, bark. Rare. Prostrate 4-10 cm. Pseudobulb 1-3 cm, elliptical in outline, depressed, obtusely 3-4 angled, pale green. Leaf 3-6 cm, elliptical - oblong, flat, stiff, green. Inflorescence 2-4 times longer than the leaf, descending. Bracts large, spreading. Flower small, dark purple. Lip mobile, densely hairy. Longer hairs with club-shaped swollen ends. Oct.-Nov. D.J. 658 (UPS).

Fig. 32. *Brachycorythis kalbreyeri.*

B. bifarium Hook. f.
Lib. (new), Iv.C., Cam.
Middle or outer parts of branches. Open shade, minor humus deposits. At altitudes above 1000 m. Rare. Erect, 5-10 cm. Pseudobulbs crowded, 1.5-2.0 cm, ellipsoid or ovoid with sharp angles or protruding ridges, green with purple stripes and spots. Leaf 4-8 cm, strap shaped, light green. Inflorescence equaling or longer than the leaves, bracts large, orange-red. Flower small, pale green. Oct.-Nov. D.J. 706 (K, UPS).

B. bufo (Lindl.) Rchb.f.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Basal parts of large branches. Open shade, humus deposits. Rather common. Erect, 15-25 cm. Pseudobulb 3-5 cm, ovoid or conical ovoid, quadrangular. Leaf 8-15 cm, oblanceolate, green. Inflorescence erect, longer than the leaves. Rachis flattened up to one cm wide. Flower small. Sept.-Oct. This and some other *B.* spp. (e.g. *B. falcatum*) form a group in which it is difficult to distinguish the species on vegetative characteristics only. D.J. 711 (K, UPS).

B. buntingii Rendle
Guin., Lib., Iv.C., N.Nig., S.Nig., Cam.
Middle parts of large branches. Full sun, bark. Rather common. Erect, 5-10 cm. Pseudobulb 1.5-2.0 cm, bluntly triangular, hard, red-brown, with a smooth or slightly reticulate surface. Leaf 4-7 cm, elliptical, obtuse, bluish-green, purplish beneath. Inflorescence erect, double the length of the leaf, densely flowered almost to the base. Flower small, white. Oct.-Nov. D.J. 688 (K, UPS).

B. calamarium Lindl.
S.L., Lib., S.Nig.
Middle or outer parts of large branches. Open shade,

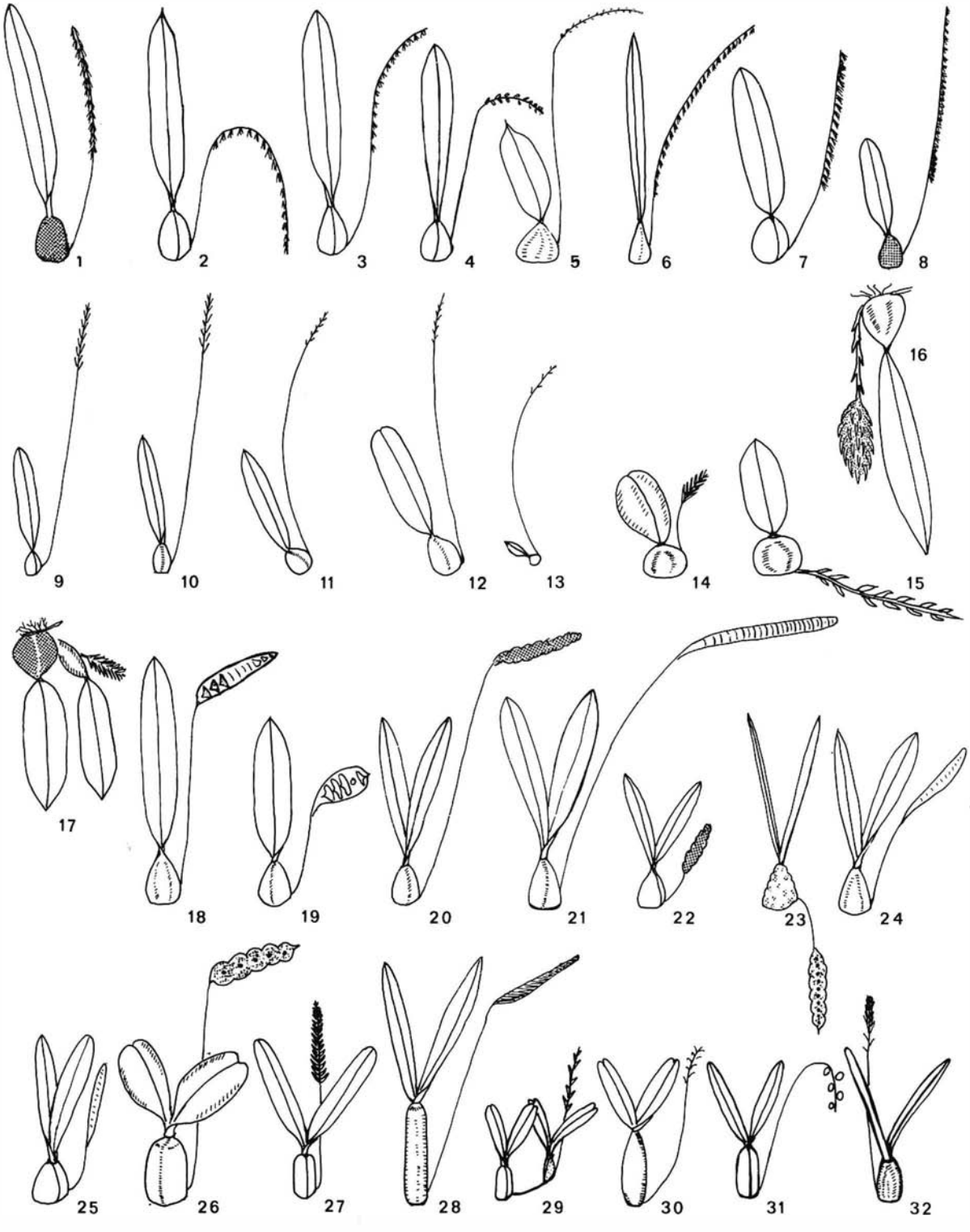


Fig. 33. Simplified drawing of the *Bulbophyllum* species in the Nimba area. (The species are not in proportion to each other.) 1. *Bulbophyllum josephii*, 2. *B. cocoinum*, 3. *B. flavidum*, 4. *B. pavimentatum*, 5. *B. recurvum*, 6. *B. nigritianum*, 7. *B. schimperanum*, 8. *B. buntingii*, 9. *B. schinzianum*, 10. *B. phaeopogon*, 11. *B. distans*, 12. *B. calamarium*, 13. *B. intertextum*, 14. *B. saltatorium*, 15. *B. barbigerum*, 16. *B. inflatum*, 17. *B. winkleri*, 18. *B. linderi*, 19. *B. magnibracteatum*, 20. *B. imbricatum*, 21. *B. falcatum*, 22. *B. melanorrachis*, 23. *B. lucifugum*, 24. *B. bufo*, 25. *B. congolanum*, 26. *B. maximum*, 27. *B. lupulinum*, 28. *B. cochleatum*, 29. *B. oreonastes*, 30. *B. rhizophorae*, 31. *B. scariosum*, 32. *B. bifarium*.

minor humus deposits. Rare. Prostrate, 15-20 cm. Pseudobulb 4-5 cm, conical or ovoid, 3-4 angled, velvety, light green. Leaf 12-15 cm, flat, stiff, oblong, green. Inflorescence 40-60 cm, bracts less than 15 mm, overlapping each other. Flower small, lip hairy, sepals strongly reflexed, yellow with purple spots. July-Aug. Difficult to distinguish from *B. schinzianum* and *B. phaeopogon* without flowers. The size of the bracts gives a possibility. D.J. 856 (UPS).

B. cochleatum Lindl.
Guin., S.L., Lib., Iv.C., N.Nig., S.Nig., Cam.
Basal or middle parts of large branches. Open shade, bark or in minor humus deposits. Common. Erect, 12-24 cm. Pseudobulbs scattered, 3-10 cm, narrowly cylindrical, bluntly quadrangular, brownish-green with brown or purple stripes or dots. Leaf 8-14 x 0.5-1.2 cm, strap-shaped, green, sometimes tinged purple. Inflorescence up to 30 cm long, curved. Flowers small, orange-red. Sept.-Oct. D.J. 631 (K, UPS).

B. cocoinum Batem. ex Lindl.
S.L., Lib., Ghana.
Basal and middle parts of large branches. Open shade, humus deposits. Rather common. Erect, 15-30 cm. Pseudobulbs crowded, 2-4 cm high, 1.5-2.0 cm broad, ovoid, sharply 3-4 angled, pale yellow. Leaf lanceolate or oblanceolate, 10-20 cm, acute, not stiff. Inflorescence long, arching, densely flowered. Flowers small, creamy white. Aug.-Sept. D.J. 541 (K, UPS).

B. congolanum Schltr.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig.
Middle parts of large branches. Full sun, bark or minor humus deposits. Rather common. Erect 8-14 cm. Pseudobulb 2-4 cm, ovoid - conical, 3-4 angled, light green-yellow. Leaf 6-10 cm, strap-shaped, green. Inflorescence erect, somewhat curved, of about the same length as the leaves. Flower, small creamy-white. Oct.-Nov. D.J. 714 (K, UPS). Fig. 58.

B. distans Lindl.
Lib., Iv.C., Ghana, S.Nig., Cam.
Middle or basal parts of large branches. Full sun - open shade, minor humus deposits. Rather common. Ascending, 10-15 cm. Pseudobulb depressed, 2-3 cm, conical-ovoid, yellow-green. Leaf 8-12 cm, oblong, flat, stiff, green. Inflorescences (often two) erect, slender, 30-50 cm. Bracts 6-10 mm. Flower small, dark purple, lip densely hairy. June-July. D.J. 855 (K), 857 (UPS).

B. falcatum (Lindl.) Rchb.f.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam., F.Po.
Middle part of large branches. Open shade, minor humus deposits. Common. Erect. Pseudobulb 1.5-5 cm long, ovoid, 3-4 angled, green. Leaves 3-12 x 0.6-2 cm, oblong-lanceolate or oblanceolate. Inflorescence very long, up to 50 cm. Rachis 0.5-0.8 cm broad. Flowers small, yellow-purple. Oct.-Nov. D.J. 668, 670 (K), 671 (UPS).

B. flavidum Lindl.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Middle part of large branches. Open shade, minor humus deposits. Rare. Erect, 8-16 cm. Pseudobulb 1-2 cm, light green, velvety. Leaf 6-12 cm, oblanceolate-narrowly oblong, acute, green. Inflorescence about the same length as the pseudobulb and the leaf, arching, densely flowered. Flower small, yellow or pink. June-July. D.J. 585 (K), 586 (UPS).

B. imbricatum Lindl.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
In the middle parts of large branches. Open shade, minor humus deposits. Rare. Erect, 15-25 cm, stout. Pseudobulbs 3-4 cm, ovoid, green, scattered along the rhizome. Leaf 12-20 cm, linear - oblong. Inflorescence longer than the leaves, erect stout. Rachis fleshy, dark purple. Flower small with purple spots. Sept.-Oct. D.J. 710 (K), 678 (UPS).

B. inflatum Rolfe
S.L., Lib.
Trunks or in the basal parts of large branches. Heavy - open shade, minor humus deposits. At altitudes above 1000 m. Rather common. Pendulous, 8-20 cm. Pseudobulb 1-3 cm, ovoid quadrangular, rhomboid in cross section, green. Leaf 7-20 x 1.5-5 cm, lanceolate - oblong or elliptical, leathery, green. Flower small, yellow-green. Jan.-Feb. Easy to recognize. The plant grow upside down. This species is very similar to *B. comatum* Lindl., in a sterile as well as fertile state. The latter has not been recorded in the Nimba Mts but from Mt Momi in the Ivory Coast. In the field work specimens without flowers that could be any of the two species have been recorded as *B. inflatum*. D.J. 717 (K, UPS).

B. intertextum Lindl.
S.L., Lib., Ghana, N.Nig., S.Nig., Cam.
Middle parts of large branches. Full sun, bark. Common. Erect, 2-5 cm. Rhizome slender, forming mats. Pseudobulbs scattered, up to one cm, elliptical - ovoid, green. Leaf 1-2.5 x 0.5-1.0 cm, elliptical, light green. Inflorescence 14-20 cm, slender. Flower minute, creamy-white. Oct.-Nov. A somewhat different form of this species occurs: Pseudobulb of similar shape and size as above, but with a purplish colour. Leaf strap-shaped, 1-4 x 0.3-0.5 cm, dark greenish-purple. Inflorescence much shorter, 4-8 cm. Flower minute, purplish. Oct.-Nov. D.J. 687, 691 (K, UPS).

B. josephii (Kunze) Summerh.
Guin., S.L., Lib. (new), Iv.C., S.Nig., Cam.
Basal parts of large branches. Open shade and humus deposits. Rare. Erect, 12-20 cm high. Pseudobulbs crowded, 2-3 cm, narrowly ovoid-conical ovoid, velvety, redbrown. Inflorescence long, slender, arching. Flower purplish-violet. July-Aug. Other species with redbrown pseudobulbs are *B. winklerii*, and *B. buntingii* D.J. 441 (K), 699 (UPS).

B. linderi Summerh.
S.L., Lib., Iv.C.
Basal or middle parts of large branches. Open shade, bark. Common. Erect, 12-20 cm. Pseudobulb 2-3 cm, ovoid, triangular, with a shiny texture, green. Leaf 8-16 cm, oblong - lanceolate, green, often red coloured along

the margin. Inflorescence erect, the apical part with the white fleshy rachis is held in a horizontal position. Flowers white. Oct.-Nov. D.J. 675 (K, UPS).

B. lucifugum Summerh.
S.L., Lib. (new).
Basal or middle parts of large branches. Open shade, minor humus deposits or on bark. Rare. Erect, 10-20 cm. Pseudobulb 2-4 cm, conical - ovoid, obtusely quadrangular, surface wavy or verrucate, greenish with purple spots. Leaf strap-shaped, green, 10-22 x 0.6-0.9 cm. Inflorescence recurved, rachis flattened, green with purple dots, crinkled at the edges. Flower small. Feb.-March. D.J. 744 (K), 730 (UPS).

B. lupulinum Lindl.
Guin., S.L., Lib. (new), Ghana, N.Nig., S.Nig.
Middle parts of large branches. Full sun, bark - minor humus deposits. Rare. Erect, 15-20 cm. Pseudobulb 4-6 cm, rectangular, yellow green. Leaf 8-18 cm, oblong, green. Inflorescence erect. Bracts large, with numerous short black or purplish hairs. Flower small, yellow with red spots. Jan.-Feb. D.J. 451 (K, UPS).

B. magnibracteatum Summerh.
Lib. (new), Ghana, S.Nig.
Middle parts of large branches. Open shade, bark. Rare. Erect. Pseudobulbs 1.5-2.0 cm long, ovoid, 3-angled. Leaves 5-7 x 1.5 cm, stiff. Inflorescence of about the same length as the plant. Rachis 0.4-0.7 cm broad with bracts as broad as the rachis. When old and dry the rachis has a characteristic obovate shape ending in a short acute apex. Flowers small, purplish. April-May. D.J. 489 (UPS).

B. maximum (Lindl.) Rchb. f.
S.L., Lib., Iv.C., Ghana, S.Nig.
Middle part of large branches. Open shade - full sun, bark. Rather common. Erect, 12-20 cm, stout. Pseudobulbs 3-7 cm, ellipsoid - conical ovoid, acutely quadrangular, green, scattered along the woody and stout rhizome. Leaf 7-10 cm, oblong - elliptical, stiff, dull green. Inflorescence 12-40 cm, rachis 1.0-1.5 cm broad, margins markedly undulate. Flowers minute, arranged along a central line of the rachis. Sept.-Oct. D.J. 656 (K, UPS).

B. melanorrachis (Rchb. f.) Rchb. f. ex De Wild.
Guin., S.L., Lib., Ghana, S.Nig.
Middle part of large branches. Open shade and minor humus deposits. Rare. Erect. Pseudobulbs 1.5-3.5 cm long, narrowly ovoid. Leaves 4-10 x 0.7-1.2 cm, oblong-oblanceolate, obtuse. Inflorescence 4-6 cm, rachis dark purple. Flowers crowded, small. Oct.-Nov. D.J. 648 (K, UPS).

B. nigritianum Rendle
S.L., Lib., Iv.C., Ghana, S.Nig.
Basal or middle parts of large branches. Open shade, minor humus deposits. Rare. Erect. Pseudobulbs 2-4 cm long, conical ovoid, velvety, dark green. Leaf narrowly strap-shaped, 10-15 x 0.7-1.0 cm. Inflorescence erect, 10-15 cm long, flowering almost to the base. Flower small, white. Oct.-Nov. D.J. 693 (K), 669 (UPS).

B. oreonastes Rchb. f.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Middle part of large branches. Open shade - full sun, bark. The most common epiphytic orchid in the Nimba area. Erect, 6-10 cm. Pseudobulbs spaced out along the rhizome, 1-3 cm, ovoid, quadrangular, yellowish-green. Leaves 2-6 cm, oblong, leathery, green. Inflorescence longer than the bulb and leaves together. Rachis narrowly winged, flowers yellowish with purple lines, lip purple. March-April. This species is vegetatively similar to *B. zenkeranum* Kraenzl. The latter species has been recorded from the Kitoma Range, south of the Nimba area. Specimens without flowers that could be any of the two species have been recorded in the field work as *B. oreonastes*. D.J. 640 (K, UPS).

B. pavimentatum Lindl.
Lib. (new), S.Nig.
Middle parts of large branches. Open shade, bark. Rare. Erect, 12-16 cm. Pseudobulbs crowded, about 2 cm long, ovoid, obscurely 2-3 angled, velvety green. Leaf 6-14 cm, oblong- elliptical, dark green. Inflorescence equal with or longer than the leaf, thin, peduncle longer than the rachis. Flower small, purplish. Oct.-Nov. D.J. 679 (UPS).

B. phaeopogon Schltr.
Lib. (new), Iv.C., Ghana, S.Nig., Cam.
Outer parts of large branches. Open shade, minor humus deposits. Rare. Erect, 12-16 cm. Pseudobulbs erect, crowded, 2-3 cm, ovoid, 3-4 angled, light green. Leaf oblong- lanceolate, 7-14 cm, stiff, green. Inflorescence 30-60 cm. Bracts more than 15 mm long, overlapping. Flower small, tepals yellow with red spots. Lip with long hairs, mobile. July-Aug. This species is hardly distinguishable from *B. schinzianum* when in a flowerless state. D.J. 811 (K), 1061 (UPS). Fig. 54.

B. recurvum Lindl.
S.L., Lib., Cam., F.Po.
Middle parts of large branches. Open shade, minor humus deposits-bark. Rare. Erect. Pseudobulbs 1-1.5 cm long, ovoid or conical ovoid, obscurely 4-angled, green to brownish green. Leaves elliptical, 3-6 x 1-2 cm, acute or obtuse. Inflorescence erect, 8-13 cm, longer than the leaves, recurved in the upper flowering half. Flower small, greenish-yellow. Oct.-Nov. D.J. 659 (UPS).

B. rhizophorae Lindl.
S.L., Lib. (new), Iv.C., Ghana, S.Nig., Cam.
On branches of small trees close to water. Open shade - full sun, bark. Rare. Pseudobulb 2-3 cm long, elliptical. Leaves oblong, ± as long as the pseuodobulbs. Inflorescence 6-10 cm, erect. Flower small, yellowish-white. Oct.-Nov. D.J. 748 (K).

B. saltatorium Lindl.
S.L., Lib. (new), Ghana.
Basal or middle parts of large branches. Open shade, bark - minor humus deposits. Rare. Prostrate, lying on the substrate, 4-7 cm. Pseudobulbs crowded, 1-2 cm, ovoid, flattened, obtusely 3-4 angled, green. Leaf 3-5 cm, falcate, oblong-elliptical, dark green. Inflorescence shorter than the plant. Flowers small, dark purple, lip hairy, almost all

flowering simultaneous. March-April. D.J. 468 (K, UPS).

B. scariosum Summerh.
Guin., S.L., Lib.
Middle or outer parts of large branches. Full sun, bark - minor humus deposits. At altitudes above 1000 m. Common. Erect, 8-16 cm. Pseudobulb 2-4 cm, ovoid, quadrangular, light green-yellow, turning redbrown when old. Leaf 4-12 cm, oblong, light green. Inflorescence erect, arching in the apical part. Flower creamy white. March-April. D.J. 716 (K, UPS).

B. schimperanum Kraenzl.
Lib. (new), S.Nig., Cam.
Middle or outer parts of large branches. Full sun, bark. Rather common. Erect. Pseudobulbs 1-2 cm long, ovoid, triangular, light green-yellow, often tinged with red. Leaf 5-10 x 1.5-2.0 cm, oblanceolate - oblong, obtuse. Inflorescence erect, 10-15 cm long, carrying flowers almost to the base. Flowers small, white. Sept.-Oct. D.J. 890 (K), 694 (UPS).

B. schinzianum Kraenzl.
Lib., Iv.C., N.Nig.
Middle parts of large branches. Open shade - full sun, bark. Rather common. Erect, 10-25 cm. Pseudobulbs crowded, erect, 2-4 cm, ovoid, sharply quadrangular, light yellow-green. Leaf 10-20 cm, oblong-elliptical, stiff, green. Inflorescence 20-60 cm. Flower small, dark purple, lip with short dense hairs. Sept.-Oct. In flowerless state similar to *B. phaeopogon*. D.J. 435 (K), 641 (UPS). Fig. 53.

B. winkleri Schltr.
Lib., N.Nig., S.Nig., Cam.
Upper parts of trunks or basal parts of large branches. Open shade, bark. Rather common. Prostrate, 8-15 cm. Pseudobulbs crowded, 1-2.5 cm, ovoid, obtusely quadrangular, surface wrinkled, red-brown. Leaf 5-12 cm long, lanceolate - oblanceolate, acute, flat, dark green. Inflorescence shorter than the leaf. Flower very small. April-May. D.J. 756 (K, UPS).

Calyptrochilum Kraenzl.

C. christyanum (Rchb. f.) Summerh.
Port.G., Guin., S.L., Lib., Iv.C., Mali, Ghana, N.Nig., S.Nig.
Basal parts of large branches. Full sun, bark. Common. Might grow to several meters in length. Stem woody. Leaf 6-12 cm, strap-shaped, bilobed, leathery. Inflorescence 3-4 cm, many flowered, rather lax, rachis ± zigzag. Flower white. Dec.-Jan. D.J. 719 (K, UPS).

C. emarginatum (Sw.) Schltr.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
On trunks of trees in villages. Rare in the primary forest. Full sun, bark. This species can grow to several meters' length. Stem woody. Leaf 8-15 x 2.5-5 cm, ovate - strap-shaped, bilobed, fleshy, green. Inflorescence short, many flowered, very dense. Flower whitish - pale purple. May-June. This plant might be confused with the closely related *Calyptrochilum christyanum,* which, however, has a zigzag rachis. D.J. 829 (K). Fig. 34.

Fig. 34. *Calyptrochilum emarginatum.*

Chamaeangis Schltr.

C. vesicata (Lindl.) Schltr.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig.
Middle parts of large branches. Full sun, bark - minor humus deposits. Common. Stem short, woody. Leaves 15-40 x 1-3 cm, linear or narrowly lanceolate, often much curved, fleshy, v-shaped in cross-section, olive green or pale yellow. Inflorescences numerous, longer than the leaves, arching or pendulous, many flowered. Flower small, pale yellow. May-June. D.J. 530 (K), 430 (UPS).

Cyrtorchis Schltr.

C. arcuata Lindl. subsp. *variabilis* Summerh.
Guin., Lib., Iv.C., Ghana, Dah., N.Nig., S.Nig.
Basal or middle parts of large branches. Open shade - full sun, minor humus deposits or bark. Common. Erect, 30-60 cm. Stem long, woody, thick, covered with old leaf sheaths. Leaf 10-20 cm long, oblong or slightly obovate, unequally bilobed at the apex. Inflorescence horizontal, equaling the length of the leaves. Flowers white, rather scattered on the raceme. Aug.-Sept. F.W.T.A., Vol. 3:1 1968, recognizes three subspecies of *C. arcuata*. The subspp. *variabilis* and *leonensis* would be impossible to separate in the field. Specimens that could be any of the two subspp. have been recorded as *C. arcuata* in the fieldwork. D.J. 627 (K, UPS).

Fig. 35. *Diaphananthe bidens.*

C. aschersonii (Kraenzl.) Schltr.
S.L., Lib. (new), Ghana, S.Nig., Cam.
Middle parts of large branches. Full sun, bark. Rather common. Erect, 20-30 cm. Stem woody, thick, covered with old leafsheaths. Leaves 6-15 x 0.5-1.0 cm, almost equally bilobed at the apex, very fleshy, rather stiff, strap-shaped. Inflorescences much shorter than the leaves. Flowers crowded on the raceme, white. Aug.-Sept. D.J. 613 (K), 576 (UPS).

C. monteiroae (Rchb. f.) Schltr.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Basal or middle parts of large branches. Open shade, minor humus deposits. Rare. Erect or pendulous, 30-60 cm. Stem long, woody. Leaf 5-20 x 2-4 cm, oblong-elliptical or oblanceolate, unequally bilobed, often with wrinkled margin. Inflorescence arching, exceeding the leaves. Flowers scattered, white. Oct.-Nov. D.J. 674 (UPS).

Diaphananthe Schltr.
D. bidens (Sw.) Schltr.
Port.G., Guin., S.L., Lib., Iv.C., Ghana, S.Nig., N.Nig., Cam.
On trunks, or in high forest in the middle parts of large branches. Open shade - full sun. Bark or minor humus deposits. Common. Up to several meters length. Stem woody. The plant grows out away from the substratum. Leaf 5-14 cm, oblong-lanceolate to narrowly ovate, apex unequally bilobed, flat, stiff, leathery, dark green. Inflorescence long, pendulous, many flowered. Flower small, salmon-pink, semi-transparent. July-Aug. D.J. 569 (UPS). Fig. 35.

Fig. 36. *Eurychone rothschildiana.*

D. densiflora (Summerh.) Summerh.
Lib. (new), Cam.
On branches of small shrubs and trees, more seldom on taller trees. Open shade, bark. Rare. Semi-pendulous. Attached to the substrate by a large number of roots at the base of a 5-40 cm long stem. Aerial roots numerous along the stem. Leaves 5-10 x 1-2 cm, lanceolate - oblong, unequally bilobed. Inflorescences 2-5 cm. Flowers crowded, small, pale green. July-Aug. D.J. 571 (K, UPS).

D. pellucida (Lindl.) Schltr.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Basal parts of large branches. Open shade, bark or minor humus deposits. Common. Stem short, woody, bearing the leaves in a dense tuft. Leaves arching, 15-70 cm, oblanceolate, unequally bilobed or almost entire at the apex, fleshy. Inflorescences numerous, pendulous, many flowered. Flower pale yellow-pinkish. July-Aug. D.J. 612 (UPS). Fig. 105.

D. rutila (Rchb. f.) Summerh.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
On trunks or branches of small trees or shrubs. Full sun - open shade, bark. Rather common. Growth habit as *D. bidens.* Stem woody. Leaves 6-15 cm, unequally and obtusely bilobed. Inflorescence long, pendulous, with a large number of small, translucent, pale yellow-purplish flowers. July-Aug. D.J. 560 (K, UPS).

Eurychone Schltr.
E. rothschildiana (O'Brien) Schltr.
Guin., S.L., Lib. (new), Iv.C., Ghana, S.Nig.
Trunks or branches of smaller trees or shrubs. Full sun - open shade, bark. Rare. Stem very short, woody. Leaves few, 7-17 cm, broadly oblanceolate, unequally bilobed at the apex, leathery. Inflorescence shorter than the leaves. Flowers large, up to 5 cm in diam., 3-6, white and green. June-July. D.J. 853 (K, UPS). Fig. 36.

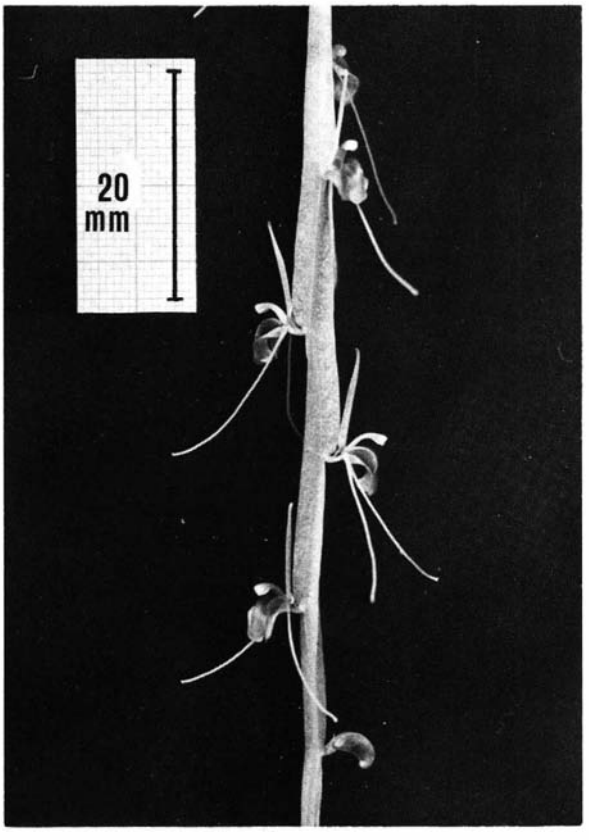


Fig. 37. *Liparis caillei.*

Genyorchis Schltr.
G. pumila (Sw.) Schltr.
S.L., Lib., Iv.C., Ghana.
Middle or outer parts of branches on small trees or shrubs. Full sun, bark. Rare. Erect, 2-3 cm. Pseudobulb 0.6-1.5 cm, ovoid, quadrangular. Leaf 1-2 cm, ligulate - oblong, green. Inflorescence slender, 5-6 cm. Flower minute, *Polystachya*-like, white-pale green. March-April. This small inconspicuous plant is similar to a *Bulbophyllum* sp. D.J. 485 (K, UPS).

Graphorchis Thou.
G. lurida (Sw.) O. Ktze.
Sen., Port.G., Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Middle parts of large branches. Full sun, bark. Common. Erect, up to 50 cm. Pseudobulbs crowded, 5-10 cm, conical - ovoid, yellow, longitudinally wrinkled, with black transverse stripes. Leaves 4-6, in a dense tuft at the tip of the mature pseudobulb, lanceolate, up to 40 cm, thin, ribbed. Inflorescence from the base of the pseudobulb appearing before the leaves, 15-50 cm, paniculate. Flower small, yellow and brown. Jan.-Feb. The yellow pseudobulb, surrounded by a dense tuft of white erect aerial roots, makes identification easy even when leaves or inflorescences are missing. D.J. 722 (UPS). Fig. 61.

Habenaria Willd.
H. leonensis Dur. & Schinz
Guin., S.L., Lib., Iv.C.
Basal parts of large trees. Full sun - open shade, humus deposits. Rare. In the investigated area epiphytic, but in the grasslands of Guineean Nimba common as terrestrial. Erect, up to 30 cm high. Leaves 6-12 x 1-2.5 cm, narrowly lanceolate. Inflorescence with a few flowers. Flower white. July-Aug. In a sterile state hard to separate from other Habenarias. D.J. 580 (K, UPS).

H. procera (Sw.) Lindl.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
On trunks of trees, but more often of oil palms. Full sun - open shade, humus deposits. Rare. Erect, up to 60 cm high. Leaves lanceolate, 12-20 x 2-3.5 cm. Inflorescence densely flowered. Flowers white. July-Aug. In a sterile state hard to separate from other Habenarias. D.J. 595 (K, UPS).

Liparis L. C. Rich.
L. caillei Finet
Guin., S.L., Lib., N.Nig., Cam.
Basal parts of trunks. Open shade, humus deposits. Rare. Pendulous. A minute plant. Total size 3-6 cm, inflorescence excluded. Pseudobulb 12-20 mm, globose, green. Leaves 2-4 cm, ovate or lanceolate, green. Inflorescence 14-18 cm long, pendulous, rachis winged, many flowered. Flower pale yellow. June-July. The leaf and pseudobulb disappear among the debris in which the plant occurs. Even when flowering the inflorescence is hard to observe. D.J. 521 (UPS). Fig. 37.

L. nervosa (Thun.) Lindl.
Syn.: *L. guineensis* Lindl., and *L. rufina* (Ridl.) Rchb. f. ex Rolfe.
Sen., Port.G., Guin., S.L., Lib., Iv.C., Ghana, Dah., N.Nig., S.Nig., Cam., F.Po.
In the forest only as an epiphyte, elsewhere often terrestrial. In the lowest parts of trunks. Open shade - full sun, humus deposits. Rare. Erect, 15-25 cm. Stem with a ± swollen base. Leaves 5-20 cm, lanceolate, thin, with undulating margins, yellow-green. Inflorescence erect, longer than the leaves. Flowers yellow. July-Aug. D.J. 556 (K, UPS).

Listrostachys Rchb. f.
L. pertusa (Lindl.) Rchb. f.
S.L., Lib., Iv.C., Ghana, S.Nig.
Middle parts of large branches. Full sun - open shade, bark. Common. Erect, 15-25 cm. Leaves arranged in a fan-shaped manner on a short, woody stem, 15-20 x 1-2 cm, strap shaped, unequally bilobed at apex, leathery, v-shaped in cross-section. Inflorescence 10-25 cm long, often longer than the leaves. Flowers small, white, arranged in two dense rows along the rachis. Aug.-Sept. This plant is of a shape similar to *Aërangis laurentii* and *Rangaëris muscicola* but has much more fleshy leaves. D.J. 700 (K), 443 (UPS). Fig. 38.

Fig. 38. *Listrostachys pertusa.*

Nephrangis Summerh.
N. filiformis (Kraenzl.) Summerh.
Lib.
Middle or outer parts of large branches. Open shade - full sun, bark. Common. Erect when small, pendulous with increasing size, 30-40 cm. Stem slender, often branched. Leaves 2-8 cm long but only 1-2 mm broad, terete, much curved, acute. Inflorescence very short, few flowered. Flower small, with a white bilobed lip. April-May. Two other species have terete leaves: *T. tridentata* and *Angraecum subulatum.* The shape of the leaves separates it from *Tridactyle tridentata,* and the pendulous growth separates it from *Angraecum subulatum.* D.J. 529 (K, UPS). Fig. 59.

Plectrelminthus Rafin.
P. caudatus (Lindl.) Summerh.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Middle or outer parts of large branches. Full sun, bark. Rather common. Erect, stout, 20-30 cm. Stem short, woody. Leaves 10-30 cm, arranged in a fan-like manner, oblong or elliptical oblong, almost equally bilobed at apex. Inflorescence longer than the leaves, erect, rachis zigzag-shaped. Flowers large, white, spur long, spirally twisted. Large capsules. April-May (Oct.-Nov.). D.J. 650 (UPS). Fig. 39.

Podangis Schltr.
P. dactyloceras (Rchb. f.) Schltr.
Guin., S.L., Lib. (new), Ghana, N.Nig., S.Nig., Cam.
Middle parts of large branches. Full sun, bark - minor humus deposits. At altitudes above 800 m. Rare. Erect, 7-12 cm. Leaves in a fan-like arrangement on top of a short woody stem, 6-10 cm, lanceolate, fleshy, green. Inflorescence arises below the leaves, and does not exceed the leaves in length. Flowers 5-10, semi-transparent, white. Feb.-March. Can be mistaken for a *Bolusiella talbotii* or a *Rangaëris rhipsalisocia.* The first, however, has a long thin inflorescence that exceeds the length of the leaves, the latter has sickle-shaped leaves. D.J. 421 (UPS).

Fig. 39. *Plectrelminthus caudatus.*

Polystachya Hook.
P. adansoniae Rchb. f.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Middle or outer parts of large branches. Full sun, bark - minor humus deposits. Common. Erect, up to 20 cm high. Pseudobulb ellipsoid, 2-4 cm, light green. Leaves strap-shaped, 8-16 cm, light green. Flowers small, yellow, arranged in a spike. May-June. D.J. 485, 858 (K), 437 (UPS).

P. affinis Lindl.
Guin., S.L., Lib., Iv.C., Ghana, S.Nig.
More or less restricted to trunks. Open shade - full sun. Rather common. Growing in a vertical position on trunks. Pseudobulbs depressed, crowded, 2.5-4.5 cm in diameter, orbicular or broadly elliptical, green. Leaf 10-20 cm, oblanceolate, dark green. Leaf and paniculate inflorescence arching. Flower yellow with red markings. Jan-Feb. D.J. 450. (K, UPS).

P. dalzielii Summerh.
Guin., S.L., Lib., Iv.C.
Middle or outer parts of large branches. Full sun, minor humus deposits. At altitudes over 1000 m. Common. A small plant. Pseudobulb around 1 cm high, conical, very hard, green. Leaf 2-6 cm, ovate-lanceolate, thin, purplish-

Fig. 40. *Polystachya elastica.*

green. Inflorescence up to 15 cm high but usually less, rising from a leafless pseudobulb. Flower white - lilac. Feb.-March. Inconspicuous in a flowerless state. Wet roots in cross-section purple-coloured. *Polystachya pobeguinii, P. elastica* and *P. saccata* have leaves and pseudobulbs of similar shape and sizes. D.J. 420 (K, UPS).

P. elastica Lindl.
S.L., Lib.
Outer parts of large branches. Full sun, bark. Rare. Erect. Pseudobulbs crowded, 1-2 cm high. Leaves narrowly lanceolate 2-5 cm long. Inflorescence 5-15 cm, born on a leafless pseudobulb. Flower rose coloured. March-April. In a flowerless state similar to the more common *P. pobeguinii.* D.J. 741 (K), 753 (UPS). Fig. 40.

P. galeata (Sw.) Rchb. f.
Guin., S.L., Lib., Iv.C., S.Nig.
Middle and basal parts of large branches. Full sun - open shade, humus deposits. Common. Erect, 20-40 cm. Pseudobulbs crowded, 5-15 cm, narrowly cylindrical, green. Leaf 10-25 cm, at the apex of the pseudobulb, elliptical - oblong, fleshy, stiff, persistant for many years. Inflorescence erect, shorter than the leaf and pseudobulb. Flower large compared to most *Polystachya* species, yellow-green, with red or purplish markings. March-April. D.J. 429 (K, UPS).

P. laxiflora Lindl.
Guin., S.L., Lib., Iv.C., Ghana, Cam.
Basal parts of large branches. Open shade, humus deposits. Common at altitudes above 1000 m, lower down uncommon. A large erect plant, up to 50 cm. Pseudobulb narrowly cylindrical. Leaves 8-20 cm long, oblanceolate.

Fig. 41. *Polystachya laxiflora.*

Inflorescence either a spreading panicle with long slender branches or, especially at higher altitudes, branches reduced to short tufts. When flowering, a large drop of clear viscid fluid is often present below each bract. Flower white - yellow. Feb.-March. This species turns black when dried and pressed. D.J. 614, 740 (K), 704 (UPS). Fig. 41.

P. leonensis Rchb. f.
Guin., S.L., Lib., Iv.C., Cam.
On trunks, or in the basal and middle parts of large branches. Open shade, minor humus deposits. At altitudes above 1000 m. Common. Erect, 12-20 cm. Pseudobulbs crowded, 1 cm, conical, covered with sheets of old leaves. Leaves 8-20 cm, lanceolate or oblanceolate, thin, green, arranged in a fan-like manner. Inflorescence paniculate. Flowers yellow-green, lip white. Feb.-March. D.J. 423 (K), 739 (UPS).

P. microbambusa Kraenzl.
Guin., S.L., Lib., Iv.C.
On trunks. Full sun, minor humus deposits. At 1200-1300 m altitudes. Rare. Common on rocks in the grasslands of the Nimba Ridge in Guinea. Erect, 5-15 cm. Pseudobulb 1-1.5 cm, cylindrical, arising from upper part of the preceeding one. Leaves 2-4 cm, lanceolate. Flower small, yellow. Jan.-Feb. D.J. 459 a (UPS).

Fig. 42. *Polystachya polychaete.*

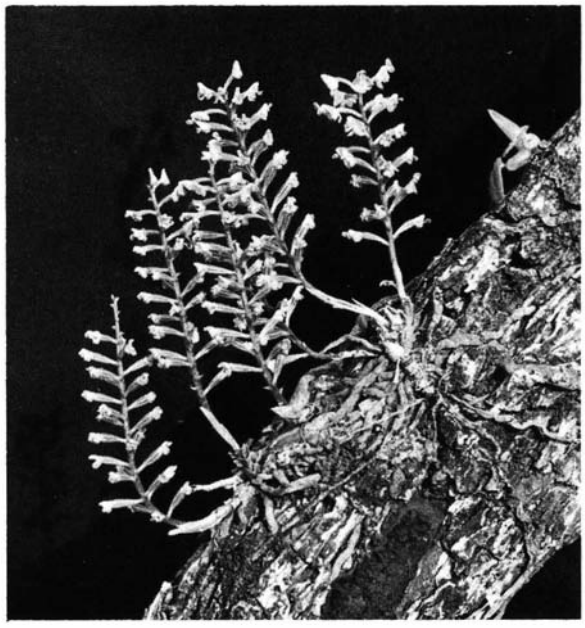


Fig. 43. *Polystachya saccata.*

P. obanensis Rendle
Lib., Iv.C., S.Nig.
Basal parts of large branches. Open shade, humus deposits. Rare. Erect, 10-20 cm. Pseudobulbs compressed, 2-4 cm, elliptical, shiny yellow, arranged in a more or less erect row, giving the impression that they are climbing on top of each other. Leaf 5-15 cm, oblong, green. One single leaf at the apex of the pseudobulb and two at the base. Inflorescence paniculate. Flower small, yellow. Scent strong, citrus-like. Sept.-Oct. D.J. 616 (K), 821 (UPS).

P. paniculata (Sw.) Rolfe
Guin., S.L., Lib., GHANAß S.Nig., Cam.
Middle parts of large branches. Full sun - open shade, bark. Common. Erect, 15-30 cm. Pseudobulbs 5-15 cm high, ellipsoid to long cylindrical, flattened, standing in a dense row, with the flattened sides towards each other, green with minute purple dots. Leaves 8-20 cm, oblong - elliptical, bluish green with a waxy layer above, purplish-green below. Flower small, orange with red markings. Oct.-Nov. D.J. 633 (K), 632 (UPS).

P. pobeguinii (Finet) Rolfe
Guin., S.L., Lib., Iv.C.
Middle parts of large branches. Open shade, humus deposits. Rare. A small plant. Pseudobulbs crowded, 0.5-1 cm, conical - ovoid, green and hard. Leaf 4-8 cm, oblong-lanceolate, green - purplish green. Inflorescence arising from a leafless pseudobulb. Flowering scape 7-15 cm long. Flowers rose or lilac, yellow hairs on the lip. Feb.-March. Inconspicuous in a flowerless state. The pseudobulb and leaves similar to those of *P. saccata* and *P. elastica.* When flowering the rose flowers attracts attention. D.J. 457 (K), 788 (UPS). Fig. 50.

P. polychaete Kraenzl.
S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Middle or basal parts of large branches. Full sun - open shade, humus deposits. Common. Erect, 15-30 cm high. Pseudobulbs 1-2 cm in cross-sect., thin, stem like, slightly inflated at the base. Leaf 8-25 cm, lanceolate - elliptic. Flowers small, arranged in a very dense simple raceme, creamy white. Oct.-Nov. D.J. 708 (K), 418 (UPS). Fig. 42.

P. puberula Lindl.
Port.G., Guinea, S.L., Lib., Iv.C.
Middle and outer parts of large branches. Full sun, minor humus deposits. Common. Erect, 30-40 cm high. Pseudobulbs crowded, 3-6 cm, conical, somewhat flattened, greenish-yellow with black transverse lines. Leaf 10-30 cm, oblanceolate - linear, thin, light green. Flowers small, yellow, in a rather large and loose panicle. May-June. D.J. 511 (K, UPS).

P. ramulosa Lindl.
S.L., Lib., Ghana, S.Nig.
On the lowest parts of trunks. Open shade, humus deposits. Rare. Erect, 5-10 cm. Pseudobulbs slightly swollen at the base. Leaf 4-8 cm, oblong - elliptical, dark green-somewhat purplish, often damaged by insects. Inflorescence much higher than the leaves. Flowers in a loose panicle, white, tinged with pink. June-July. D.J. 552 (K, UPS).

Fig. 44. *Polystachya tessallata* and *Platycerium stemaria.*

P. rhodoptera Rchb. f.
S.L., Lib., Iv.C., S.Nig.
Almost exclusively found on the lowest parts of trunks. Open shade, humus deposits. Rare. Erect, 20-40 cm high. Leaf 7-12 x 1 cm, narrowly lanceolate. Inflorescence somewhat branched. Flower pale rose. Sept.-Oct. Leaves held in a more or less vertical position. Empty capsules, 15-20 mm long, persist on the inflorescence for a year. D.J. 447 (K), 462 (UPS).

P. saccata (Finet) Rolfe
Port.G., Guin., Lib. (new), N.Nig.
This is one of the few species that frequently occur on the upper parts of trunks. Full sun - open shade, bark. Rather common. A minute plant. Pseudobulb 0.5 cm, conical, green. Leaf 2-5 cm, oblong - lanceolate, green - purplish green. Inflorescence 3-8 cm, arising from the leafless pseudobulb. Flower white and rose. Feb.-March. Inconspicuous in a flowerless state. Leaves and pseudobulbs similar to those of *P. pobeguinii* and *P. elastica.* D.J. 460 (K), 456 (UPS). Fig. 43.

P. subulata Finet
Guin., S.L., Lib. (new), Iv.C., N.Nig.
Middle or basal parts of large branches. Open shade, minor humus deposits. Rare. Erect, 12-25 cm high. Pseudobulb 5-8 cm high but less than 0.5 cm in cross-section, narrowly cylindrical, green. Leaf 6-10 cm, ligulate or oblanceolate, dark purplish-green. Inflorescence simple or seldom somewhat branched. Flower pale yellow-green with purple dots. Capsules large. June-July. D.J. 859 (K, UPS).

P. tenuissima Kraenzl.
Lib. (new), Iv.C., Ghana.
Middle parts of large branches. Full sun - open shade, bark - minor humus deposits. Rare. Erect, 10-20 cm. Pseudobulbs 2-6 cm, terete, green. Leaves terete, slightly falcate. Inflorescence paniculate. Flower minute, pale yellow. July-Aug. D.J. 657 (UPS).

Fig. 45. *Rangaëris brachyceras.*

P. tessallata Lindl.
Guin., S.L., Lib., Iv.C., Ghana, N.Nig., S.Nig., Cam.
Basal and middle parts of large branches. A tolerant species. Full sun - open shade, bark - large humus deposits. Common. Erect, up to 50 cm. Pseudobulb 1 cm, conical brown-yellow. Leaves 10-25 cm, oblanceolate or oblong-elliptic, dark green, often somewhat purplish. Inflorescences much longer than the leaves, somewhat branched, branches secund. Flower small, greenish-yellow with purple markings. May-June. D.J. 522 (K, UPS). Fig. 44.

Rangaëris Summerh.
R. brachyceras (Summerh.) Summerh.
Guin., S.L., Lib. (new), Iv.C., S.Nig.
Middle or outer parts of large branches. Full sun, minor humus deposits. At altitudes above 1200 m. Rare. Erect, 10-20 cm. Stem woody, short. Leaves in a fan-like arrangement, 6-16 x 1-2 cm, ligulate or slightly wider in the upper part, v-shaped in cross-section. Inflorescence longer than the leaves, slender. Flower pale, yellowish white. June-July. D.J. 594 (K). Fig. 45.

R. muscicola (Rchb. f.) Summerh.
Guin., S.L., Lib., Iv.C., S.Nig., Cam.
Middle parts of large branches. Full sun, bark. Common. Erect, 8-15 cm. Stem short, woody. Leaves 10-20 x 1-2 cm, v-shaped in cross-section. Inflorescence straight, longer than the leaves. Flower white, star-shaped, with a long spur. Capsules 3-5 cm long and narrow. June-July. This plant might be confused with *Aërangis laurentii,* which, however, has a zigzag inflorescence. D.J. 540 (K, UPS). Fig. 59.

R. rhipsalisocia (Rchb. f.) Summerh.
Sen., Guin., S.L., Lib., Iv.C., Ghana, S.Nig., Cam.
Middle or outer parts of large branches. Full sun, bark. Rare. Erect, 8-15 cm. Stem short, woody. Leaves arranged in a fan-shaped manner, 5-10 cm, fleshy, flattened, much curved, waxy, bluish green. Inflorescences longer than the leaves, stout. Flower white, rather small. Jan.-Feb. May resemble *Podangis dactyloceras* or *Bolusiella talbotii.* D.J. 724 (K, UPS).

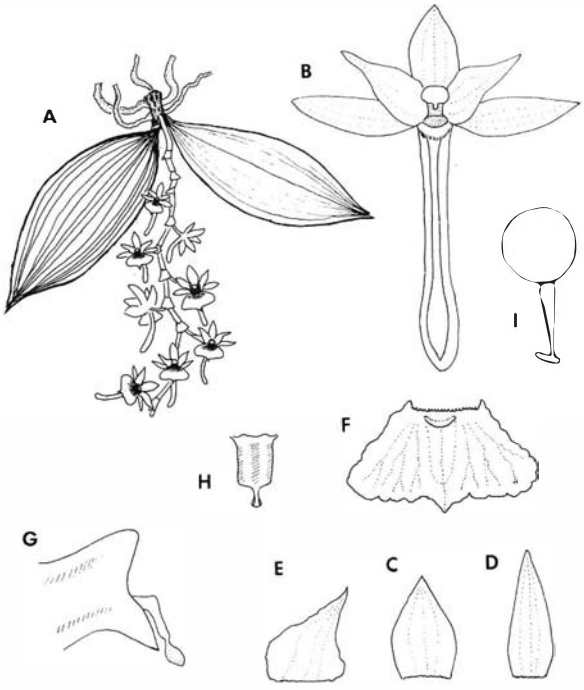


Fig. 46. *Rhipidoglossum paucifolium.* (A) Flowering plant, (B) Flower with lip removed, front view, (C) Dorsal sepal, (D) Lateral sepal, (E) Petal.(F) Lip, (G) Column with anther cap and pollinia removed, side view, (H) Rostellum, front view, (I) Pollinium. (From Johansson 1974.)

Rhipidoglossum Schltr.

R. paucifolium Dick Johanss.
Lib. (New).
Basal parts of large trees and on small trees and shrubs. Open shade, bark. Rare. Stem very short, with a very large root system. Leaves few, 4-6 x 1.5-2.0 cm, oblong-lanceolate. Inflorescences pendulous. Flowers crowded, semi-transparent, pale green. Aug.-Sept. This species is only known from the Nimba area (Johansson 1974). D.J. 572 (K, UPS). Fig. 46.

Stolzia Schltr.

S. repens (Rolfe) Summerh.
Lib. (new), S.Nig., Cam.
Middle or outer parts of large branches. Open shade - full sun, minor humus deposits. Rare. Prostrate. Pseudobulb clubshaped, looking like a swollen part of the rhizome. Leaves elliptical or nearly orbicular, two at each pseudobulb. Never seen flowering in the Nimba area. F.W.T.A. 1968, 3:1 describes the penduncle as stout,very short, flower small,orange, ochra-coloured or reddish. Its creeping habit makes it hard to detect. It can be mistaken for a *Peperomia rotundifolia,* since both grow in similar habitats. D.J. 604 (UPS).

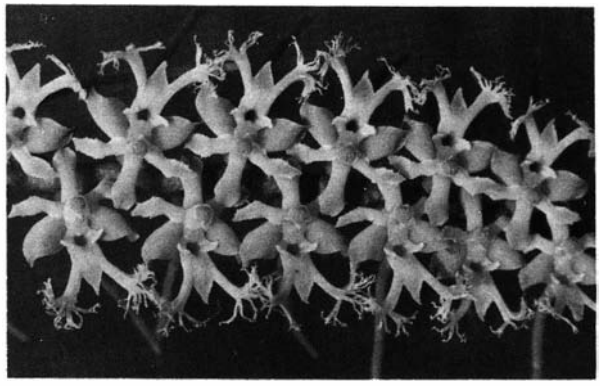


Fig. 47. *Tridactyle bicaudata.*

Tridactyle Schltr.

T. anthomaniaca (Rchb. f.) Summerh.
S.L., Lib., Iv.C., S.Nig., Cam.
Middle or outer parts of large branches. Full sun, bark. Common. Climbing or hanging. A rather large plant, branching in many directions. Stem stout, woody. Leaf 2-8 cm, oblong or elliptical oblong, broadly and obtusely bilobed at the apex, flat, somewhat fleshy but stiff, leathery. Inflorescences less than 0.5 cm, carrying 1-3 flowers. Flower small, yellow-brown. Oct.-Nov. D.J. 676 (K, UPS).

T. armeniaca (Lindl.) Schltr.
Guin., S.L., Lib., Ghana.
Basal parts of large branches. Open shade, bark - minor humus deposits. Common. Erect, often branching and creating dense 'stands'. Stem long, woody in the basal part. Leaf 5-12 x 1.0-1.5 cm, oblong - lanceolate, unequally bilobed at apex, flat, rather thin. Inflorescence mostly below the leaves. Flowers small, yellow or apricot. Feb.-March. *T. fusifera* Mansf. and *T. tridactylites* are vegetatively similar to this species. The first species has not been observed although F.W.T.A. 1968 3:1, gives two records from the Nimba area. The latter species only occurs at altitudes above 1000 m where *T. armeniaca* is rare. D.J. 452 (K, UPS).

T. bicaudata (Lindl.) Schltr.
S.L., Lib., Iv.C., Ghana, N.Nig.
Middle or basal parts of large branches. Open shade, bark - minor humus deposits. Rather common. Erect. 30-50 cm. Stem long, woody. Leaf 10-20 x 1-2 cm, narrowly ligulate, unequally bilobed. Inflorescence from the leaf axils or below the leaves. Flower pale yellow-orange. Oct.-Nov. Vegetatively similar to *T. armeniaca.* It is easy to identify by the very strong aromatic, somewhat vanilla-like scent that is emitted from the roots, particularly when the plant is pulled off it's substrate. D.J. 684 (UPS). Fig. 47.

T. crassifolia Summerh.
Lib. (new), Ghana.
On the trunk or anywhere on the large branches. Full sun, bark. Rare. Erect, or sometimes hanging, with a stout

woody stem. Leaf 3-8 x 0.6-1.0 cm, unequally bilobed, v-shaped in cross-section, the upper surface concave with a narrow groove along the centre, the lower surface convex, very fleshy, stiff. Surface waxy, bluish green. Inflorescences very short. Flowers greenish yellow. March-April. D.J. 695 (K).

T. tridactylites (Rolfe) Schltr.
Guin., S.L., Lib. (new), Iv.C., N.Nig., S.Nig., Cam., F.Po.
Basal or middle parts of large branches. Open shade, minor humus deposits. At altitudes above 1000 m. Common. Erect, often branching, forming large masses of growths. Stem woody. Leaves strap-shaped, distichous, deeply notched. Inflorescences short and few-flowered, in the lower leafless part of the stem. Flower yellow. Jan.-Feb. In vegetative parts similar to *T. armeniaca,* but has, however, never been observed at altitudes below 1000 m. The possible confusion of the two species is therefore limited to high altitudes. In observations of distribution (> 1000 m), *T. tridactylites* is considered the only species present. D.J. 726 (UPS). Fig. 86.

T. tridentata (Harv.) Schltr.
Guin., S.L., Lib. (new), Ghana.
Middle or outer parts of large branches. Full sun, bark. Rather common. Pendulous, 30-50 cm. Leaves 6-10 x 0.1-0.3 cm in cross-section, terete, distichous, with a shallow groove running along their entire length. Inflorescence short, few-flowered. Flower pale yellowish. Aug.-Sept. This species can be confused with *Nephrangis filiformis* which, however, has leaves that are shorter and markedly falcate. D.J. 591 (K, UPS). Fig. 59.

Vanilla Mill.
V. crenulata Rolfe
Guin., S.L., Lib., Iv.C., Ghana, S.Nig.
Climbs the basal parts of the trunks. Open shade, large humus deposits. Rare. Climber. Sizes up to three meters in length have been observed. Stem slender. Leaf 5-10 cm, oblong - elliptical, waxy, yellow-green. Inflorescence a long hanging raceme. Flowers large, white or yellow with purple markings on the lip. July-Aug. In a flowerless state this species is difficult to differentiate from *Vanilla africana* Lindl. D.J. 723 (K, UPS). Fig. 51.

Other vascular epiphytes

Begonia L. (Begoniaceae)
B. mannii Hook.
S.L., Lib. S.Nig., Cam., F.Po.
Basal part of large branches. Open shade, humus deposits. Rare. D.J. 551 (K, UPS).

B. polygonoides Hook. f.
Guin., Lib., Iv.C., S.Nig., Cam.
Basal parts of large branches. Heavy - open shade, humus deposits. Rather common. D.J. 545 (K) 735 (UPS).

B. rubro-marginata Gilg.
Lib. (new), Cam.
Basal or middle parts of large branches. Open shade - full sun, humus deposits. Common. D.J. 736 (K), 733 (UPS). Fig. 65.

Fig. 48. Left: A strangling fig. (*Ficus anomani*) established as an epiphyte in the crown of a palm. Later it will send roots to the ground and continue as an independent plant. Nimba Range 600 m. Right: A strangling fig when the roots have reached the ground. The original phorophyte is dead and has left a hollow formed by the decayed trunk.

Calvoa Hook. f. (Melastomataceae)
C. monticola A. Chev. ex Hutch. & Dalz.
Guin, S.L., Lib., Iv.C.
The lowest parts of the trunks. Heavy shade, humus deposits. Common. D.J. 785 (K, UPS).

C. trochainii Jac.-Fél.
Guin., Lib.
Basal parts of trunks or middle parts of large branches. Open shade, minor humus deposits. Common. D.J. 573 (UPS).

Medinilla Gaud. (Melastomataceae)
M. mannii Hook. f.
Lib., F.Po.
Middle or basal parts of large branches. Open shade, humus deposits. At altitudes above 1000 m, often solitary. At lower altitudes, often associated with *Drynaria laurentii*. Common. D.J. 725 (UPS).

Peperomia Ruizd & Pav. (Piperaceae)
P. fernandopoiana C. DC.
Guin., Lib., Iv.C., S.Nig., Cam., F.Po.
In all sections of the phorophyte in a wide range of habitats. Common. D.J. 475 (UPS).

P. molleri C. DC.
Lib., Ghana, Togo, S.Nig., Cam., F.Po.
Basal parts of trunks. In heavy shade, minor humus deposits. Rare. D.J. 882 (K).

P. rotundifolia (L) H.B. & K.
S.L., Lib., Iv.C., Ghana, Togo, Cam.
Basal or middle parts of large branches. Open shade, humus deposits. Rather common. D.J. 498 (UPS). Fig. 59.

Preussiella Gilg. (Melastomataceae)
P. chevalieri Jac.-Fél.
Guin., Lib., Iv.C.
Basal parts of large branches. Open shade, humus deposits. Rather common. D.J. 785 (K).

P. kamerunensis Gilg.
Lib., Cam.
Basal parts of large branches. Open shade, humus deposits. At altitudes above 1000 m. Rare. D.J. 824 (K).

Remusatia Schott. (Araceae)
R. vivipara (Roxb.) Schott.
Guin., S.L., Lib., Iv.C., Cam.
Basal parts of large branches or trunks. Open shade, large humus deposits. Rare. D.J. 491 (K).

Rhipsalis Gaertn. (Cactaceae)
R. baccifera (J. Mill.) W.T. Stearn
S.L., Lib., Iv.C., Ghana, S.Nig., Cam., F.Po.
Middle or outer parts of branches. Full sun - open shade, bark or minor humus deposits. Common. D.J. 793 (UPS). Fig. 59.

Table 7. Facultative epiphytes and filmy ferns in the Nimba area.

FACULTATIVE EPIPHYTES

Pteridophytes
Asplenium variable Hook var. variable
Bolbitis fluviatilis (Hook.) Ching
Bolbitis salicina (Hook.) Ching
Lygodium smithianum Presl ex Kuhn
Pityrogramma calomelanos (L.) Link
Selaginella blepharophylla Alston
Selaginella molleri Hieron.
Selaginella myosurus (Sw.) Alston
Selaginella versicolor Spring
Selaginella zechii Hieron.

Other vascular epiphytes
Araceae
Cersestis afzelii Schott
Culcasia angolensis Welw. ex Schott
Culcasia liberica N.E.Br.
Raphidophora africana N.E.Br.

Begoniaceae
Begonia oxyloba Welw. ex Hook.
Begonia quadrialata Warb.

Melastomataceae
Tristemma incompletum Benth.

Moraceae
Ficus anomani Hutch. (Fig. 48)
Ficus kamerunensis Warb. ex Mildbr. & Burret.
Ficus leprieurii Miq.
Ficus sagittifolia Warb. ex Mildbr. & Burret.

Urticaceae
Urera oblongifolia Benth.
Urera rigida (Benth.) Keay

FILMY FERNS
Hymenophyllum kuhnii C.Chr.
Trichomanes africanum Christ
Trichomanes chamaedrys Tanton
Trichomanes erosum Willd.
Trichomanes guineense Afzel. ex Sw.
Trichomanes mannii Hook.

III. Biology of vascular epiphytes

Reproduction biology

Flowering periods of orchids

The flowering periods are of particular interest since they may indicate an interbreeding barrier between closely allied species.

The general pattern in the flowering of the orchids is presented in two-month-periods for the year 1969 (Fig. 49). Two flowering peaks are easily noticed. In his studies of the Nigerian rain forests Richards (1939) found this bimodal culmination of flowering to be a general rule for the vegetation. A similar pattern in flowering times of West African orchids is reported by Sanford (1971:166): "Casually, the two blooming peaks seem to follow the long and short dry seasons. Such coincidence has probably lead to the belief that dry seasons trigger flowering in trees (see Ashton 1969) . . ., however, there is no evidence for orchids that it is either the dry season or the following moisture that actually induces flowering." (Cf. Arditti 1966.)

The genera *Bulbophyllum* and *Polystachya,* accounting for about half of the number of species, show a marked difference in their blooming peaks (Fig. 49). The Polystachyas have the most frequent blooming late in the dry season or early in the rainy season, while the Bulbophyllums have a very pronounced peak during the end of the rainy season.

Most of the *Bulbophyllum* species flower on mature shoots, e.g. at the end of the rainy season. *Bulbophyllum winkleri* and *B. oreonastes* are two exceptions. They flower on new growths early in the growing season.

Among the Polystachyas that flower during the dry season there are four species bearing their flowers on leafless pseudobulbs (Curtis 1943), viz. *P. dalzielii, P. elastica, P. pobeguinii,* and *P. saccata.* At the end of the rainy season in Nov.-Dec. the

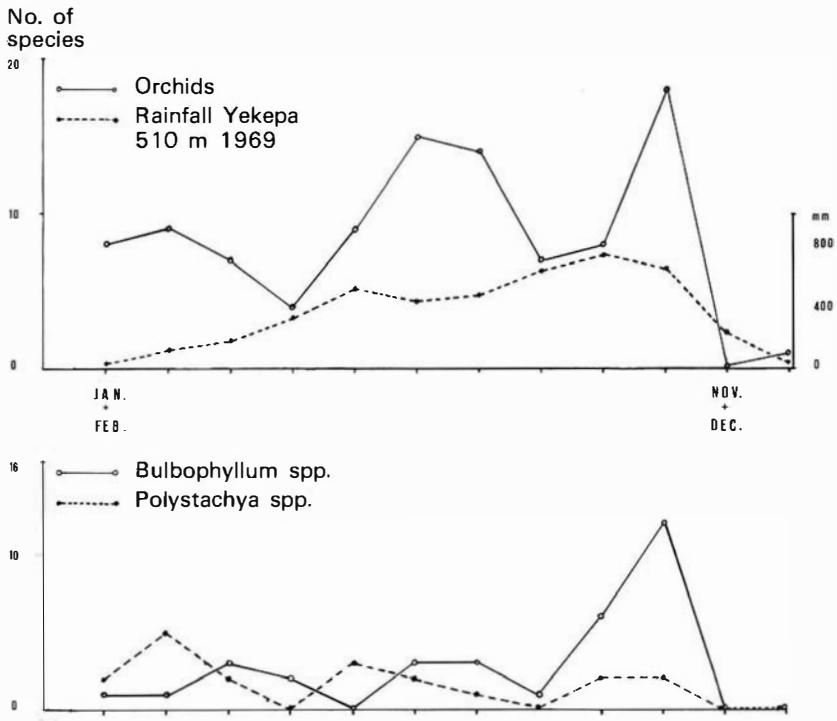


Fig. 49. Flowering periods. Upper figure: Total number of flowering orchids in two-month-periods during a year in relation to the rain fall. Lower figure: Number of flowering species of the genera *Bulbophyllum* and *Polystachya.*

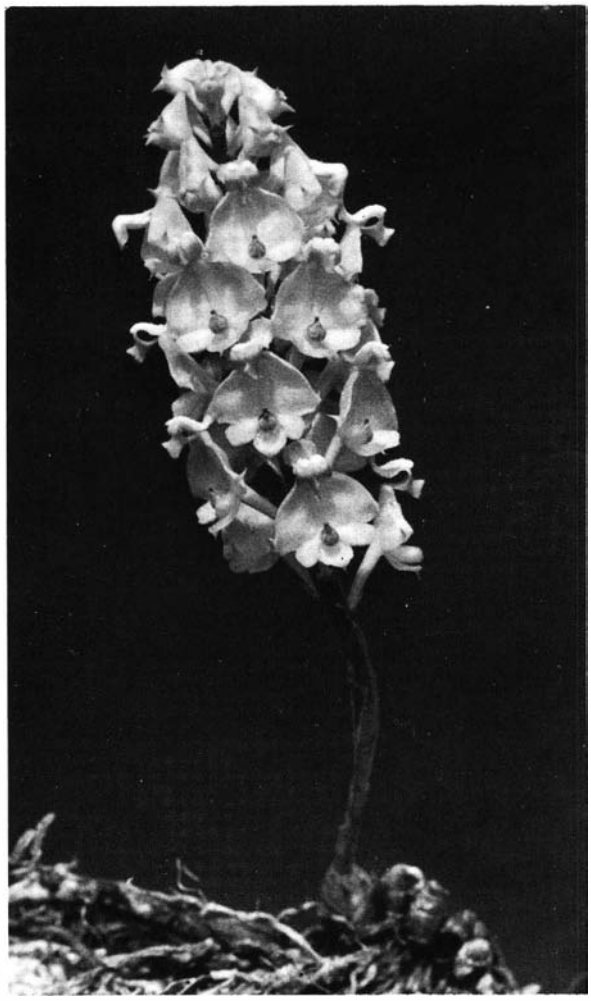


Fig. 50. *Polystachya pobeguinii.*

leaves are shed, and the plant seemingly disappears since the pseudobulbs are very small (less than one centimeter) and the root system is hidden in cracks in the bark or covered by debris, lichens and mosses. Thus when the inflorescence appears one gets the impression that it is growing straight out of the bark (Fig. 50).

It is evident that the species of some genera flower during a limited period of the year, while others have a more prolonged flowering time. The six species of the genus *Angraecum* flower in the middle of the rainy season. In July all of them flower simultaneously. In August the four *Diaphananthe* species have a similar synchronous blooming time. The genus *Tridactyle,* on the other hand, includes species that flower during every month of the year. The many closely allied species especially in the

Fig. 51. *Vanilla crenulata.*

genus *Bulbophyllum* which flower simultaneously favour the possibilities of hybridization.

There are also examples of closely related species with different flowering times e.g. *Calyptrochilum emarginatum* and *C. christyanum.* These grow in the same habitat under non-limiting conditions (as in the Nimba area), but there are considerable intervals between their flowering periods.

Observations of orchid pollination

Since in sexual flowering plants pollination is a prerequisite for the seed formation, any limitation in this process will effect the total number of seeds. However, among the angiospermous epiphytes of Nimba all species seem to be pollinated with one exception. *Vanilla crenulata* has never been observed with capsules. Two plants of this species which were observed during three years produced a large number of flowers each year (Fig. 51) but no signs of pollination were noted. The flowers simply wilted away after the anthesis. No actual observation of the pollinators of any *Vanilla* species seems to exist, even if various insects and hummingbirds are said to participate in the process (Childers et al. 1959:483). The possibility of the *Vanilla* species being autogamous has also been considered (Van der Pijl

Table 8. Insects caught on orchid flowers cultivated in Yekepa.

Orchid	Insects frequently visiting the flower
Bulbophyllum buntingii	Syntomis sp.
Bulbophyllum calamarium	Trigona sp.
Bulbophyllum schinzianum	Polybiodes tabida (Tab.), Polistes marginalis (Tab.)
Cyrtorchis aschersonii	Bradylema sp., Gabonia nudeus (Weise)
Diaphananthe pellucida	Euchromia lethe (F.)
Polystachya pobeguinii	Trigona sp.
Tridactyle tridentata	Gabonia nudeus (Weise)

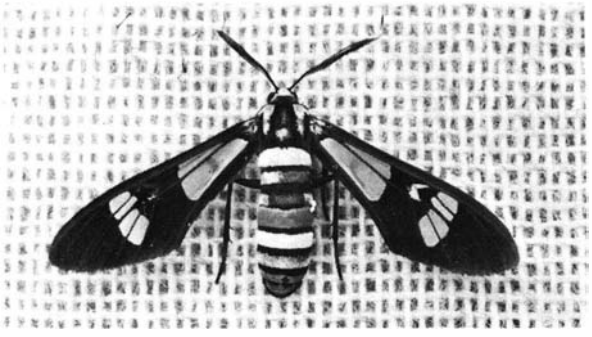


Fig. 52. *Euchromia lethe.*

& Dodson 1969:125). Whether insufficient pollination is a limiting factor to this species is hard to tell from the few observations available.

A list of some insect species caught visiting orchid flowers at Yekepa is given in Table 8. If all of these insects are effective in the pollination process is doubtful, but two of them, *Euchromia lethe* (Fig. 52) and *Polybiodes tabida* were observed with pollinia attached to them from the orchids visited.

Diaspore size and dispersal

Judged by the types of diaspores (Table 9) among the epiphytes one may assume that the dispersal is mostly done by wind (cf. Oliver 1930, Curtis 1933). The seeds of the Peperomias and *Rhipsalis baccifera,* which have fleshy fruits said to be edible (Moreau 1935:20), are probably dispersed by animals (Fig. 55).

Orchid seeds are usually small, reduced, and very numerous. One seed weighs from 0.3 to 14 µg (Arditti 1967:3). Ames (1946) estimated the number of seeds to 3,770,000 in one single capsule of *Cynoches chlorochilon.* The sizes of the orchid seeds of the species in the Nimba area varies generally between 100-400 µm. Particularly small seeds were found in *Angraecum classensii* (15-50 µm) and *A. podochiloides* (20-50 µm). *Bulbophyllum* seeds are between 100-250 µm in size, and among the *Polystachya* species between 200-400 µm. Particularly large seeds are noticed for *Liparis nervosa* (500-660 µm) a species of the lower parts of the trunks. Fern spores are in general considerably smaller than orchid seeds, e.g. *Drynaria laurentii* (40 µm) and *Asplenium barteri* (40-50 µm).

Table 9. Diaspores of the epiphytes in the Nimba area.

Diaspores	No. of species Total	%	Categories
Minute spores	39	25.5	Pteridophytes
Minute seeds	109	71.2	Orchidaceae, Melastomataceae, Begoniaceae
Seeds with viscid coating	1	0.7	Cactaceae
Fleshy fruits	4	2.6	Araceae, Piperaceae

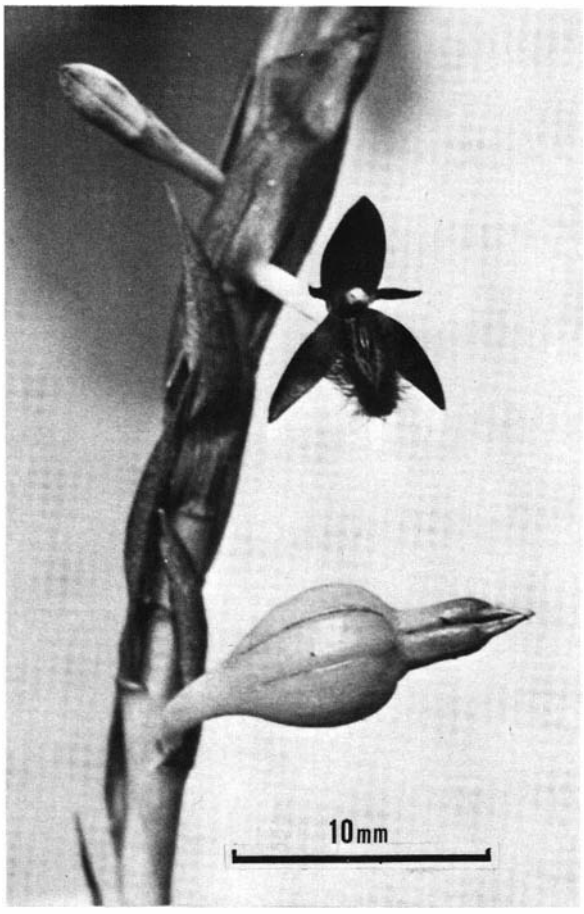


Fig. 53. Capsule, flower and bud of *Bulbophyllum schinzianum.* Several orchids open their flowers singularly or a few at a time. This may favour the possibility of pollination by insects.

Germination and establishment

After the diaspore has reached the phorophyte the germination and further development may be inhibited for several reasons. The dryness of the substrate can be assumed to be a usual reason for such a failure. However, there are some reports that other properties of the bark may prevent germination. The influence of the substrate on the epiphyte flora will be discussed more specifically in chapter V. A list of factors that might influence the germination of orchid seeds has been presented by Arditti (1967).

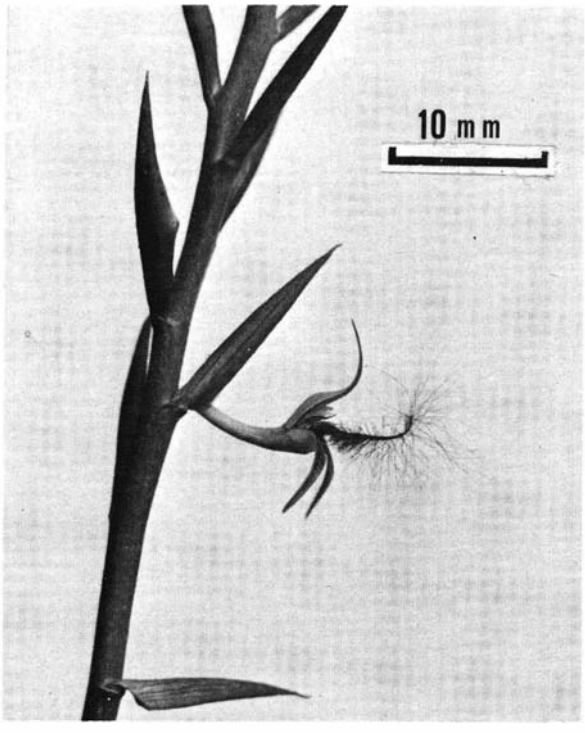


Fig. 54. *Bulbophyllum phaeopogon.* The hairy lip is mobile in a vertical direction and the slightest breeze will initiate a movement.

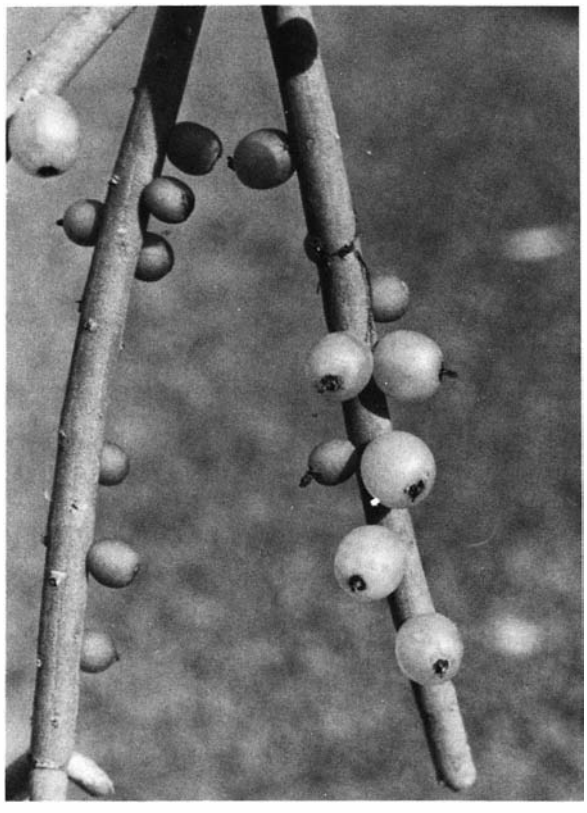


Fig. 55. *Rhipsalis baccifera* with berries, each holding a large number of small seeds.

The seeds of the orchids are dependent on certain mycorrhizal fungi for their development (Heagarty 1955, Arditti et al. 1972), although it is possible to grow them asymbiotically in vitro (Knudson 1922, Burgeff 1936, 1959). Thus, the presence of these fungi on the phorophyte is a prerequisite for the establishment of orchids (Withner 1959:317).

All the fungi belong to the Hymenomycetes. The majority are members of the imperfect genus *Rhizoctonia,* and as such are probably haploid mycelia of Corticiae (Burgeff 1959:376).

Rhizoctonias are present in all green orchids. No specific relation between fungus species and orchid host seems to exist (Curtis 1939). The possibility for orchid seeds to be inoculated with mycorrhizal fungi in the early stages of germination at a temporary resting place, e.g. at the root system of the mother plant, and then blown to a final resting place, has been suggested (Ames 1922). Ames considers the slow germination of the orchid seeds to be of advantage, increasing their possibilities to get in contact with the fungi. "If orchid seeds germinated quickly and gained weight rapidly, if the embryo immediately put forth roots and in a brief time secured a firm hold on the substratum, the likelihood of dispersal after the entrance of the mycorrhizal fungi would be diminished and opportunities for successful dispersal severely limited." (Ames 1922:232.)

The disadvantage for the seed in becoming a little heavier with their fungal freight is regarded to be of little importance. More critical is desiccation, but experiments with *Goodyera pubescens* R. Br. showed that the seeds in their early stages of germination easily could withstand a journey of twenty to thirty miles without lethal desiccation.

Life forms

The many strange life forms among epiphytes attracted attention early (Goebel 1888, Schimper 1888, Karsten 1895, 1925). A life form system has been created by Hosokawa (1943, 1949, 1955). Objections towards this system have been raised by Holtum (1960). In a dense forest a general pattern can be observed. The epiphytes of the lowest parts of the trees are living under rather constant conditions

Fig. 56. *Asplenium nidus* is an exceptionally large epiphyte. The fronds may reach a length of two metres. Amani 950 m, Usambara Mts, Tanzania.

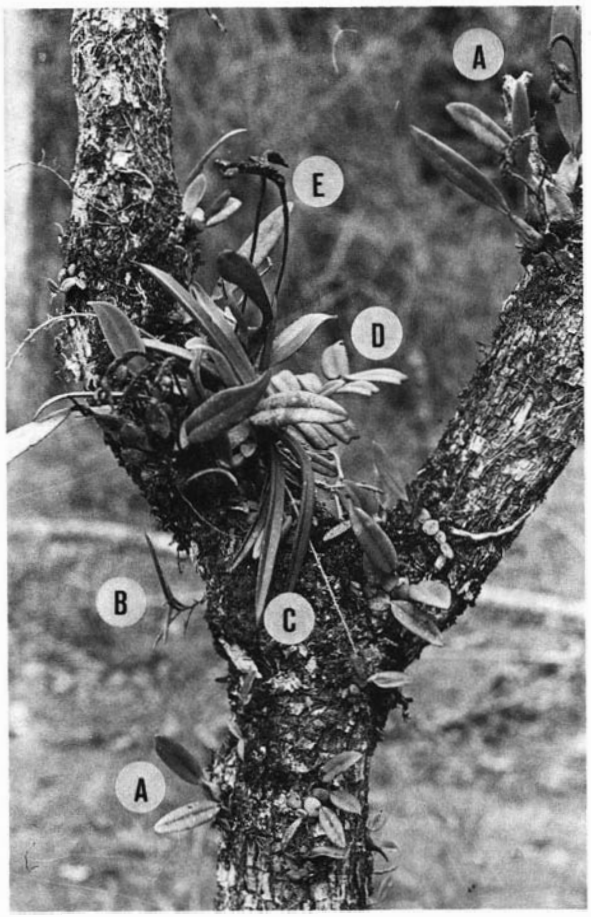


Fig. 57. Xeromorphic epiphytes on the outer part of a branch of *Lophira alata.* Nimba Range 600 m. (A) *Bulbophyllum schimperanum,* (B) *Nephrangis filiformis,* (C) *Chamaeangis vesicata,* (D) *Tridactyle anthomaniaca,* (E) *Bulbophyllum linderi.*

of humidity. There is little need for adaptations against desiccation (Fig. 56).

The filmy ferns, *Trichomanes* and *Hymenophyllum* that are common on the lowest parts of trunks, represent the most drought-sensitive epiphytes. Higher up on the trees the epiphytes with somewhat fleshy leaves establish themselves. A reduction of transpiration surface compared to the volume of the plant can also be observed. In more exposed habitats, the size and total number of leaves are reduced (Fig. 57).

The common *Bulbophyllum* species have only one or two leaves with the basal part of the leaf developed into a pseudobulb (Fig. 58). Xeromorphic structures e.g. succulent and terete leaves are common in the most exposed habitats (Fig. 59).

The number of stomata and their distribution on the leaves may also be of adaptative importance. A study of several orchids (Table 12) revealed that the stomata in general are located on the lower side of the leaves. The highest number of stomata per sq. mm (108) was observed for *Plectrelminthus caudatus,* which grows in exposed habitats, while the lowest number was found in *Habenaria leonensis* from a more protected habitat. However, *Aërangis laurentii,* which occurs in the same habitat as *Plectrelminthus caudatus,* has only about half the number of stomata per sq. mm of the latter. From this scanty material it is hard to draw any conclusion, but the number of stomata may well prove to be of minor importance as an environmental adaptation.

Drought tolerant and drought avoidant epiphytes

One may divide the epiphytes into two major groups, the drought tolerant and the drought avoidant (cf. Jarvis & Jarvis 1963). The shape and texture of the leaves often indicate to which group a certain species

Fig. 58. *Bulbophyllum congolanum.*

belongs. The leaves of the drought avoidant epiphytes, being deciduous, are not adapted to survive the dry season. Examples of such plants are the ferns *Davallia chaerophylloides, Drynaria laurentii,* and *Nephrolepis undulata.* Among the orchids the species belonging to the genera *Brachycorythis, Graphorchis, Habenaria,* and *Liparis* are all deciduous, as well as many Polystachyas. *Begonia rubro-marginata* and *Remusatia vivipara* also exhibit this adaptation.

The drought tolerant epiphytes often have a reduced number of leaves, e.g. *Eurychone rothschildiana;* succulent leaves, e.g. *Microsorium punctatum, Angraecum distichum, Peperomia rotundifolia;* or terete leaves, e.g. *Angraecum subulatum, Nephrangis filiformis, Tridactyle tridentata.*

The combination of few and succulent leaves are exemplified by *Bolusiella talbotii* and *Rangaëris rhipsalisocia. Rhipsalis baccifera* represents the stem succulents.

Sympodial and monopodial growth

The two largest orchid genera, *Bulbophyllum* and *Polystachya,* have sympodial growth. This means that the plants develop a shoot which is limited in apical growth. Thus the development of pseudobulbs and leaves takes place during the wet season, each shoot terminating in an inflorescence. The following wet season a new shoot will appear. This growth form is generally considered to be favourable for epiphytes (Holtum 1960) apart from giving them an indefinite length of life. (The Botanical Gardens of Copenhagen have a living plant of *Oncidium sphacelatum* from Mexico, which has been in cultivation for 127 years, Anonymus:1968.)

One should expect that among the orchids with sympodial growth there would be no need of advanced adaptations towards desiccation. It is therefore somewhat surprising to find advanced adaptation against drought among e.g. the *Bulbophyllum* species. The Polystachyas give examples of leaves that have no adaptations and are deciduous, e.g. *P. puberula,* as well as succulent leaves that remain on the pseudobulb during the dry season, e.g. *P. tenuissima.* Whether or not these succulent leaves remaining on the plant during the dry season are an asset or liability in the survival of the new shoot is hard to tell. They naturally lose water through transpiration, but their photosynthetic activity is difficult to estimate. Thus the adaptations against drought among the sympodials could be considered as much an adjustment to drought periods of varying length during the wet season as an adjustment to the dry season proper.

The orchids with monopodial growth, where each stem has an indefinite apical growth, are subject to a more serious threat to desiccation, since they keep their leaves during the dry season. Holtum (1960) states that monopodial orchids are therefore found mainly in regions which have no long dry season.

In the Nimba area there are 60 species of sympodial orchids compared to 41 monopodial species.

Water economy

Water uptake

Most of the substrates used by epiphytes have a limited storage capacity for water. This means that the epiphytes themselves must be able to effect a rapid water uptake during the limited period when

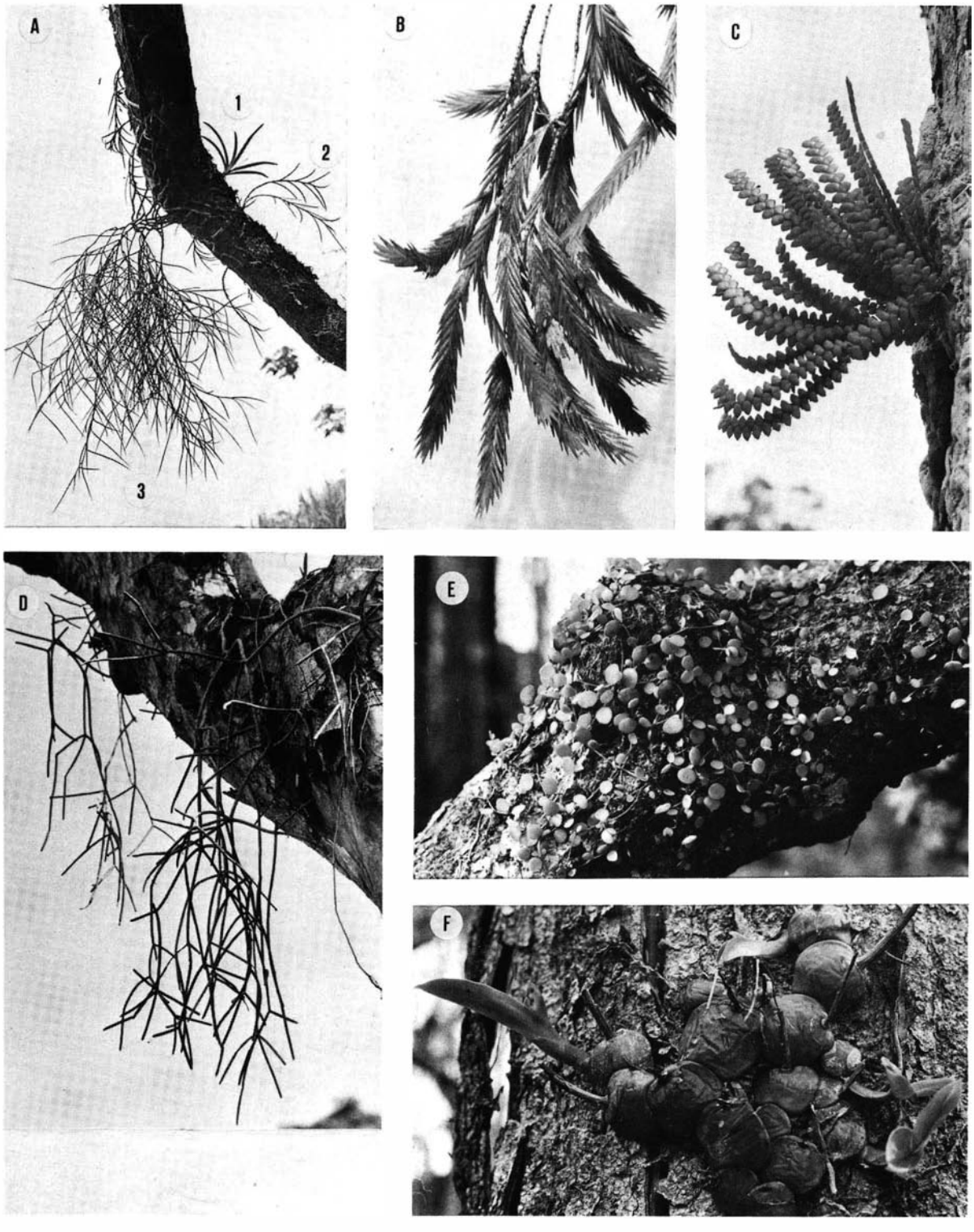


Fig. 59. Life forms of some epiphytes. (A) 1. *Rangaëris muscicola*, 2. *Nephrangis filiformis*, 3. *Tridactyle tridentata*, (B) *Angraecum podochiloides*, (C) *A. distichum*, (D) *Rhipsalis baccifera*, (E) *Peperomia rotundifolia*, (F) *Polystachya affinis*.

Fig. 60. Roots of *Aërangis laurentii.*

Fig. 61. *Graphorchis lurida,* aerial roots in the fore ground. Yekepa 500 m.

the substrate is wet, or collect the water in small pools between the leaves (tank or cistern epiphytes among many bromeliads of the Americas). Water absorbed in humus may also serve as a water supply (Fig. 113).

The osmotic potential of epiphytes seem to be high (Harris 1918, 1934, Blum 1933). Walter (1971:136-137) found that orchids with tubers had a value of −2.0 bar. Somewhat lower values (−4.7 to −6.7 bar), were found in orchids without tubers and the lowest values were found among epiphytic ferns (−9.1 to −33.7 bar).

Non-vascular epiphytes such as mosses and lichens are well known for their rapid water uptake. Indirectly their moisture holding capacity may be of importance for the vascular epiphytes. The filmy ferns have a water uptake similar to the mosses.

The roots of epiphytic orchids exhibit several specialized features in their morphology and anatomy. The aerial roots are surrounded with a white, papery or spongy layer of dead cells called the velamen. Went (1940:91) claims that the velamen has an important role in the uptake of water and mineral nutrients: "Es ist nun klar, dass das Velamen sich direkt mit dem ersten mineralreichen Sickerwasser füllt . . ." Dycus and Knudson (1957) found that the uptake of water was approximately equal to the rate of water lost by evaporation in the aerial roots of orchids. The absorption was equivalent to that required to saturate the velamen (cf. Wallach 1939). Condensation of water vapor by living roots could not be proved. If condensation did occur, it was so limited in comparison to the evaporation that it could not be detected. The principal roles of the velamen in free aerial roots were considered to be a mechanical protection and the prevention of an excess loss of water from the cortex. Goebel (1922) reports that roots of *Epidendron nocturnum* that had their velamen carefully removed, lost 20 % of their water content in 24 hrs as compared to a 7 % loss by roots with their velamen untouched.

However, when an aerial root comes in contact with a solid surface the velamen cells at the point of attachment become markedly modified. Certain salts are absorbed by the modified part of the root and

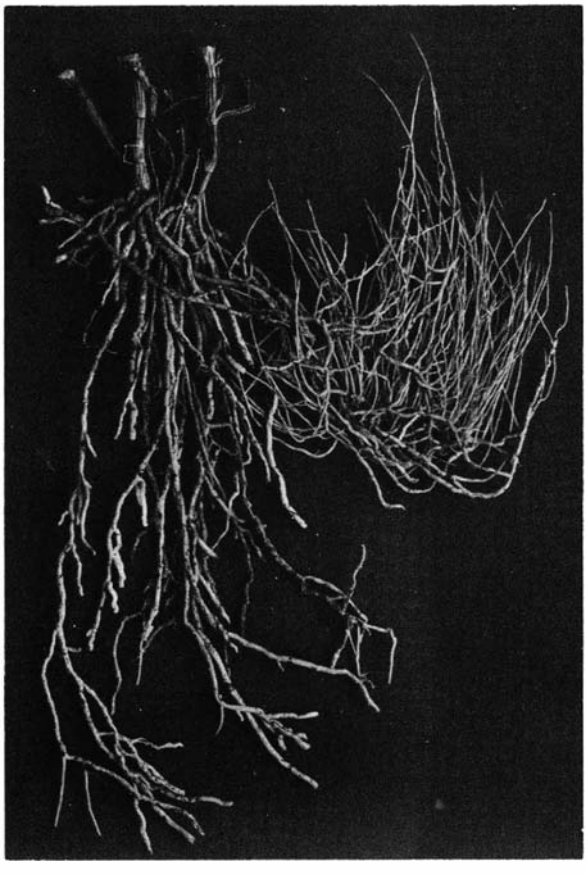


Fig. 62. Root system of *Ansellia africana* (D.J. 412 UPS).

may enter the cortex. (Dycus & Knudson 1957.)

In the Nimba area the velamen is particularly well developed among the species that grow in exposed positions on substrates with insignificant amounts of humus depostis, e.g. *Aërangis laurentii* (Fig. 60), *Plectrelminthus caudatus,* and *Rangaëris rhipsalisocia.* A conspicuous habit of the aerial roots is exhibited by *Ansellia africana* and *Graphorchis lurida* (Fig. 61).

From the "normal" aerial roots attached to the substrate numerous negatively geotropic roots arise (Fig. 62). These erect roots which are covered with velamen form a dense 'tussock'. No function has been shown for these erect roots, although Sanford (quoted from Sanford & Adanlawo 1973) suggested that they might be advantageous in catching and holding organic debris.

Very recently an anatomical study of the erect roots of *Ansellia africana* (Sanford & Adanlawo 1973:312) showed that the exodermal cells have very little thickening of their walls. The authors consider it very probable that these roots are more permeable than the others and so may have a special absorptive function. The geographical distribution of these two orchids (Fig. 63), (*Ansellia africana* occurs in deciduous forest or wooded grasslands and *Graphorchis lurida* in exposed habitats in dry and wet forest types), might also indicate that such roots may participate in the water uptake. The existence of these roots greatly increases the surface area of the root system towards the air. Water vapour might condensate on the roots during the night and then be transferred to the living tissues of the plants. This could be one explanation to the occurrence of these two species in dry habitats. Incidentally, *Ansellia gigantea* (Fig. 102), which is closely related to *A. africana,* occurs in (for epiphytes) extremely dry habitats in East Africa (Piers 1968:158).

Storage of water

By comparing the total weight of various organs and their water content the distribution of water in the plant may be obtained. In most cases it is very difficult to remove the total root system, which naturally limits the use and exactness of this method. Another problem is that the variation in water content during the year may be unproportional between various parts of the plants. This method, however, will give an idea of what part of the plant holds the bulk of the water (cf. Gessner 1956). The water con-

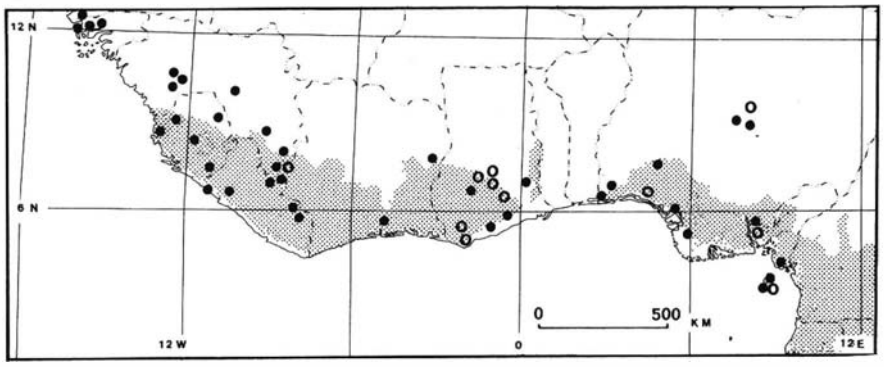


Fig. 63. Records of *Ansellia africana* (○), and *Graphorchis lurida* (●) in West Africa.

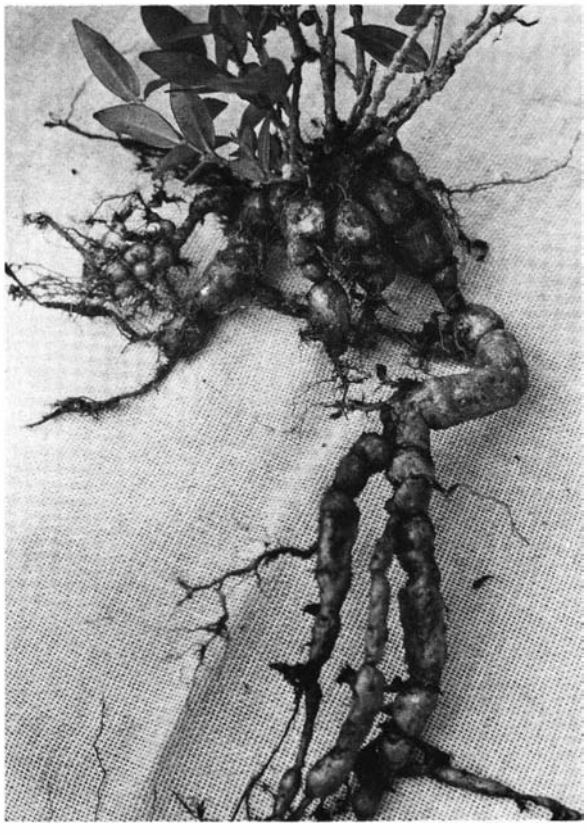


Fig. 64. *Medinilla mannii*. Collected from a *Drynaria laurentii* - *Asplenium megalura* epiphyte community. Nimba Range 700 m.

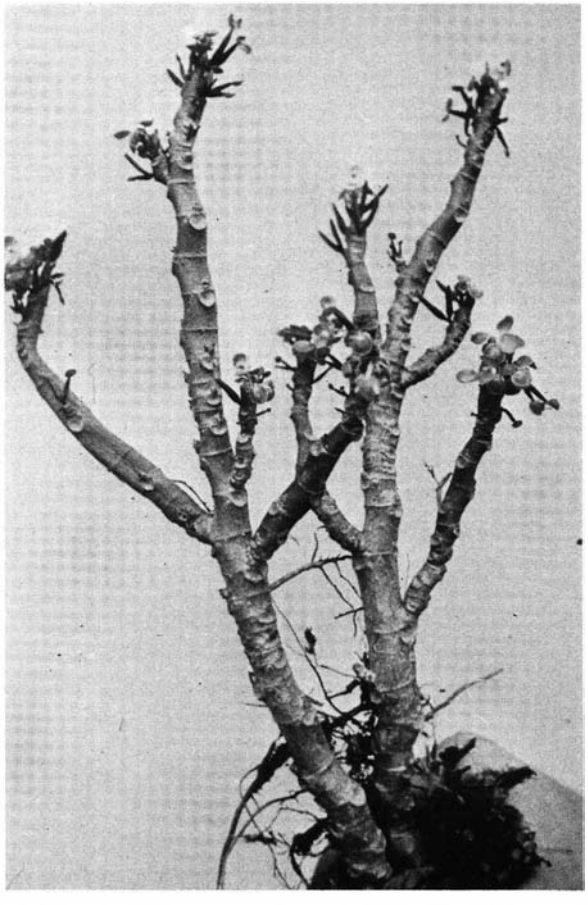


Fig. 65. *Begonia rubro-marginata* exemplifies stem succulence among the epiphytes. Grassfield, december 1964.

tent is determined as the difference in weight between the fresh weight and the dry weight (24 hrs in 105°C) expressed as percentage of the fresh weight.

The figures presented refer to the mean of five separate investigations of the species concerned.

In the root system

Some epiphytes with a large root system compared to the stem and leaves, e.g. *Medinilla mannii* (Fig. 64) naturally hold a major part of the water in the roots. Orchids with a proportionally large volume of the water supply in the roots are e.g. *Plectrelminthus caudatus* and *Tridactyle armeniaca* (Table 10).

Table 10. Water content in different parts of some orchids as a percentage of the total water content in the plant. Mean of five samples.

	Root	Stem	Leaves
Calyptrochilum christyanum	29.9	10.2	59.9
Plectrelminthus caudatus	72.0	1.2	26.8
Tridactyle armeniaca	70.7	6.5	22.8

Bulb-like tubers occur on *Medinilla mannii* and *Remusatia vivipara*. Small bulbs are frequently found on the roots of *Nephrolepis undulata;* their function is unknown.

In the stem

As a rule the stem and rhizomes of most epiphytic orchids are woody and hold only minor amounts of the water supply. *Ansellia africana,* with its spindle-shaped stem is an exception. *Begonia rubro-marginata* (Fig. 65) and *Rhipsalis baccifera* are good examples of stem succulence. The rhizome of certain ferns is utilized for water storage, e.g. *Drynaria laurentii* which holds 85.4 % of the total water content in the roots + rhizome (7.4 % and 7.2 % respectively in the fertile and sterile leaves).

In the leaves

The *Bulbophyllum* orchids have a part of the leaf developed into a pseudobulb which is built up by

Table 11. Water content in different parts of some Bulbophyllum species as a percentage of the total water content in the plant. Mean of five samples.

	Root + rhizome	Leaf proper	Pseudo-bulb
Bulbophyllum cocoinum	7.9	29.3	62.8
Bulbophyllum congolanum	13.9	34.1	52.0
Bulbophyllum winkleri	3.5	31.9	64.6

water holding tissues. The proportions between the water in the anatomical leaf (leaf proper + pseudobulb) and the rest of the plant were roughly 9:1 for three species examined (Table 11).

The fleshy leaves of *Calyptrochilum christyanum* hold approximately 60 % of the total water content of this species (Table 10). The Peperomias have fleshy leaves, particularly *Peperomia rotundifolia* (Fig. 59). Due to a poorly developed root system and a thin trailing stem the plant appears to consist mainly of the discoid leaves.

Expenditure of water

The transpiration of epiphytic orchids was found to be low by Kamerling (1912). It was for some time thereafter assumed that this was a typical feature for epiphytic plants. Later, Spanner (1939) showed that certain epiphytes, e.g. *Myrmecodia,* have high transpiration rates, and the opinion was established that the epiphytes, as most other ecological groups, provide examples of great variation in transpiration rates. Short period transpiration tests by Coutinho in a virgin forest in Brazil, quoted from Walter (1971:135-136), gave very low transpiration rates for orchids and bromeliads.

Coutinho (1964) also observed the 'De Saussure effect', i.e. the absorption of atmospheric CO_2 during the night and its assimilation in daylight, in epiphytic bromeliads and orchids. Similar observations in fleshy orchid leaves have been reported by Arditti & Dueker (1968:866).

The 'true' transpiration value is rather difficult to obtain and this requires extensive instrumentation. When the aim is to establish transpiration differences between various species simpler methods can be used.

In this study the detached leaf method, or quick weigh technique, was used (Iwanoff 1928, Stocker 1929, Willis & Jefferies 1963, Swanson & Lee 1966, Rutter et al. 1963). This method is based upon the observation that a leaf will temporarily continue its transpiration after it has been detached. This transpiration is noticed as a decrease in weight.

Loss in weight of plant material is often regarded as a measure of water loss, since changes in water content involve greater weight changes in the plant

Table 12. Transpiration rates and some records of stomata numbers in the detached leaves of some epiphytes. The transpiration rates are given as the loss of weight per hour in percentage of the fresh weight. All figures refer to the mean of five samples.

Species	No. of stomata per sq. mm Upper epidermis	Lower epidermis	Transpiration rates
Polystachya dalzielii	0	70	20.0
Graphorchis lurida	0	72	11.2
Polystachya puberula	0	58	11.2
Asplenium geppii	–	–	10.7
Polystachya leonensis	0	82	8.6
Begonia rubro-marginata	–	–	6.9
Medinilla mannii	–	–	6.7
Preussiella chevalieri	–	–	6.3
Arthropteris orientalis	–	–	5.6
Ancistrochilus rothschildianus	0	52	5.5
Brachycorythis kalbreyeri	0	52	6.3
Polystachya affinis	0	66	4.9
Drynaria laurentii (fertile leaf)	–	–	4.5
Nephrolepis undulata	–	–	4.2
Tridactyle tridactylites	12	52	3.7
Elaphoglossum isabelense	–	–	3.5
Phymatodes scolopendria	–	–	2.9
Plectrelminthus caudatus	0	104	2.9
Polystachya rhodoptera	0	62	2.8
Oleandra distenta	–	–	2.4
Angraecum subulatum	–	–	2.3
Microsorium punctatum	–	–	2.0
Aërangis laurentii	0	58	1.7
Angraecum distichum	–	–	1.5
Polystachya laxiflora	–	–	1.4
Habenaria leonensis	0	34	1.0
Rhipsalis baccifera (stem)	–	–	1.0
Listrostachys pertusa	–	–	0.9
Cyrtorchis arcuata	–	–	0.8
Angraecum podochiloides	0	66	0.7
Diaphananthe pellucida	0	42	0.7
Diaphananthe bidens	0	56	0.6
Tridactyle anthomaniaca	10	60	0.6
Bulbophyllum linderi	0	46	0.5
Bulbophyllum winkleri	–	–	0.4
Bulbophyllum saltatorium	12	48	0.4
Bulbophyllum bufo	8	70	0.4
Bolusiella talbotii	–	–	0.3
Chamaeangis vesicata	–	–	0.3
Nephrangis filiformis	–	–	0.3
Calyptrochilum christyanum	–	–	0.3

than do changes in the content of any other substances present. The transpiration rate at the time of cutting the leaf may be obtained by extrapolation from the values in weight decrease during the first three minutes. The effects of abscission and placing the leaf in a different environment for the weighing make the accuracy of the result questionable (Iwanoff 1928, Rufelt 1963, Willis et al. 1963). But to the extent that these effects are similar for different species, the method is valuable as an indexing technique (Kochenderfer & Lee 1973:177).

Since the transpiration rate is influenced by the temperature, relative humidity and even time of day, all results given refer to a vapour pressure deficit (V.P.D.) of 20-25 mb. The experiments were carried out in daylight in the afternoon (14^{00}-16^{00}).

After detachment the scar at the base of the leaf was sealed with nail-varnish. The leaf was then placed on a torsion balance (sensitive to 0.1 mg) and the decrease in weight during the first three minutes was recorded. The values given refer to extrapolations of these recordings.

The water loss may be given as the rate of transpiration compared to the weight of the leaf (Table 12). Three species of orchids (*Polystachya dalzielii, Graphorchis lurida* and *Polystachya puberula*) showed a loss of more than 10 % of their fresh weight per hour. During the dry season with non-existent rainfall and the substrate drying up, it is impossible to maintain such a rate of transpiration and these three species are all deciduous.

Polystachya dalzielii which showed the highest rate of transpiration grow on the highest, cool and mist-swept parts of the range, an environment that helps to keep the transpiration low.

It is more difficult to understand how *Graphorchis lurida* is able to replace the heavy water losses, since it occurs in very exposed habitats, mostly on bark, which naturally can only supply a very limited amount of water. The special root system, previously discussed, may well be the answer to the ability of this species to maintain its water balance.

Table 13. Transpiration rates in the detached leaves of some orchids. Given as the loss of weight per hour in percentage of the fresh weight, and in absolute figures (g/dm²/hr).

Species	Transpiration (water loss)	
	% of fresh weight/hr	g/dm²/hr
Graphorchis lurida	11.21	0.14
Bulbophyllum linderi	0.72	0.08
Bulbophyllum winkleri	0.41	0.05
Calyptrochilum emarginatum	0.36	0.04
Diaphananthe pellucida	0.66	0.03
Cyrtorchis arcuata	0.56	0.02

The high transpiration rates of *Polystachya puberula* that occurs on more humid substrates is less surprising. The leaves are very thin and lack visible adaptations towards desiccation.

Ferns from humid environments could naturally be expected to have high transpiration rates, as found for *Asplenium geppii.*

Three orchid species showed rates of 5-10 %. *Polystachya leonensis* occurs at the same altitudes as *P. dalzielii,* while the two others, *Brachycorythis kalbreyeri* and *Ancistrochilus rothschildianus,* belong to moist, drought-protected habitat. *Begonia rubro-marginata, Preussiella chevalieri* and *Medinilla mannii* also belong to this group. All these species are deciduous. Transpiration rates below 1.0 % have only been found among the orchids, even if *Rhipsalis baccifera* is close (1.0 %).

Particularly the orchids with a monopodial growth, i.e. that keep their leaves during the dry season, exhibit low transpiration values, e.g. *Bolusiella talbotii, Calyptrochilum christyanum, Chamaeangis vesicata* and *Nephrangis filiformis.*

Transpiration can also be given in absolute figures, e.g. as g/dm²/hr (Table 13). This method also results in the lowest transpiration rates for the xeromorphic types of monopodial orchids, e.g. *Cyrtorchis arcuata, Diaphananthe pellucida,* and *Calyptrochilum emarginatum.*

IV. The occurrence of epiphytes

Epiphytes on forest trees

The occurrence of epiphytes in a particular region has been expressed in several ways:

1. Total number of epiphytic species in the region as documented from floras or extensive collections.
2. The quotient between the number of epiphytes and the number of other vascular plants.
3. Percentage of trees of a certain minimum height carrying epiphytes.
4. Highest total number of epiphytic species on one tree.
5. Number of individuals ('stands') of epiphytic species on one tree.

Combinations between these methods have often been used.

1. Total number of epiphytic species known

In the area investigated a total of 101 epiphytic orchid species were recorded. From Nimba Range outside Liberia Schnell (1952:530-534) recorded 27 species of epiphytic orchids which probably represent less than 25 % of the total number. It is significant that Schnell only observed four *Bulbophyllum* species (versus 32 in this study). Most members of this genus are concealed in the crowns of the tallest trees and are not likely to be found, except when specifically sought for. One of the few reports of this kind from Africa refers to the Budongo rain forest in Uganda (Eggeling 1947:55-56): "Excluding hemi-epiphytic figs nearly one hundred species of vascular epiphytes have been collected from Budongo." This method is reliable only in regions where the flora is very well-known. With rare exceptions it is not useful in the tropics.

2. Quotient epiphytes/other vascular plants

The presence of epiphytes may also be expressed as a comparison to the non-epiphytic plants. Hosokawa (1943, 1950) has introduced this method, called the Epiphyte quotient (Ep.Q.), which is simply the quotient between the number of species of 'Epiphyta typica' (Table 1) and the number of species of all vascular plants. A similar quotient called 'l'indice épiphytique' has been used by Schnell (1952:338). In the Nimba Mts outside Liberia the figures from the mountain forest (forêt montagnardes) are given as 0.31-0.33 compared to 0.04-0.16 for the forests at the base of the mountains (forêts inférieurs). The results received with this method are dependent on knowledge of the entire flora in a certain area. As stated earlier the epiphytic flora tends to be underestimated, which limits the credibility of this method.

3. Percentage of tall trees carrying epiphytes

High forest

In the Nimba area the percentage of trees in high forest that carried epiphytes was investigated in three sample plots (clear-felling plots according to Richards' terminology, 1939:19). Each plot was 50 m long and 15 m wide. To simplify the recording, trees smaller than ten meters were excluded since they seldom carry epiphytes. The plots were surveyed in advance, involving the limitation, marking and numbering of the trees. Each of the trees 10 m or higher was drawn on a sketch figure at its proper place along the profile (Figs. 66, 67, 68). The crowns have been drawn as if they were compact. This is seldom the case. After the trees had been felled the size of the trunk and the crown were recorded with a measuring tape.

In these three plots the felling of the trees was done for other purposes than vegetation studies. This meant that once the felling operation started, it continued with high speed and therefore limited the time available for the examination of the phorophytes. The marking of the trees is very important since in all three cases trees outside the sample strips were also felled. The trees fell in various directions, knocking down parts of branches from one another and often ending up on top of each other on the ground.

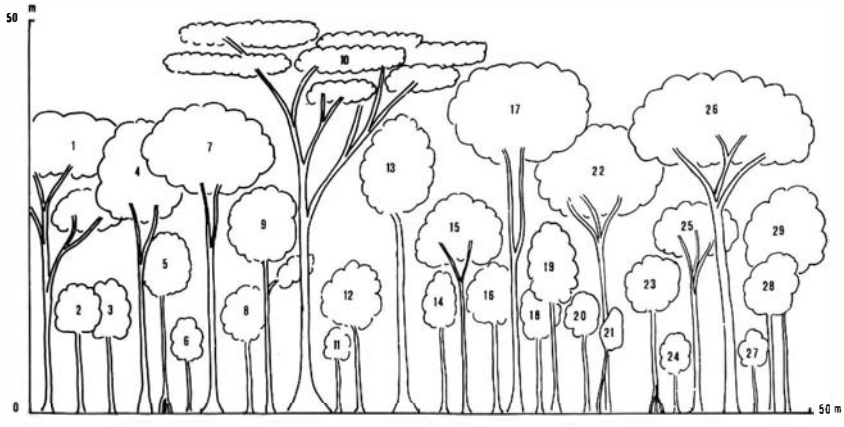


Fig. 66. Sample plot I. (See text.) Profile diagram representing a 50 m long and 15 m wide strip of the forest. Trees < 10 m are excluded. The figures refer to Table 14.

Table 14. Occurence of epiphytes on the trees (10 m or taller) in sample plot 1. The number mark the position of the tree in the profile diagram (Fig. 66).

Species of tree	No.	Height (m)	No. of species			
			Pteridophytes	Orchids	Others	Total
Piptadeniastrum africanum	1	38	1	1	–	2
Chlorophora regia	2	17	–	–	–	–
Chlorophora regia	3	17	–	–	–	–
Lophira alata	4	37	3	4	1	8
Heritiera utilis	5	23	6	1	–	7
Piptadeniastrum africanum	6	13	–	–	–	–
Lophira alata	7	39	4	4	2	10
Heritiera utilis	8	26	2	–	1	3
Mitragyna ciliata	9	29	5	3	2	10
Piptadeniastrum africanum	10	50	4	7	1	12
Parinari excelsa	11	11	–	–	–	–
Parinari excelsa	12	19	3	1	1	5
Nauclea diderrichii	13	38	6	4	1	11
Calpocalyx aubrevillei	14	18	–	–	1	1
Erythrophleum ivorense	15	28	3	3	1	7
Piptadeniastrum africanum	16	19	–	–	–	–
Lophira alata	17	44	2	3	1	6
Calpocalyx aubrevillei	18	16	–	–	–	–
Calpocalyx aubrevillei	19	25	–	–	2	2
Erythrophleum ivorense	20	15	1	2	1	4
Chidlowia sanguinea	21	13	–	–	–	–
Parinari excelsa	22	37	9	4	4	17
Uapaca guineensis	23	20	2	2	2	6
Heritiera utilis	24	10	–	–	–	–
Chlorophora regia	25	26	1	–	1	2
Parinari excelsa	26	43	9	8	5	22
Chidlowia sanguinea	27	10	–	–	–	–
Calpocalyx aubrevillei	28	21	2	–	2	4
Parkia bicolor	29	29	2	–	–	2
Total	29		11	22	4	37

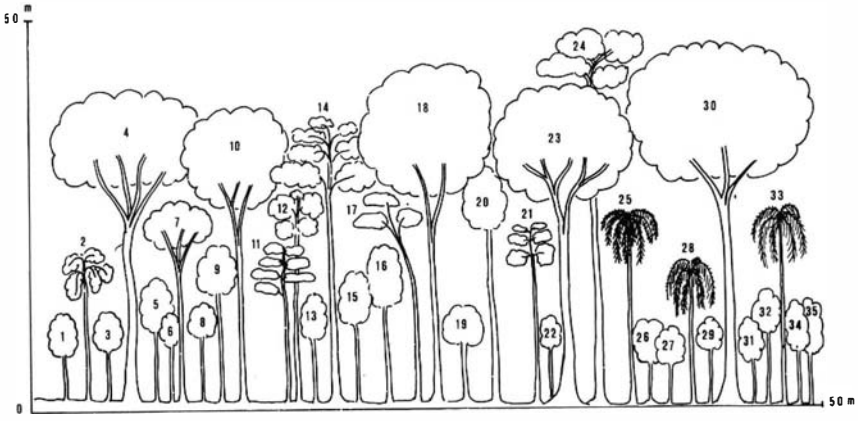


Fig. 67. Sample plot II. (See text.) Profile diagram representing a 50 m long and 15 m wide strip of the forest. Trees < 10 m are excluded. The figures refer to Table 15.

Table 15. Occurrence of epiphytes on the trees (10 m or taller) in sample plot II. The number mark the position of the tree in the profile diagram (Fig. 67).

Species of tree	No.	Height (m)	No. of species			
			Pteridophytes	Orchids	Others	Total
Anthocleista nobilis	1	12	–	–	–	–
Pycnanthus angolensis	2	19	–	–	–	–
Anthocleista nobilis	3	12	–	–	–	–
Parinari excelsa	4	39	6	7	2	15
Parinari excelsa	5	16	–	–	–	–
Chidlowia sanguinea	6	12	–	–	–	–
Heritiera utilis	7	35	2	1	–	3
Chidlowia sanguinea	8	13	–	–	2	2
Heritiera utilis	9	21	2	–	–	2
Lophira alata	13	38	6	5	1	12
Terminalia ivorensis	11	20	–	–	–	–
Fagara tessmannii	12	26	–	–	–	–
Klainedoxa gabonensis	13	14	–	–	–	–
Terminalia ivorensis	14	37	–	–	–	–
Lophira alata	15	17	–	–	–	–
Calpocalyx aubrevillei	16	20	–	1	1	2
Piptadeniastrum africanum	17	27	–	–	–	–
Lophira alata	18	43	3	9	3	15
Parinari glabra	19	13	–	–	1	1
Heritiera utilis	20	31	–	1	–	1
Alstonia boonei	21	23	–	–	–	–
Calpocalyx aubrevillei	22	11	–	–	–	–
Parkia bicolor	23	42	2	–	–	2
Fagara tessmannii	24	45	–	–	–	–
Elaeis guineensis	25	25	4	–	–	4
Lophira alata	26	11	–	–	–	–
Lophira alata	27	10	–	–	–	–
Elaeis guineensis	28	18	3	–	–	3
Anthocleista nobilis	29	12	–	–	–	–
Chlorophora regia	30	46	5	–	6	11
Antiaris toxicaria	31	11	–	–	–	–
Anthonotha fragrans	32	15	2	2	–	4
Elaeis guineensis	33	25	3	–	–	3
Chlorophora regia	34	14	–	–	–	–
Chlorophora regia	35	14	–	–	–	–
Total	35		14	19	4	37

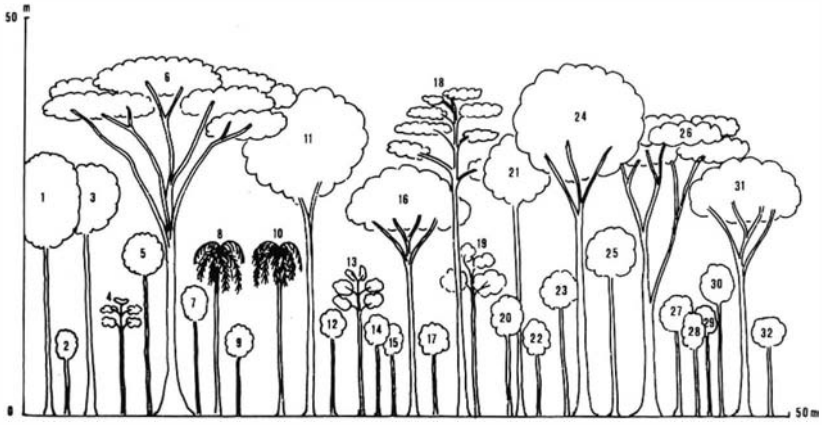


Fig. 68. Sample plot III. (See text.) Profile diagram representing a 50 m long and 15 m wide strip of the forest. Trees < 10 m are excluded. The figures refer to Table 16.

Table 16. Occurrence of epiphytes on the trees (10 m or more) in sample plot III. The number mark the position of the tree in the profile diagram (Fig. 68).

Species of tree	No.	Height (m)	No. of species			
			Pteridophytes	Orchids	Others	Total
Cryptosepalum tetraphyllum	1	33	2	3	–	5
Albizia zygia	2	11	–	–	–	–
Cryptosepalum tetraphyllum	3	32	2	3	–	5
Terminalia ivorensis	4	15	–	–	–	–
Triplochiton scleroxylon	5	23	1	–	–	1
Piptadeniastrum africanum	6	45	6	8	–	14
Anthocleista nobilis	7	16	–	–	–	–
Elaeis guineensis	8	23	5	–	–	5
Anthocleista nobilis	9	12	–	–	–	–
Elaeis guineensis	10	23	4	–	1	5
Lophira alata	11	42	3	7	3	13
Lophira alata	12	14	–	–	–	–
Terminalia ivorensis	13	19	–	–	–	–
Pentadesma butyracea	14	13	–	–	–	–
Lophira alata	15	12	–	–	–	–
Parinari excelsa	16	32	9	4	5	18
Calpocalyx aubrevillei	17	12	–	–	2	2
Terminalia ivorensis	18	42	–	–	–	–
Piptadeniastrum africanum	19	22	–	–	–	–
Lophira alata	20	16	–	–	–	–
Cryptosepalum tetraphyllum	21	36	3	3	1	7
Coula edulis	22	13	1	–	1	2
Heritiera utilis	23	18	2	–	–	2
Lophira alata	24	45	7	7	3	17
Canarium schweinfurthii	25	24	–	–	–	–
Piptadeniastrum africanum	26	38	1	2	–	3
Cryptosepalum tetraphyllum	27	15	–	–	–	–
Cryptosepalum tetraphyllum	28	13	–	–	–	–
Cryptosepalum tetraphyllum	29	14	–	–	–	–
Cryptosepalum tetraphyllum	30	19	–	–	–	–
Parinari excelsa	31	33	6	8	4	18
Parinari excelsa	32	12	–	–	–	–
Total	32		12	26	6	44

The plots were situated on level ground and on well-drained soils. It is doubtful if any of these forests are so called primary, i.e. untouched by human activities. However, they represent the highest and oldest sections of forest at this level. In any case the dominance of *Piptadeniastrum africanum, Lophira alata, Parinari excelsa* and *Heritiera utilis* in the plots corresponds very well with their presence in well-drained forest in the whole area investigated. Almost no terrestrial herbs occurred in any of the plots. The trees and shrubs below 10 m height consisted of straight poles with small, thinly foliated crowns.

The first plot (Fig. 66) was located 5.5 km SW of Grassfield at approximately 500 m altitude. This plot is close to the areas surveyed by Adam (1969) and Gorgla (1969) (see chapter I). The plot examined went through a section of high and dense forest that was surrounded by patches of forest of lesser height.

The second plot (Fig. 67) was situated 1 km east of the water purification plant in Yekepa, not far from the river Yah, at approximately 600 m altitude. This section of the forest was rather rich in oil palms (*Elaeis guineensis)* and Terminalias. The presence of several trees common to secondary forest, e.g. *Pycnanthus angolensis* and *Fagara tessmannii,* might suggest recent human influence.

The third plot (Fig. 68) was located 3 km NW of Zulowie in the foothills of Mt Tokadeh at roughly 500 m altitude. This forest was not as dense as the two others. More light penetrated through the canopy and small-sized shrubs and trees were more numerous.

On the average every second tree ten m or higher carried epiphytes (Tables 14-17).

Secondary forest

A survey by telescope (distance observation) was undertaken in a secondary forest, east of the Grassfield airstrip in Nimba. A total of twenty-seven trees in sizes from 10-29 m were studied. The presence of a high number of pteridophytes compared to the number of orchid species was observed. The quotient between pteridophytes and orchids was 3:1 as compared to 1:2 in the high forest (Table 17).

There are few remarks in the literature on epiphytes in secondary or degraded forests. Eggeling (1947:56) gives some interesting figures from Uganda. In a colonizing, secondary forest (*Maeopsis)* 11.7 % of the trees bore epiphytes of 14 species. In an older secondary forest ('mixed') 16.3 % of the trees carried epiphytes of 25 species, while in a primary or climatic climax 'Ironwood' forest, 22.7 % of the trees were colonized by epiphytes of 35 species. In this steady rise of both the occurrence and the number of species from the colonizing forest to the climatic climax forest, some interesting details can be noticed. Nearly the whole increase in the number of epiphytic species between the 'mixed' and the 'Ironwood' forests can be traced back to the increase of the orchid species in the latter. In the mixed forest there were 15 species of orchids constituting 60 % of the epiphytic flora, while in the climax forest there were 24 species (68 %). There were even fewer species of ferns in the Ironwood forest than in the mixed forest, seven compared to eight.

Table 17. Occurrence of epiphytes on phorophytes (10 m or taller) in high and secondary forest. (High forest figures from Tables 14, 15 and 16.)

Forest type	No.of trees	Trees with epiph. %	No. of epiphyte species			
			Pterid.	Orch.	Others	Total
High						
I	29	62.1	11	22	4	37
II	35	40.0	14	19	4	37
III	32	50.0	12	26	6	44
Total	96	52.1	19	38	8	65
Secondary	27	14.8	9	3	1	13

Results from the use of this method, either as an indication of the occurrence of epiphytes or as a characterization of the vegetation, are available from several places (Table 18).

The method is an approximate one that preferably can be used when the determination of species is difficult, or there is a shortage of time. It may refer to investigations made on felled trees, or in more open and low-growing forest types to trees standing. The accuracy is in the latter case naturally somewhat lower. It must be observed that the minimum of height of the trees that are included in the study is of utmost importance. The smaller the trees included in the study the lower will be the percentage of trees with epiphytes observed. The minimum height must be adapted to the structure of the forest investigated, a fact that makes comparisons between different areas hard to achieve (Grubb et al. 1963:592).

4. Highest number of epiphytic species on one tree

The highest number of epiphytes on one tree in the

Table 18. Aspects on the presence and abundance of epiphytes as reported from various parts of the world.

Country and author	Min. height of trees being considered	Total no. of trees being considered	% of trees with vasc. epiphytes	Max. no. of ep. on any one tree	Total no. of ep. in the area (est.)
Nigeria. (Richards, 1939)	15 ft	67	15	13	35
Nigeria. (Richards, 1939)	15 ft	75	24	13	35
Uganda. (Eggeling, 1947)	15 ft	44	22.7	26	100
Sarawak. (Richards, 1932)	25 ft	91	13	—	—
Sarawak. (Richards, 1932)	25 ft	44	11	—	—
British Guiana. (Davies & Richards, 1933, 1934)	5 m	193	16	11	200
British Guiana. (Davies & Richards, 1933, 1934)	14 m	55	38	11	200
Ecuador, Lowland. (Grubb et al., 1963)	20 ft	42	60	—	—
Ecuador, Mountain (Grubb et al., 1963)	20 ft	52	96	—	—
Liberia, Rain forest. (This publication.)	10 m	29	62.1	22	153
Liberia, Rain forest. (This publication)	10 m	35	40.0	15	153
Liberia, Rain forest. (This publication)	10 m	32	50.0	18	153
Tanzania, Riparian forest. (This publication)	5 m	20	60.0	2	7
Tanzania, Wooded grassland. (This publication)	5 m	24	8.3	1	7
Tanzania. Wooded grassland. (This publication)	4 m	50	100.0	2	2

three (sample) plots was 22 (9 ferns, 8 orchids, 5 other epiphytes) observed on a 43 m high *Parinari excelsa,* but a higher number of epiphytic species on certain trees has been observed (Table 19). During a brief visit to the Usambara Mts in Tanzania, I was able to count 25 species of epiphytes on a *Parinari excelsa* (Table 27).

Eggeling (1947:55) reports from the Budongo rain forest in Uganda: "... In these plots the maximum number of species of epiphytes on a single tree is twenty-six but elsewhere in the forest I have collected between forty and forty-five species from an especially suitable host." Richards (1964:113) probably underestimates the richness of epiphytes on certain trees: "The number of species of epiphytes on a single tree is seldom very large even in rich districts. The largest number of species recorded by the

Table 19. Highest number of epiphytic species recorded (close obs.) on single individuals of some phorophytes common in the Nimba area.

Phorophyte	Height (m)	Number of epiphyte species			
		Pterid.	Orch.	Others	Total
Heritiera utilis	36	9	20	1	30
Mitragyna ciliata	33	14	10	4	28
Chlorophora regia	42	6	20	1	27
Parinari excelsa	38	7	14	6	27
Lophira alata	42	6	12	4	22
Piptadeniastrum africanum	49	7	13	1	21

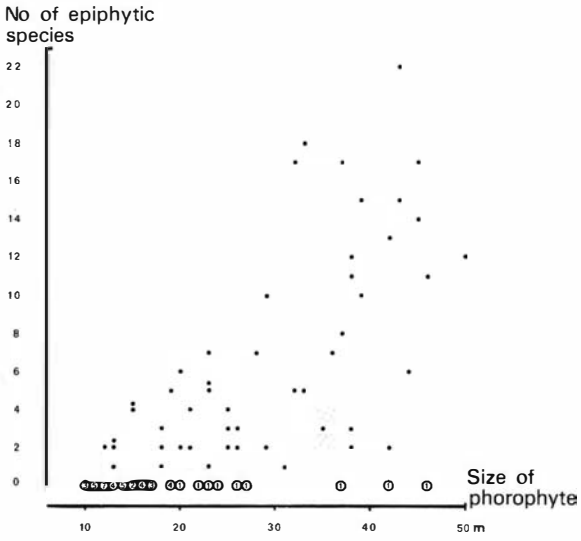


Fig. 69. Correlation between the size of the phorophyte and the occurrence of epiphytes in sample plots I-III (Tables 14-16). Figures in circles indicate the number of trees in each size class that were devoid of epiphytes.

Table 20. Number of epiphyte 'stands' (a) and their distribution (b) on a 43 m tall Heritiera utilis. Seka Valley 700 m. The distribution is given as a percentage of the total number of 'stands'.

(a) *Species*	*'Stands'*
Bulbophyllum oreonastes	443
Bulbophyllum linderi	361
Listrostachys pertusa	274
Tridactyle armeniaca	153
Elaphoglossum salicifolium	105
Bulbophyllum saltatorium	109
Elaphoglossum isabelense	88
Tridactyle anthomaniaca	78
Rangaëris muscicola	49
Cyrtorchis arcuata	49
Polystachya polychaete	37
Bulbophyllum schinzianum	27
Polystachya saccata	21
Nephrolepis undulata	20
Asplenium megalura	18
Bulbophyllum barbigerum	16
Begonia rubro-marginata	8
Raphidophora africana	6
Polystachya tessallata	5
Drynaria laurentii	4
Begonia mannii	3
Graphorchis lurida	2
Remusatia vivipara	1
Total	1857

(b) *Section*	I	II	III	IV	V
Distribution of the 'stands'	—	5.7	50.7	39.3	4.3

author is about fifteen in British Guiana and about 13 in Nigeria." From Brazil 53 species of epiphytes on one tree has been reported (Focke 1893).

In the clear-felling plots the number of species of epiphytes on each phorophyte correlated to the height of the phorophyte is shown in Fig. 69. The age, species and environment of the trees investigated naturally exert a strong influence on the number of species of epiphytes that will be present. Thorold (1952), however, found no appreciable change in epiphyte rating (see enumeration methods) between cocoa trees, 15 respectively 60 years of age, while Richards (1939:30) states "epiphytes occur chiefly on the largest individuals of each species of tree".

The usefulness of this method as an instrument for comparison of the epiphyte flora in various regions is limited. Comparison must be performed on the same species and sizes of phorophytes due to the strong correlation between epiphyte flora and the phorophyte. For instance in the first plot a *Parinari excelsa* (no. 26) carried 62 % of the total number of epiphytic species (that also occurred on other phorophytes) in that plot. Similar results are found in the two other strips. A *Lophira alata* (no. 18) in the second plot and *Parinari excelsa* (no. 31) in the third carried 40.5 % and 40.9 % respectively of the species in their plots.

5. Number of epiphytic specimens or 'stands' on one tree

In the Nimba area it was observed that certain species of trees may harbour a very high number of epiphytic individuals. A total of 1857 individuals ('stands') were counted on a *Heritiera utilis* (Table 20), and on a *Parinari excelsa*.with one large branch excluded, 1171 individuals ('stands') were recorded.

Enumeration of the total number of individuals ('stands') of epiphytic species that occur on a tree is made difficult due to the inaccessibility and the growth habits of many epiphytes. Richards (1964:113) states: "No information is available as to the number of individuals of epiphytes for the tropics, but in New South Wales, Turner quoted by Longman & White (1917:64) counted over 200 individuals of epiphytic orchids on one tree."

The number of epiphytes in this sense is not very useful in determining their occurrence in a particular geographical region because of the same reasons as presented in the previous method. Grubb et al.

(1963:592) notices this in Ecuador: "Amongst twenty-five trees bearing vascular epiphytes on the lowland plot three trees bore 40 % of the total number."

However, records of this nature are valuable when analyzing the correlation between the phorophyte and its epiphytic flora.

Epiphytes on other substrates

On cultivated trees

Trees, many of them of exotic origin, that are kept in cultivation in and around the villages seem to be of varying suitability as phorophytes. The common mango tree, *Mangifera indica,* has a very poor or non-existent epiphyte flora. *Citrus* trees (grapefruit, orange and tangerine) seem to carry epiphytes only occasionally, their bark, however, is covered with white crustaceous lichens to such a degree that it often gives a whitish impression.

Coffee trees may be observed with a substantial number of epiphytes.

Table 21. Epiphytes recorded on Hevea brasiliensis in Firestone plantations at Harbel, Liberia.

Pteridophytes	Bulbophyllum cochleatum
Arthropteris monocarpa	Bulbophyllum cocoinum
Arthropteris orientalis	Bulbophyllum congolanum
Asplenium megalura	Bulbophyllum falcatum
Davallia chaerophylloides	Bulbophyllum intertextum
Drynaria laurentii	Bulbophyllum linderi
Elaphoglossum barteri	Bulbophyllum nigritianum
Elaphoglossum salicifolium	Bulbophyllum oreonastes
Lomariopsis guineensis	Bulbophyllum pavimentatum
Loxogramme lanceolata	Bulbophyllum recurvum
Lycopodium warneckei	Calyptrochilum emarginatum
Microgramma owariensis	Cyrtorchis arcuata
Microsorium punctatum	Cyrtorchis monteiroae
Nephrolepis biserrata	Diaphananthe bidens
Nephrolepis undulata	Graphorchis lurida
Oleandra distenta	Listrostachys pertusa
Phymatodes scolopendria	Polystachya tessallata
Platycerium stemaria	Tridactyle anthomaniaca
Vittaria guineensis	Tridactyle armeniaca
Orchids	*Other vascular epiphytes*
Aërangis biloba	Begonia polygonoides
Ancistrorhynchus cephalotes	Peperomia sp.
Angraecum distichum	Preussiella chevalieri
Bulbophyllum bufo	Rhipsalis baccifera

Fig. 70. Epiphytes on a rubber tree (*Hevea brasiliensis*). Firestone Rubber Plantation, Harbel, Liberia. (A) *Microgramma owariensis,* (B) *Graphorchis lurida,* (C) *Bulbophyllum falcatum,* (D) *Drynaria laurentii.*

The cocoa trees in the Nimba area seem to offer a rather good environment for epiphytes. A total of 13 species of epiphytes have been observed on this phorophyte. Thorold (1952) reported 32 species on cocoa trees in Nigeria.

The cola tree that is found outside almost every village shows a striking richness in epiphytes. Not less than 21 species of ferns, 39 species of orchids and 5 species of other vascular epiphytes have been recorded on this small tree.

Ornamental trees, e.g. *Delonix regia* (the flamboyant tree), *Jacaranda* sp., *Terminalia catappa,* and *Sphatodea campanulata* P. Beauv., all seem to offer a poor milieu for epiphytes. This may be a local effect since, in Douala, Cameroon, the flamboyant trees that line the streets are overgrown with epiphytes, *Microgramma owaroides* and *Polystachya odorata* Lindl. among others.

The rather young rubber trees in the plantations in

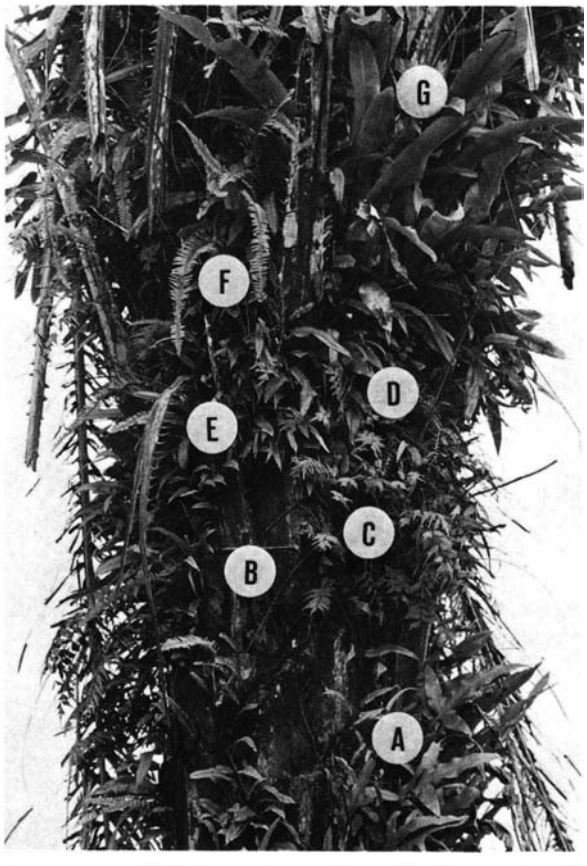


Fig. 71. Epiphytes on an oil palm (*Elaeis guineensis*). Yekepa 600 m. (A) *Phymatodes scolopendria*, (B) *Vittaria guineensis*, (C) *Asplenium megalura*, (D) *Lycopodium warneckei*, (E) *Oleandra distenta*, (F) *Nephrolepis undulata*, (G) *Microsorium punctatum*.

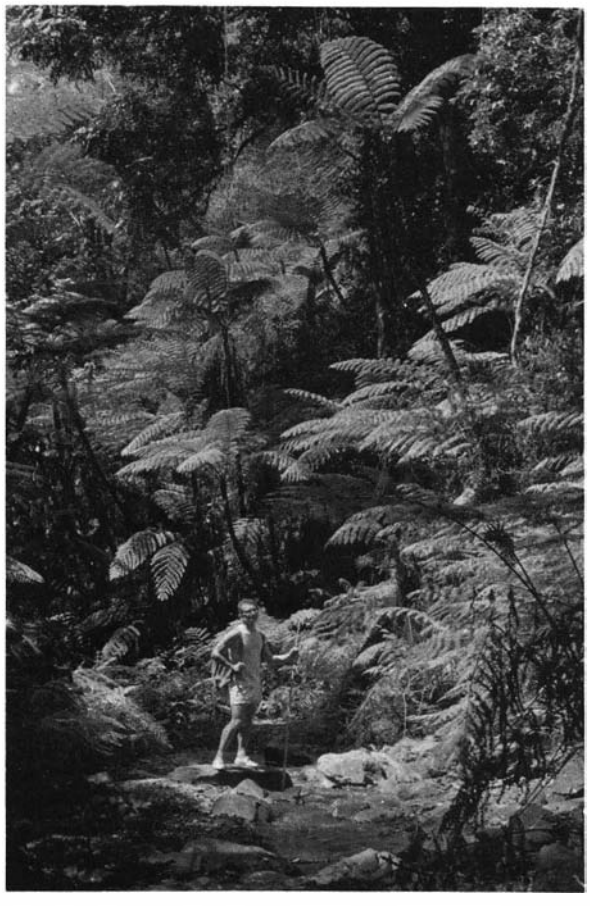


Fig. 72. *Cyathea manniana*. Iti river valley. Nimba Range 800 m.

the Nimba area hold very few epiphytes, but old trees in the Firestone rubber plantation at Harbel are very rich in eiphytes (Table 21) (Fig. 70). A total of 45 species were observed.

When the forest is cut for farming the oil palms are spared for their economic value and they are generally able to survive the farm-burning. Thus in clearings and secondary bush the palms are conspicuously numerous. As the older fronds die, the persistent woody bases remain adherent to the trunk, covering its length with horny stubs sharply angled upwards, so that large quantities of dead plant material are collected. In these humus deposits many epiphytic pteridophytes are growing (Fig. 71). Only one epiphytic orchid, *Habenaria procera*, was observed on the oil palm. Several species of other vascular plants, both "true" epiphytes and occasional or ephemeral (facultative) ones, utilize this habitat (cf. Van Oye 1921, Vanderyst 1922).

On tree-ferns

Two species of tree-ferns are present in the Liberian Nimba, *Cyathea camerooniana* Hook. and *C. manniana* Hook. *Cyathea camerooniana* is found in deep shade, in gullies often near streams, or close to small swamps from 500 m to 1200 m altitude. It has a short stem usually between 1-2 m high. The fronds reach up to four meters in length. No epiphytic vascular plants have been noticed growing on these stems.

Cyathea manniana forms veritable 'forests' in suitable places along the streams (Fig. 72). This tree-fern is rather common, particularly at higher altitudes. It is like a slender oil palm in shape. The stem may reach a length of 10 m with a diameter of only 5-6 cm. The stem is built up by persistent leaf-bases and matted adventitious roots which form an excellent substrate for the roots of the epiphytic plants. As a matter of fact the stem from tree-ferns is considered by professional orchid growers to be one of the best potting media for epiphytic orchids.

Table 22. Epiphytes recorded on 25 Cyathea manniana, (2 m or taller). Nimba Range 700 m. The figures refer to the percentage of the total number of tree ferns that carried each species of epiphyte.

Species	% of tree ferns carrying each sp. of epiphyte
Arthropteris monocarpa	64
Asplenium dregeanum	52
Asplenium barteri	32
Raphidophora africana	32
Impatiens sp.	32
Begonia oxyloba	28
Peperomia sp.	24
Asplenium variable var. paucij.	16
Nephrolepis biserrata	16
Nephrolepis undulata	12
Tectaria angelicifolia	12

The translucent crowns of these gigantic ferns permit a certain amount of light to penetrate to the ground creating an almost uniform light intensity. On a sunny day the light intensity at ground level is around three times greater in a tree fern forest than in a high forest.

Twenty-five tree ferns (*C. manniana*), 2 m or higher growing in a stream-bed at 700 m alt., were examined as to the presence of epiphytes on their stems (Table 22). No orchids were recorded or ever observed on *Cyathea manniana,* but the presence of pteridophytes and other vascular epiphytes was striking. 84 % of the tree ferns examined carried at least one species of epiphyte.

On 'herbs'

No epiphytes have been observed growing on herbs in the Nimba area. Guillaumet (1967:57) reports that the curious looking *Afrotrilepis pilosa* (Böck.) J. Raynal., (Cyperaceae), which has stems covered with closely packed persistent old leaf sheets, may support an epiphyte flora. Eleven species of epiphytic orchids are reported to occur on old *Trilepis pilosa* 'trunks' on the slopes of Carter Peak in Nigeria (Richards 1957:568). One of these is *Polystachya odorata* Lindl. var. *trilepidis* Summerh., which is known only as an epiphyte on *Trilepis* (Richards 1957:568). The stems of *Vellozia splendens* Rend., (Velloziaceae), are covered in the same manner as described for *Afrotrilepis.* Epiphytic orchids very frequently occur on *Vellozia splendens* in Malawi (Morris 1968, 1970:13).

Table 23. The epiphytic flora on eleven dead trees. Yekepa 500 m.

Group	Species		'Stands'	
	Total no.	%	Total no.	%
Pteridophytes	8	16.7	43	4.2
Orchids	38	79.2	966	95.2
Other vasc. plants	2	4.1	6	0.6
Total	48	100.0	1015	100.0

Both these perennial herbs occur among rocks in areas that for one reason or another are more or less devoid of trees. In this milieu they simply act as a substitute for trees.

On dead trees

The epiphytic flora of eleven dead trees was studied (close or distance observation) (Table 23). The trees had no humus deposits, and in some cases even the bark had slipped off forcing the epiphytes to grow directly on the wood. Since there was no foliage the plants were subject to full sunlight.

The ratio between the species of pteridophytes and orchids was nearly 1:5 (8:38). The number of individuals shows more clearly the effect of the extreme environmental conditions on the epiphytic fern flora. Only 4.2 % of the total number of individuals ('stands') of the epiphytes were pteridophytes. Some species occur in large numbers. On a 14 m high tree 416 epiphytic individuals were found, with the dominance of two species, *Polystachya puberula* (181) and *P. paniculata* (121) (Table 24).

Table 24. Number of epiphyte 'stands' on a 14 m tall dead tree. Yekepa 500 m.

Species	'Stands'
Bolusiella talbotii	7
Bulbophyllum maximum	19
Bulbophyllum oreonastes	17
Chamaeangis vesicata	31
Diaphananthe rutila	4
Plectrelminthus caudatus	16
Polystachya adansoniae	7
Polystachya obanensis	3
Polystachya paniculata	121
Polystachya puberula	181
Polystachya tessallata	5
Rangaëris rhipsalisocia	5
Total	416

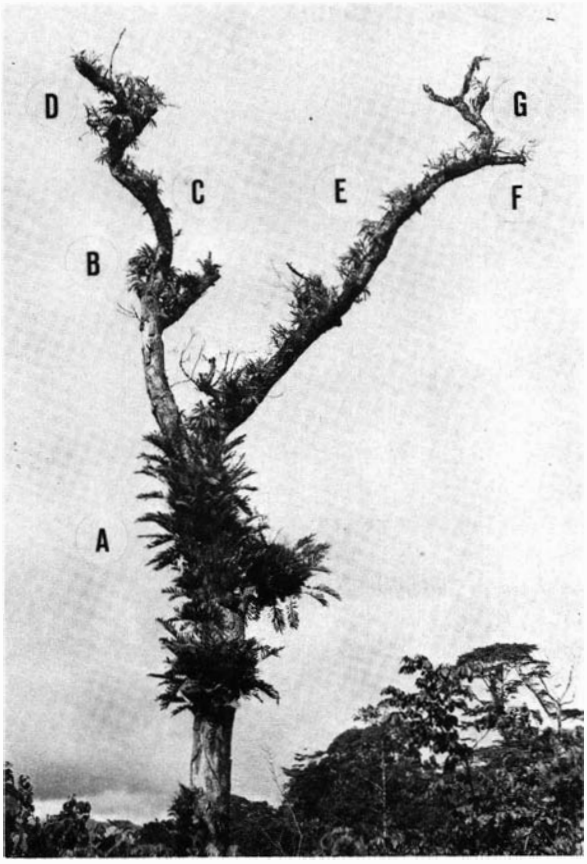


Fig. 73. Epiphytes on a small dead tree. A total of 17 species were recorded (2 pteridophytes and 15 orchids). (A) *Drynaria laurentii,* (B) *Graphorchis lurida,* (C) *Chamaeangis vesicata,* (D) *Polystachya tessallata* and *Phymatodes scolopendria,* (E) *Polystachya puberula,* (F) *Rangaëris rhipsalisocia,* (G) *Ancistrorhynchus cephalotes.*

The rich epiphyte flora that frequently can be found on recently dead trees has mostly established itself several years earlier when the tree was alive. During the dying process of trees many epiphytes take advantage of the increased light intensities, (caused by the falling of the leaves) but probably also by a beginning decomposition of the bark (Went 1940:91). When the trees are dead the epiphytes will flourish during the first rainy season.

The very exposed habitat will rapidly exert a strong influence on the species composition of the epiphyte flora favouring the drought resistant orchids (Fig. 73). In a few years the altered environmental conditions combined with an exhaustion of the substrate will result in an impoverished epiphyte flora, even if certain species will occur in a very large number of individuals.

Some species of phorophytes that have a sparse epiphytic flora such as *Terminalia ivorensis* have frequently been observed to carry a larger number of epiphytes when dead. Similar observations are also reported from Uganda: "Smooth barked species e.g. *Cynometra* rarely carry epiphytes until they are so old that the branches have begun to die back, when they too may be fairly heavily colonized." (Eggeling 1947:56.)

On rocks and soil

In the Nimba area several species of epiphytes occur on sloping rock surfaces and bare soil patches at 1100-1200 m altitude on Mt Gbahm. This habitat is created by human activities (road construction) and sooner or later the ground will be colonized by terrestrial plants with *Dissotis* spp. (Melastomataceae) as pioneers. Presently (1970) a large number of epiphytes are thriving there. The most common are *Polystachya dalzielii, P. leonensis, P. laxiflora* and *Bulbophyllum oreonastes,* which can all be seen by the hundreds. Less frequent are *Lycopodium warneckei, Angraecum birrimense, A. distichum, Bulbophyllum magnibracteatum, B. scariosum, Graphorchis lurida, Polystachya paniculata, P. pobeguinii, P. rhodoptera, P. saccata, P. tessallata, Rangaëris muscicola, Tridactyle armeniana,* and *T. anthomaniaca.*

It is well known that epiphytic species under special circumstances will grow on rocks or on the ground (Oliver 1930:2, Polack 1933:26, Richards 1936:32, 1964:122, Jaeger & Adam 1972). This behavior is natural in areas devoid of suitable phorophytes and where the microclimate fits the requirements of the epiphytes. It is in relatively dry areas that one will find epiphytes on the ground due to lack of trees and weak competition from other terrestrial plants. In humid areas the opposite effect appears, i.e. habitually terrestrial plants grow as facultative epiphytes.

From the Loma Mts in Northern Sierra Leone, Jaeger et al. (1968) report no fewer than 34 species of epiphytes of which 13 also were found growing on rocks, e.g. *Polystachya dalzielii, Bulbophyllum scariosum* and *B. bifarium.* Four species of epiphytes are reported occurring on granite boulders in the southern Ivory Coast (Guillaumet 1967:57).

From Kenya, Piers (1968 a:158) gives an example of a healthy establishment of an *Ansellia gigantea* (Rchb. f.) var. *nilotica* (Baker) Summerh.: "An ex-

ceptional specimen plant, a gigant covering some 20 square metres and growing intermingled with Aloes, Euphorbias and other xerophytic terrestrials, grows near the shores of Lake Elmenteita in the Rift Valley in soil which is almost pure volcanic ash."

Rangaëris muscicola which in dry areas of East Africa occurs on rocks is often connected to the presence of lichens as judged by notes on herbarium sheets: "On lichens on the huge granite boulders at the bottom of Njombe river cascade, Tanzania" Lynes 1931 (K), "Covering rocks in a mass. Clinging to rock surface with lichens" Zambia, Abercorn Distr. H.M. Richards 8404 (K), "on lichen-covered rocks" Malawi, Mlanje, Morris 91 (K), "Epiphytic or lithophytic orchid, always in association with grey lichens" N. Rhodesia, Ika Hills, Morze 1961 (K).

One might speculate that the lichens with their water-absorbing and water-holding capacity could create a suitable microclimate for the germination of orchid seeds. The microclimate could also be of major importance in the possibilities for the young orchid plants to survive dry periods.

The epiphytic orchids, with their slow growth and small leaf surface, combined with a root system adapted to superficial growth, appear suitable for this kind of habitat.

Distribution of epiphytes on the phorophytes

The first impression one gets, when looking at the distribution of epiphytic plants within a tropical rain forest, is the lack of order. It seems that the epiphytes are able to grow at any place on the trees. There are many reasons that help to create this impression. One of these is the limited sector of the trees that can be observed from the ground, another that many observations are done in areas where human activities have disturbed the original stratification, i.e. bright light may penetrate to the lowest level of the forest. In such cases one often finds species normally belonging to the topmost layer of the forest growing close to the ground. Many other influences may contribute towards an impression of randomness in the distribution of the epiphytes. A regular pattern emerges first when one has the possibility of examining a substantial number of trees in an undisturbed environment from the outermost branches in the crown down to the base of the stem.

Such a pattern has been observed by several authors. Schimper (1903) states that the epiphytic plants on a tree in a virgin forest are not the same from its base to its topmost branches but exhibit a well-marked differentiation. Moreau (1943:8): "A few small species e.g. *Angraecum viride* are found always on twigs rather than branches." Holtum (1960) observed that some small epiphytes grow only on the smaller branches of trees or shrubs. Richards (1964:118): "Large epiphytic ferns such as *Asplenium nidus* and *A. africanum* tend to prefer the trunks to the branches, but many epiphytes show the opposite preference." Morris (1970:5): "On all trees there is a pronounced stratification of the epiphytic flora." But where an existence of some distribution patterns has been documented no actual investigation has previously been done to describe or analyze them.

Ecological subdivision of the phorophyte

Previous schemes

To make it possible in a short time to record accurately the epiphytes it is necessary to use some kind of subdivision of the tree.

Van Oye (1924 b) divides the oil palm (*Elaeis guineensis*) into five zones. This zonation is useful for the oil palms and other palms whose crowns are built up by large leaves. For the often extensive crowns of the large rain forest trees this zonation is less useful. In Europe Ochsner (1928) uses the same zonation as Van Oye, excluding the submedian zone.

Richards (1939) in certain cases used the height above the ground, in others a more relative description, e.g. base of the first branch, in the records of the growing site of the epiphyte. Sometimes these two pieces of information are combined. The use of a large number of relative terms, without strict definition, is rather confusing. In 28 felled trees, recorded as bearing epiphytes, Richards used no less than eleven such relative 'localities'.

Hosokawa (1954 a) divides the phorophyte into four sections. An arbitrary system of 15 ft (4.5 m) zones from the ground upwards has been used by Grubb et al. (1963:592-593).

Tixier (1966) works with three large sections, but uses 5 subunits within the 'base of the trunk section'. The study of epiphytic lichens and bryophytes in temperate climates has caused many subdivisions of the phorophytes. Barkman (1958:31-32) has made a valuable compilation of that terminology. The lower

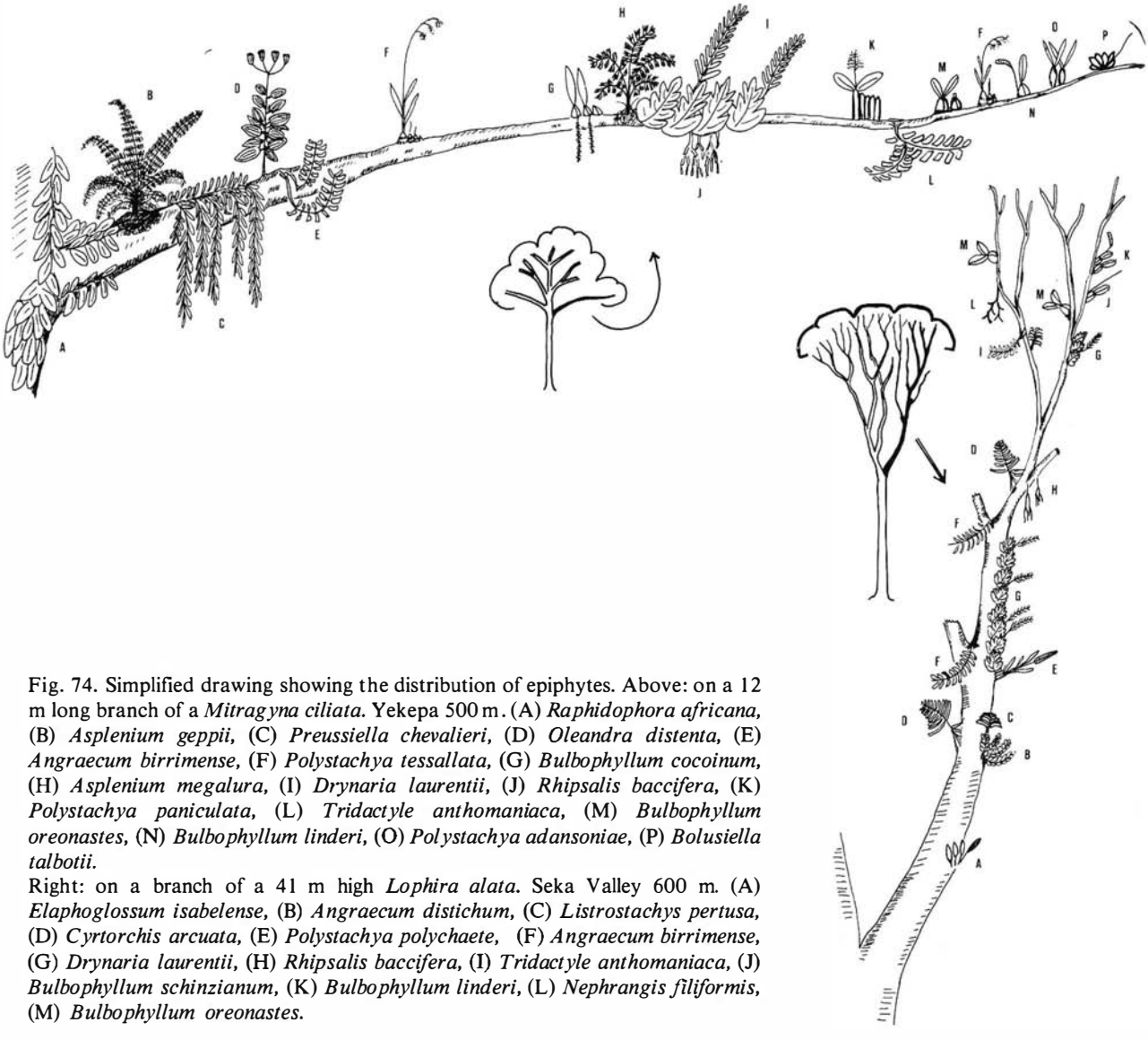


Fig. 74. Simplified drawing showing the distribution of epiphytes. Above: on a 12 m long branch of a *Mitragyna ciliata*. Yekepa 500 m. (A) *Raphidophora africana*, (B) *Asplenium geppii*, (C) *Preussiella chevalieri*, (D) *Oleandra distenta*, (E) *Angraecum birrimense*, (F) *Polystachya tessallata*, (G) *Bulbophyllum cocoinum*, (H) *Asplenium megalura*, (I) *Drynaria laurentii*, (J) *Rhipsalis baccifera*, (K) *Polystachya paniculata*, (L) *Tridactyle anthomaniaca*, (M) *Bulbophyllum oreonastes*, (N) *Bulbophyllum linderi*, (O) *Polystachya adansoniae*, (P) *Bolusiella talbotii*.
Right: on a branch of a 41 m high *Lophira alata*. Seka Valley 600 m. (A) *Elaphoglossum isabelense*, (B) *Angraecum distichum*, (C) *Listrostachys pertusa*, (D) *Cyrtorchis arcuata*, (E) *Polystachya polychaete*, (F) *Angraecum birrimense*, (G) *Drynaria laurentii*, (H) *Rhipsalis baccifera*, (I) *Tridactyle anthomaniaca*, (J) *Bulbophyllum schinzianum*, (K) *Bulbophyllum linderi*, (L) *Nephrangis filiformis*, (M) *Bulbophyllum oreonastes*.

parts of the phorophytes have generally been subject to many subdivisions, while as a rule the whole crown has been regarded as one section. This can in many cases be traced back to poor knowledge of the epiphytes of the crown rather than being based upon real observations. A number of subdivisions used in studies of vascular epiphytes is presented in Table 25.

Biotopes on the phorophytes in the Nimba area

In the tropical rain forest there is a pronounced stratification of the vegetation. The crowns of the trees form one or more 'strata' and it is in the topmost of these 'strata' that the main part of the epiphytes appear. This stratification of the rain forest is by no means uniform, but rather large variations can be found (Foggie 1947, Newman 1954, Robbins 1959, Holdridge 1970). As a rule the crowns are rather small compared to the length and size of the trunks, but a few species of trees with the ramification close to the ground give rise to crowns of large dimensions.

Usually the emergent (superstory; Odum 1970 a) trees have more flattened and expanding crowns than the trees in the lower 'strata' of the forest.

The richness in biotopes which can be found in the crowns of the large trees is in sharp contrast to the more uniform environment in the lower 'strata' of the

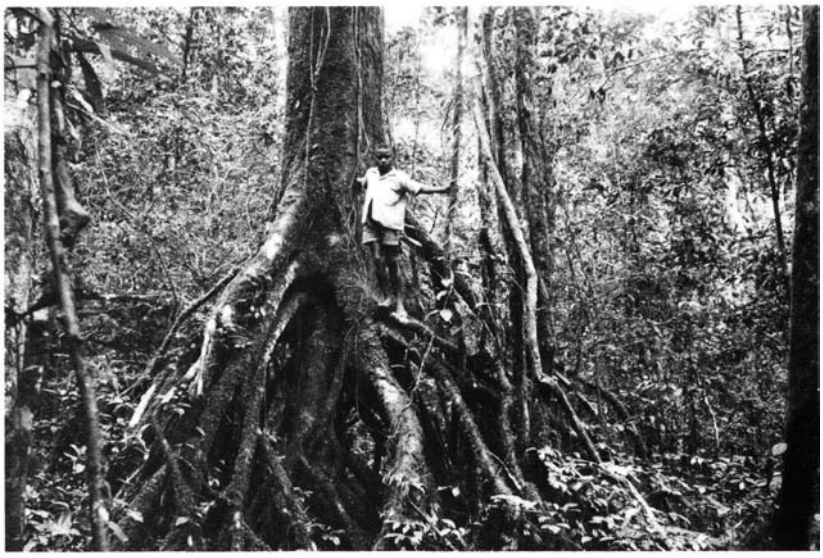


Fig. 75. Plank buttresses of *Piptadeniastrum africanum* (above) and stiltroots of *Uapaca guineensis* (below). Yekepa.

Table 25. Subdivision of the phorophyte by some authors

Author	'Trunk'	'Crown'
Van Oye 1924	region basale, r. sous-mediane, r. mediane, r. sous-coronaire	region coronaire
Ochsner 1928	basis-teil, mittelteil, subkronenteil.	kronenteil
Schnell 1950	strate épiphytique inférieure	strate épiphytique supérieure
Hosokawa 1954a	Trunk-bases, trunks	Crown-bases, crowns
Tixier 1966	Base de troncs, strate fructescente	Cîme

forest. This fact is reflected in the zonation used in this study.

Subdivision used in this study

A subdivision must conform to the varying size and shape of the trees to make comparisons between various phorophytes meaningful. Any simple system of height zones will inevitably fail to correspond with natural 'zones' of environmental conditions, because of the uneven nature of the canopy as pointed out by Richards (1964:116) and Grubb et al. (1963:592).

Hosokawa (1954 a) noticed two zones on the branches, crown-bases and crowns. One also finds these two zones on the phorophytes in the Nimba area. However, there is very frequently in the middle

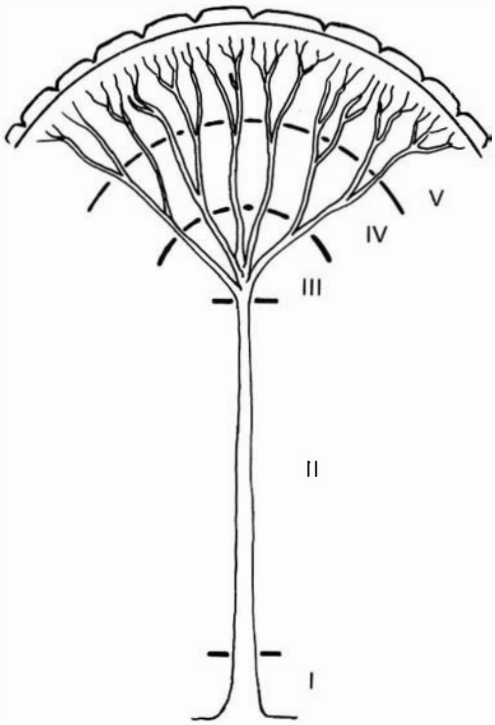


Fig. 76. Subdivision of the phorophyte.
Section:
I The basal parts of the trunk (0-3 m)
II The trunk from three m up to the first ramification
III The basal part of the large branches (1/3 of the total length of the branch)
IV The middle part of the large branches (1/3 of the total length of the branch)
V The outer part of the large branches (1/3 of the total length of the branch)

part of a branch an epiphytic flora of a different composition than the one occurring at the base of the branch, or in the outermost parts (Fig. 74). This irregular distribution of the epiphytes can be found on trees of varying sizes. The branches have therefore been divided into three sections of equal size.

The trunk has been divided into a short section close to the ground, and a considerably longer section that includes the rest of the trunk up to the first ramification. This division is based upon the easily observed difference between the epiphytic flora at the base of the tree and the one occurring on the upper part of the trunk (Fig. 75). The division of the phorophytes into sections used in this study are summarized in Fig. 76.

Recording and registration of epiphytes

The very limited knowledge of the ecology of the epiphytic plants in the rain forest is, as previously mentioned, connected with the difficulties in studying them in the field (Fig. 77). As a matter of fact a large part of the epiphytes described from the rain forest are species naturally occurring on the lowest part of the trunks.

Under ordinary circumstances it is from the ground level difficult to even get a limited view of the crowns of the highest trees. The shorter trees, together with lianas and other climbers, form a layer of varying thickness that can be looked through only here and there. This means that even if it is possible to study a certain part of the crown, the overall picture is not discernible.

The possibility of a definite host specificity also greatly complicates any attempt of random sampling, as has been pointed out by Curtis (1952:551). One may of course study the epiphytes that occur on the trees along roads, at the edge of the high forest etc. In these cases one will find an epiphytic flora that is by no means representative for the high forest proper.

To be able to compare the epiphytes from the high forest, observations have also been performed on phorophytes in other environments (e.g. around villages and in plantations).

To enable the use of all possible information three different observation methods have been applied in the recording of the epiphytic flora. They may simply be called the close observation, distance observation and occasional observation methods. One separate record was produced for each phorophyte that was examined.

Close observation

This method means that the investigation has been performed on a tree lying on the ground. The access to felled trees was limited, but occasionally road construction, landscaping or forestry operations produced useful material. Trees knocked down by natural causes are very seldom found.

The investigation of a felled tree must be carried out almost instantly, since many plants will either die or be favoured by the change in the environment. Commonly the orchids suffer from too low light intensities, while certain species of pteridophytes have an advantage with the higher relative humidity close to the ground. The practice of shifting cultivation

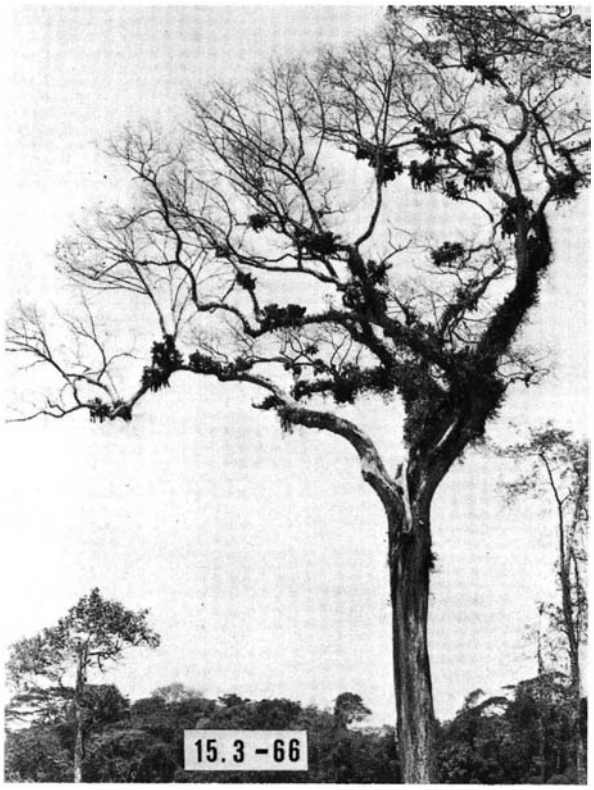


Fig. 77. The concealment of the epiphytes by the foliage as illustrated by a *Triplochiton scleroxylon*. This tree is deciduous for a short period when the epiphytes are easily observed. Note the distribution of the large *Platycerium* ferns.

might seem to offer an immense material. Unfortunately these farming activities are to the largest extent carried out in so-called secondary forests. Here the vegetation is after repeated destruction kept in various young secondary growth stages.

When the tree is lying on the ground it is relatively simple, at least when one knows well enough the vegetative parts of the epiphytes to make determinations, to map the distribution and to study the ecology of the various species. Certain large branches can be used to illustrate the continuous changes in the epiphytic flora from the base to the outermost parts, so-called 'transects'.

In the description of vegetative change along an environmental gradient the 'transects' are of a considerable importance. But since neither the trunks nor the branches represent straight lines a transect of traditional type is not easy to work with. Therefore a modified type of transect has been used. The method is simply to let a measuring tape follow the twistings and bends of the stretch to be examined. This stretch is later presented as if it was a straight line. Most of the monopodial orchids grow out from the branches, and thus a very minute part of the plant, aside from the extensive root system, covers the sampling area. The scale constructed is therefore based on the actual number of plants rather than the area covered.

The transects can preferably be drawn along the branches in the crown, since it is here that the most substantial changes occur in substrate, light and microclimate. From the point of ramification, where the branch is relatively broad, the transect as it runs along the branch, covers a smaller and smaller area. This fact should be considered when reading the transect results (Fig. 79).

Distance observation

Such investigations have been performed on a standing phorophyte on which it has been possible to investigate the trunk and at least one complete branch (or more seldom the whole phorophyte). This method, described by Went (1940), allows the recording of the epiphytic flora from the ground. With the aid of field glasses, or rather a telescope on a tripod,

it is possible to identify the majority of epiphytes. An advanced knowledge of the vegetative parts of the plants is a prerequisite since you seldom find the plants in a flowering state. To acquire that knowledge a sample of almost every epiphyte was collected and kept alive. They thrived growing on substrate similar to the one they were collected from, (in small wooden boxes, 20 x 20 x 5 cm, with broad slots in the bottom). The boxes were kept on shelves in a specially constructed 'frame house'. Species difficult to classify were also kept in this manner until a safe determination could be made.

From this collection of living epiphytes information was extracted which proved useful in the field work. Through a telescope at a magnification of 40x even small details can be observed, and epiphytes a few centimeters in size can be identified on the branches of the highest trees. As a rule characteristics, such as remaining floral parts pseudobulbs etc., are of great help in the determination process. (A description of the vegetative parts of the orchids has been presented in chapter II.)

However, for certain orchids, there are sometimes only small details in the flowers that separate two species from one another. In these cases the generic name only has been used in telescopic surveys.

The pteridophytes were, for the most part, easier to separate from each other than the orchids. There are very few morphologically similar species that could cause problems in the identification.

Among the other vascular epiphytes the *Peperomia* species are difficult to determine.

There are certain disadvantages with this method. It is very time consuming. The plants growing in the most exposed places will easier be discovered than those in more obscure habitats. Large growing species will be spotted more often than minute plants. Many more objections can be raised. It is therefore important to separate the observations with the distance method from those performed in other ways.

The distance recording served two purposes. Certain species of epiphytes were never observed in the studies of felled trees. The distribution on the phorophytes and habitat conditions for these species must therefore be based upon information from this type of investigation. Furthermore, the records obtained from the distance recordings, can be used to determine the accuracy of this method in comparison to the close investigation method.

Occasional observation

It is normally possible to study the epiphytic flora only on a limited part of the phorophyte. Such records that may refer to close as well as distance observations, are called occasional observations. From the lowest parts of the phorophytes a large number of observations may easily be obtained and parts of branches that have fallen down from the crowns also offer abundant material.

For most species these records add little or nothing to the knowledge achieved from close and distance observations, but for certain species this is ± the only information about their distribution and general ecology that has been possible to obtain. The records from this latter group of species are listed under Occasional observations (Table 29).

Registration

The traditional way of determining the abundance or presence is not particularly useful for epiphyte rating. In most cases, the limited presence, and the stout and rather large size of many epiphytes, make it possible to count the individual plants, or groups of plants.

The sympodial plants with their vegetative multiplication present a special problem. These plants often form dense 'mats' of rhizomes and stems mixed with immature plants. This makes it very difficult to determine the number of individual plants that are present.

An arbitrary system of epiphyte rating, primarily qualitative and only quantitative in so far as importance is attached to the presence of one or more colonies has been used by Thorold (1952).

Grubb et al. (1963:591) works with the term 'an individual' for each clearly separated clump of plants. Sanford (1968b:56) has given an accurate description of the problems concerning the enumeration of epiphytic orchids: "Actual counting of orchid plants on a tree presents special difficulty. Many plants such as *Bulbophyllum* spp. forms mats of pseudobulbs connected by relatively long rhizomes. It is impossible to determine where one plant ends and another begins. Other species, such as those of the genus *Calyptrochilum,* form great masses of pendulous stems, and again determination of individuals is arbitrary. For this reason a special usage of 'stand' is used in these enumerations. A stand is taken to mean a collection of individual stems or/and plants spatially separated from another group of the same

species either by an area on the tree devoid of orchids or occupied by another species. In the case where the same area is occupied by an intermingling of more than one species, one stand is counted for each species present."

During the investigation the same unit (called 'group'), as described by Sanford, was used. In order not to cause confusion by adding one more name for the same thing, the term 'stand' sensu Sanford is adopted.

Ecological observations

In order to get a rough idea of the importance of certain environmental influences on the distribution of the epiphytes within the forest, attention has been paid to light and substrate. For each epiphyte that was recorded, the light intensity and type of substrate at its growing site were recorded in a three-graded scale.

Light

Light intensity was divided into three classes: heavy shade, open shade and full sun. The amount of light available varies of course with the time of the day and cloudiness of the sky, and also somewhat with the time of the year. Since the light intensity was only estimated, mistakes cannot be excluded. However, the main bulk of the observations are easy to group.

Light intensities regarded as heavy shade normally appear in the lower strata of the rain forest. In exceptional cases this intensity can be found higher up in the trees due to dense foliage. In most cases there is no problem to separate heavy shade from open

Table 26. The trees (10 m or taller) of the high forest included in the study. Trees with epiphytes are marked

	Close observation			Distance observation		
Phorophytes	No.	% with epiphytes	Sizes	No.	% with epiphytes	Sizes
Albizia glaberrima	4	50.0	36,38,38,40´	–	–	–
A. zygia	3	100.0	17,21,26´	5	60.0	12,13,18,21,24´
Alstonia boonei	8	50.0	12,14,17,21,25,27,29,30	6	33.3	13,15,18,19,22,31´
Amphimas pterocarpoides	4	50.0	11,14,14,34´	4	50.0	12,16,29,32´
Anthocleista nobilis	7	28.5	11,14,14,15,16,17,18	12	16.7	10,10,11,11,12,12,13,13,15,15,16,19´
Anthonotha fragans	1	100.0	17´	7	85.8	11,15,16,20,21,26,32´
Antiaris toxicaria	2	100.0	34,35´	6	66.7	22,24,28,29,30,34´
Berlinia confusa	3	66.7	14,33,41´	2	50.0	13,17´
Bombax buonopozense	3	66.7	24,30,41´	1	0.0	26
Bussea occidentalis	3	66.7	21,22,26´	–	–	–
Calpocalyx aubrevillei	13	46.2	11,11,12,12,14,16,18,20,23,23,25,26,29´	2	50.0	14,18´
Canarium schweinfurthii	5	40.0	13,14,21,29,38´	5	60.0	17,20,23,26,34´
Ceiba pentandra	2	100.0	19,31´	12	83.3	20,25,26,29,30,34,36,37,40,40,40,42´
Chidlowia sanguinea	14	42.9	11,12,12,12,13,13,14,14,14,15,15,16, 18,18´	12	75.0	12,12,13,14,16,17,17,18,20,20,21,24´
Chlorophora regia	5	60.0	17,18,28,39,42´	8	75.0	18,23,25,27,29,29,30,39´
Chrysophyllum perpulchrum	4	75.0	23,26,31,31´	1	100.0	28´
Combretodendron macrocarpum	4	75.0	14,14,27,31´	7	71.4	12,12,14,17,19,19,34´
Coula edulis	3	66.7	16,26,30´	4	75.0	23,25,30,34´
Cryptosepalum tetraphyllum	6	66.7	10,21,23,24,25,27´	6	66.7	14,26,28,28,29,34´
Daniellia ogea	7	42.9	14,16,19,20,26,34,37´	4	75.0	21,23,26,34´
Distemonanthus benthamianus	3	33.3	26,27,30	–	–	–
Entandrophragma utile	3	100.0	29,38,60´	3	66.7	21,40,42´
Erythrophleum ivorense	4	75.0	15,28,32,36´	4	75.0	12,14,18,41´
Fagara tessmannii	6	33.3	29,31,32,36,38,42	6	0.0	14,21,21,34,40,42
Guarea cedrata	3	66.7	21,32,36´	2	100.0	19,25´
Heritiera utilis	7	85.7	13,16,18,26,32,35,43´	14	92.3	17,22,24,27,29,30,30,31,31,31,33,34,34,37´
Khaya anthotheca	2	100.0	34,36´	3	33.3	14,16,19
Lophira alata	7	71.4	11,16,39,42,43,44´	4	50.0	12,13,24,38´
Lovoa trichilioides	5	60.0	19,24,27,33,38´	1	100.0	36´
Mammea africana	3	66.7	14,16,33´	3	66.7	13,20,27´
Mitragyna ciliata	5	100.0	11,22,32,33´	5	100.0	12,14,26,28,30´
Nauclea diderrichi i	3	100.0	28,32,38´	1	0.0	24
Parinari aubrevillei	2	100.0	21,23´	–	–	–
P. excelsa	5	80.0	12,21,22,38,42´	18	83.3	12,14,14,18,20,21,25,26,28,33,34,35,35,36, 39,39,40,44´
P. glabra	4	75.0	19,20,23,23´	–	–	–
Parkia bicolor	7	28.5	21,23,26,29,29,30,32´	9	33.3	11,23,25,26,27,30,31,32,33´
Pentaclethra macrophylla	4	75.0	20,22,27,34´	2	100.0	27,36´
Pentadesma butyracea	2	100.0	31,40´	2	50.0	18,23
Piptadeniastrum africanum	6	50.0	12,18,34,43,49,54´	19	52.6	13,16,20,20,21,24,26,26,28,28,32,34,35,38, 42,43,44,51,53´
Pycnanthus angolensis	6	33.3	16,20,21,23,24,27´	6	16.7	14,19,24,26,30,34´
Rhodognaphalon brevicuspe	4	75.0	21,27,32,35´	1	100.0	33´
Sacoglottis gabonensis	2	50.0	14,39´	4	100.0	29,33,34,40´
Terminalia ivorensis	9	22.2	14,21,31,32,38,40,40,42,43´	9	11.1	16,18,23,30,33,40,41,41,41´
T. superba	7	28.5	28,32,33,35,41,42,42´	5	20.0	17,28,42,43,44
Triplochiton scleroxylon	7	57.1	12,15,22,30,32,41,44´	7	57.1	10,11,16,20,39,42,45´
Uapaca guineensis	3	100.0	17,20,21´	5	80.0	12,12,18,25,27´
Vitex micrantha	2	50.0	13,24´	4	100.0	10,12,17,23´
Total	222			241		

shade intensities. The light in a tropical rain forest is not gradually increasing from the ground level up to the crowns of the emergent trees. It is rather discontinuous, as many author have pointed out, e.g. Richards (1939:30). In the crowns of the trees of the topmost stratum high light intensities are formed by open shade. The limit between full sun and open shade is also easy to observe, since only plants in very exposed positions receive light intensities regarded as full sun.

In a study of the epiphytic societies in Java, Went (1940) used a relative scale to judge the light intensity at the growing sites of the epiphytes. He estimated the light intensity at the growing site in per cent of the light outside the forest.

Substrate

The substrate was divided into three classes: bark, e.g. bark without humus attached, minor humus deposits, e.g. bark with thin and scattered humus layer, and large humus deposits. Humus is here regarded as dead organic material in various stages

Table 27a. Total number of records, according to the close observation method, of pteridophytes and other vascular epiphytes in the high forest.

	No of observ.	Section of the phorophytes					Heavy shade			Open shade			Full sun		
		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Pteridophytes															
Antrophyum immersum	3	33.3	66.7	•	•	•	•	33.3	•	•	66.7	•	•	•	•
A. mannianum	2	•	•	•	100.0	•	•	•	•	•	•	•	•	100.0	•
Arthropteris monocarpa	7	57.1	•	28.6	14.3	•	14.3	42.9	•	•	14.3	28.6	•	•	•
A. orientalis	27	•	•	70.4	29.6	•	•	•	•	14.8	48.1	29.6	7.4	•	•
A. palisoti	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Asplenium aethiopicum	2	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•	•
A. africanum	7	•	14.3	57.1	28.6	•	•	•	•	14.3	42.9	28.6	•	•	14.3
A. barteri	16	56.2	6.2	37.5	•	•	37.5	25.0	37.5	•	•	•	•	•	•
A. dregeanum	93	4.3	25.8	38.7	29.0	2.1	•	2.1	16.1	2.1	38.7	26.9	•	10.7	3.2
A. geppii	22	•	9.1	86.4	4.5	•	•	•	4.5	•	27.3	68.2	•	•	•
A. hemitomum	2	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
A. megalura	172	•	1.2	34.9	51.2	12.8	•	•	•	1.7	12.2	21.5	2.9	23.8	37.8
A. variable var. paucijugum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Davallia chaerophylloides	45	•	8.9	28.9	51.1	11.1	•	•	•	17.8	33.3	4.4	22.2	17.8	4.4
Drynaria laurentii	499	•	3.8	48.3	41.9	6.0	•	•	•	31.3	6.2	•	53.9	8.6	•
Elaphoglossum barteri	7	28.6	28.6	42.8	•	•	•	28.6	•	•	14.3	57.1	•	•	•
E. chevalieri	20	20.0	50.0	25.0	5.0	•	•	25.0	50.0	•	15.0	•	•	•	10.0
E. isabelense	160	•	16.2	30.0	53.7	•	•	•	•	26.2	20.0	4.4	28.1	21.2	•
E. kuhnii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
E. salicifolium	208	•	22.1	45.2	22.1	10.6	•	•	•	26.4	17.8	•	47.1	8.6	•
Lomariopsis guineensis	1	100.0	•	•	•	•	100.0	•	•	•	•	•	•	•	•
Loxogramme lanceolata	32	15.6	37.5	12.5	25.0	9.4	9.4	15.6	•	31.2	43.7	•	•	•	•
Lycopodium mildbraedii	11	•	•	18.2	81.8	•	•	•	•	•	63.6	9.1	9.1	18.2	•
L. warneckei	13	•	•	•	92.3	7.7	•	•	•	7.7	23.1	•	15.4	38.5	15.4
Microgramma owariensis	80	•	16.2	50.0	27.5	6.2	•	•	•	40.0	36.2	6.2	13.7	3.8	•
Microsorium punctatum	143	•	8.4	44.1	41.2	6.3	•	•	•	14.0	37.1	9.8	16.1	22.4	0.7
Nephrolepis biserrata	16	•	•	87.5	12.5	•	•	•	•	•	18.7	37.5	•	31.2	12.5
N. undulata	300	•	2.7	56.3	39.7	1.3	•	•	•	3.3	31.0	26.7	3.7	20.7	14.7
Oleandra distenta	184	•	4.3	59.8	35.9	•	•	•	•	10.9	35.3	33.7	8.1	10.9	1.1
Phymatodes scolopendria	226	•	5.7	52.6	41.6	•	•	•	•	30.1	40.7	4.9	16.4	8.0	•
Platycerium angolense	222	•	3.1	19.4	60.8	16.7	•	•	•	15.8	9.5	0.9	47.7	24.3	1.8
P. stemaria	142	•	•	25.3	60.6	14.1	•	•	•	8.4	16.9	5.6	39.4	29.6	•
Pyrrosia mechowii	40	•	•	30.0	70.0	•	•	•	•	5.0	40.0	5.0	15.0	30.0	5.0
Tectaria angelicifolia	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
T. fernandensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Vittaria guineensis	247	6.1	12.6	44.1	29.9	7.3	1.6	3.6	•	20.2	38.9	8.1	9.7	15.8	2.0
Xiphopteris oosora	46	•	•	52.2	39.1	8.7	•	•	•	21.7	54.3	23.9	•	•	•
X. serrulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
X. villosissima	5	•	•	60.0	40.0	•	•	•	•	•	100.0	•	•	•	•
Total no. of observations	3000														
Other vasc. epiphytes		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Begonia mannii	10	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
B. polygonoides	3	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
B. rubro-marginata	72	•	1.4	45.8	48.6	4.2	•	•	•	8.3	27.8	27.8	1.4	18.1	16.7
Calvoa monticola	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
C. trochainii	6	50.0	16.7	33.3	•	•	16.7	33.3	•	•	16.7	33.3	•	•	•
Medinilla mannii	67	•	4.5	31.3	64.2	•	•	•	•	14.9	38.8	17.9	6.0	17.3	4.5
Peperomia fernandopoiana	148	16.9	19.6	30.4	30.4	2.7	11.5	12.2	3.4	15.5	22.3	16.2	6.8	6.8	5.4
P. molleri	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. rotundifolia	9	•	•	11.1	66.7	22.2	•	•	•	22.2	55.6	•	22.2	•	•
Preussiella chevalieri	39	•	2.6	53.8	35.9	7.7	•	•	•	•	28.2	41.0	•	12.8	17.9
P. kamerunensis	34	•	11.8	50.0	35.3	2.9	•	•	•	•	29.4	47.1	•	•	23.5
Remusatia vivipara	6	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
Rhipsalis baccifera	109	•	0.9	14.7	54.1	30.3	•	•	•	19.3	15.6	3.7	27.5	27.5	6.4
Total no. of observations	503														

The distribution of the records between (1) the different sections of the phorophytes and (2) the different light and substrate classes each refer to a percentage of the total number of records. A = Bark, B = Minor humus deposits, C = Large humus deposits.

Table 27 b. Total number of records, according to the close observation method, of orchids in the high forest. (Explanation in Table 27 a.)

	No. of observ.	Section of the phorophytes					Heavy shade			Open shade			Full sun		
		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Orchids															
Aërangis biloba	27	•	•	51.8	48.1	•	•	•	•	22.2	7.4	•	44.4	25.9	•
A. laurentii	23	•	•	39.1	30.4	30.4	•	•	•	•	•	•	100.0	•	•
Ancistrochilus rothschildianus	53	•	•	56.6	35.8	7.5	•	•	•	11.3	49.1	9.4	9.4	20.7	•
Ancistrorhynchus capitatus	22	•	13.6	45.4	31.8	9.1	•	•	•	40.9	27.3	•	4.5	27.3	•
A. cephalotes	7	•	57.1	•	42.9	•	•	•	•	•	•	•	100.0	•	•
A. clandestinus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. recurvus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Angraecopsis elliptica	25	•	•	48.0	52.0	•	•	•	•	4.0	28.0	68.0	•	•	•
Angraecum birrimense	29	•	•	48.3	44.8	6.9	•	•	•	•	17.2	62.1	•	13.8	6.9
A. chevalieri	19	•	•	73.7	26.3	•	•	•	•	57.8	10.5	•	15.8	15.8	•
A. classensii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. distichum	54	•	•	29.6	53.7	16.7	•	•	•	18.5	11.1	3.7	48.1	14.8	3.7
A. podochiloides	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•
A. subulatum	6	•	•	50.0	50.0	•	•	•	•	16.7	66.7	•	•	16.7	•
Ansellia africana	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•
Bolusiella talbotii	73	•	4.1	•	24.7	71.2	•	•	•	4.1	•	•	91.8	4.1	•
Brachycorytis kalbreyeri	•	•	•	•	+	+	•	•	•	•	•	•	•	•	•
Bulbophyllum barbigerum	21	•	4.8	19.0	61.9	14.3	•	•	•	33.3	9.5	•	47.6	9.5	•
B. bifarium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. bufo	67	•	•	71.6	28.4	•	•	•	•	10.4	52.2	19.4	3.0	11.9	3.0
B. buntingii	58	•	•	10.3	75.9	13.8	•	•	•	20.7	6.9	•	69.0	3.4	•
B. calamarium	2	•	100.0	•	•	•	•	•	•	•	•	•	100.0	•	•
B. cochleatum	94	•	•	54.3	45.7	•	•	•	•	37.2	36.2	9.6	13.8	3.2	•
B. cocoinum	34	•	•	52.9	44.1	2.9	•	•	•	8.8	47.0	29.4	•	2.9	11.8
B. congolanum	19	•	•	31.6	68.4	•	•	•	•	•	•	•	57.9	42.1	•
B. distans	33	•	•	42.4	48.5	9.1	•	•	•	3.0	42.4	•	24.2	30.3	•
B. falcatum	6	•	•	•	100.0	•	•	•	•	•	66.7	•	33.3	•	•
B. flavidum	6	•	•	33.3	66.7	•	•	•	•	16.7	50.0	•	•	33.3	•
B. imbricatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. inflatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. intertextum	36	•	•	19.4	58.3	22.2	•	•	•	22.2	•	•	69.4	8.3	•
B. josephii	21	•	4.8	61.9	33.3	•	•	•	•	•	90.5	9.5	•	•	•
B. linderi	810	•	0.5	44.3	45.5	9.6	•	•	•	34.7	6.7	•	48.5	9.9	0.2
B. lucifugum	76	•	•	44.7	47.4	7.9	•	•	•	40.8	47.4	•	5.3	6.6	•
B. lupulinum	11	•	•	18.2	63.6	18.2	•	•	•	•	18.2	•	54.5	27.3	•
B. magnibracteatum	2	•	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•
B. maximum	31	•	•	19.3	67.7	12.9	•	•	•	61.3	•	•	38.7	•	•
B. melanorrachis	2	•	•	•	100.0	•	•	•	•	•	100.0	•	•	•	•
B. nigritianum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. oreonastes	1185	•	2.1	23.7	54.3	19.9	•	•	•	33.6	6.7	1.3	44.4	12.9	1.0
B. pavimentatum	3	•	33.3	•	66.7	•	•	•	•	•	•	+	100.0	+	•
B. phaeopogon	11	•	•	36.4	+	63.6	•	•	•	18.2	•	18.2	18.2	45.4	•
B. recurvum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. rhizophorae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. saltatorium	28	•	7.1	64.3	28.6	•	•	•	•	42.9	50.0	+	7.1	•	•
B. scariosum	199	•	•	6.5	45.2	48.2	•	•	•	9.5	12.1	1.0	32.2	42.2	3.0
B. schimperanum	45	•	•	13.3	55.5	31.1	•	•	•	24.4	+	+	71.1	4.4	•
B. schinzianum	86	•	•	31.4	59.3	9.3	•	•	•	40.7	5.8	+	38.4	15.1	•
B. winkleri	30	•	26.7	56.7	16.7	•	•	•	•	53.3	20.0	•	20.0	6.7	•
Calyptrochilum christyanum	33	•	•	60.6	24.2	15.1	•	•	•	24.2	•	•	75.8	•	•
C. emarginatum	2	•	50.0	•	50.0	•	•	•	•	50.0	•	•	50.0	•	•
Chamaeangis vesicata	18	•	•	5.3	94.7	•	•	•	•	5.3	•	•	52.6	42.1	•
Cyrtorchis arcuata	176	•	•	50.6	44.9	4.5	•	•	•	27.3	34.7	4.5	19.9	10.2	3.4
C. aschersonii	25	•	•	32.0	52.0	16.0	•	•	•	12.0	8.0	16.0	64.0	•	•
C. monteiroae	•	•	•	•	•	•	•	•	•	•	+	•	+	•	•
Diaphananthe bidens	35	•	2.9	28.6	57.1	11.4	•	•	•	31.4	17.1	5.7	31.4	14.3	•
D. densiflora	2	•	•	•	100.0	•	•	•	•	•	•	•	50.0	50.0	•
D. pellucida	9	•	•	66.7	33.3	•	•	•	•	22.2	66.7	11.1	•	•	•
D. rutila	2	•	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•
Eurychone rothschildiana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Genyorchis pumila	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Graphorchis lurida	139	•	4.3	24.5	57.5	13.7	•	•	•	18.7	2.9	•	67.6	10.1	0.7
Habenaria leonensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
H. procera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Liparis caillei	1	•	•	•	100.0	•	•	•	•	•	•	•	•	100.0	•
L. nervosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Listrostachys pertusa	389	•	5.9	26.0	46.8	21.3	•	•	•	24.9	9.2	•	55.5	10.3	•
Nephrangis filiformis	193	•	•	19.1	60.6	20.2	•	•	•	34.7	19.7	•	38.3	7.3	•
Plectrelminthus caudatus	9	•	•	•	66.7	33.3	•	•	•	•	•	•	100.0	•	•
Podangis dactyloceras	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Polystachya adansoniae	268	•	•	15.3	44.0	40.7	•	•	•	17.9	16.8	1.9	25.0	34.3	4.1
P. affinis	•	•	•	•	•	•	•	•	•	•	•	•	+	+	•
P. dalzielii	93	•	•	7.5	49.5	43.0	•	•	•	3.2	25.8	•	26.9	44.1	•
P. elastica	•	•	•	•	+	•	•	•	•	•	•	•	•	+	•
P. galeata	56	•	•	33.9	55.4	10.7	•	•	•	7.1	25.0	25.0	3.6	28.6	10.7
P. laxiflora	21	•	9.5	57.1	33.3	•	•	•	•	9.5	38.1	47.6	•	4.8	+
P. leonensis	48	2.1	10.4	39.6	43.7	4.2	•	•	•	14.6	37.5	14.6	16.7	12.5	4.2
P. microbambusa	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•
P. obanensis	8	•	•	62.5	37.5	•	•	•	•	•	75.0	25.0	•	•	•
P. paniculata	161	•	•	18.6	60.9	20.5	•	•	•	24.2	6.8	14.3	37.3	17.4	•
P. pobeguinii	1	•	•	100.0	•	•	•	•	•	•	100.0	•	+	•	•
P. polychaete	222	•	3.6	39.2	42.3	14.9	•	•	•	6.3	26.6	21.6	9.0	25.2	11.3
P. puberula	232	•	•	18.4	51.3	30.3	•	•	•	7.3	23.1	1.7	13.7	49.1	5.1
P. ramulosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. rhodoptera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. saccata	85	•	49.4	30.6	17.6	2.3	•	•	•	42.3	3.5	•	50.6	3.5	•
Polystachya subulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. tenuissima	4	•	•	•	100.0	•	•	•	•	50.0	•	•	50.0	•	•
P. tessallata	158	•	2.5	42.4	39.9	15.1	•	•	•	15.2	31.6	19.0	9.5	15.8	8.9
Rangaëris brachyceras	1	•	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•
R. muscicola	143	•	2.1	20.3	58.7	18.9	•	•	•	14.0	4.2	•	62.9	18.9	•
R. rhipsalisocia	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Rhipidoglossum paucifolium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Stolzia repens	4	•	•	•	100.0	•	•	•	•	•	50.0	•	+	50.0	•
Tridactyle anthomaniaca	650	•	0.6	24.5	46.6	28.3	•	•	•	16.2	4.8	0.3	73.7	4.6	0.5
T. armeniaca	363	•	6.1	51.8	33.6	8.5	•	•	•	41.3	31.9	7.2	11.0	6.6	1.9
T. bicaudata	4	•	+	25.0	75.0	•	•	•	•	75.0	25.0	•	+	•	•
T. crassifolia	16	•	37.5	25.0	18.7	18.7	•	•	•	•	25.0	•	75.0	•	•
T. tridactylites	62	•	4.8	37.1	35.5	22.6	•	•	•	24.2	43.5	6.4	3.2	21.0	1.6
T. tridentata	53	•	•	17.0	54.7	28.3	•	•	•	7.5	•	•	90.5	1.9	•
Vanilla crenulata	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•
Total no. of observations	6940														

of decay. This subdivision of substrates was easy to work with during the recording.

Each epiphyte or group of epiphytes has thus been recorded in one of the nine possible light-substrate classes. The idea was to provide a base for a quantitative judgment of each species' dependence of light and substrate. However, it should be emphasized that many other influences effect the presence and distribution of epiphytes.

General distribution pattern

The distribution pattern was recorded on 463 individual trees (⩾ 10 m in height) of the high forest, representing 47 species of 21 genera. 222 trees were investigated according to the close observation method and 241 by distance observation (Table 26). The quantitative figures from this investigation for each species of epiphyte is presented in Tables 27, 28 and 29.

It became evident that most species of epiphytes are ± restricted to one or two particular section(s) of the phorophyte, while a few occur more evenly in a number of sections (Fig. 78). An analysis of the results from this investigation will later be presented, correlated to certain environmental influences (Chapter VI).

Table 28 a. Total number of records, according to the distance observation method, of pteridophytes and other vascular epiphytes in the high forest. (Explanation in Table 27 a.).

	No. of observ.	Section of the phorophytes					Heavy shade			Open shade			Full sun		
		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Pteridophytes															
Antrophyum immersum	10	30.0	70.0	•	•	•	70.0	30.0	•	•	•	•	•	•	•
A. mannianum	4	•	•	•	75.0	25.0	•	•	25.0	•	•	•	50.0	25.0	•
Arthropteris monocarpa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. orientalis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. palisoli	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Asplenium aethiopicum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. africanum	19	•	10.5	73.7	15.8	•	•	•	•	10.5	42.1	47.4	•	•	•
A. barteri	26	57.7	23.1	11.5	7.7	•	19.2	30.8	11.5	3.8	30.8	3.8	•	•	•
A. dregeanum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. geppii	22	•	4.5	77.3	18.2	•	•	•	•	•	9.1	90.9	•	•	•
A. hemitomum	1	•	•	100.0	•	•	•	•	•	•	100.0	•	•	•	•
A. megalura	183	•	•	20.2	62.3	17.5	•	•	•	1.1	22.9	10.9	3.3	32.8	29.0
A. variable v. paucijugum	7	71.4	28.6	•	•	•	•	100.0	•	•	•	•	•	•	•
Davallia chaerophylloides	63	•	20.6	41.3	31.7	6.3	•	•	•	22.2	31.7	3.2	15.9	22.2	4.8
Drynaria laurentii	929	•	2.8	42.6	42.1	12.5	•	0.2	•	28.3	14.8	2.3	45.5	8.8	•
Elaphoglossum barteri	6	16.7	•	83.3	•	•	•	16.7	16.7	•	•	66.7	•	•	•
E. chevalieri	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
E. isabelense	76	•	7.9	27.6	57.9	6.6	•	•	•	14.5	46.1	5.3	15.8	15.8	2.6
E. kuhnii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
E. salicifolium	144	•	9.7	14.6	59.0	16.7	•	•	•	34.0	20.8	•	31.9	13.2	•
Lomariopsis guineensis	1	100.0	•	•	•	•	•	•	•	100.0	•	•	•	•	•
Loxogramme lanceolata	14	7.1	42.9	35.7	14.3	•	•	•	•	28.6	71.4	•	•	•	•
Lycopodium mildbraedii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
L. warneckei	39	•	•	5.1	76.9	17.9	•	•	•	7.7	10.3	5.1	10.3	59.0	7.7
Microgramma owariensis	47	•	8.5	51.1	40.4	•	•	•	•	36.2	42.6	10.6	2.1	6.3	2.1
Microsorium punctatum	178	7.3	•	50.6	39.3	2.8	•	•	•	14.0	44.3	12.4	5.6	19.7	3.9
Nephrolepis biserrata	42	•	•	64.3	35.7	•	•	•	•	•	7.1	21.4	4.8	45.2	21.4
N. undulata	342	•	1.5	46.5	47.7	4.4	•	•	•	6.4	36.3	30.7	5.6	14.6	6.4
Oleandra distenta	352	•	4.8	64.8	30.1	0.3	•	0.6	•	17.0	39.2	35.8	2.8	3.4	1.1
Phymatodes scolopendria	174	•	9.2	57.5	28.7	4.6	•	•	•	21.8	53.4	5.7	6.9	12.1	•
Platycerium angolense	264	•	3.8	24.6	53.4	18.2	•	•	•	24.2	17.0	1.1	44.7	12.9	•
P. stemaria	126	•	0.8	11.9	61.9	25.4	•	•	•	15.9	25.4	0.8	48.4	9.5	•
Pyrrosia mechowii	16	•	•	•	62.5	37.5	•	•	•	•	37.5	•	•	62.5	•
Tectaria angelicifolia	4	75.0	25.0	•	•	•	•	50.0	50.0	•	•	•	•	•	•
T. fernandensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Vittaria guineensis	265	2.6	8.7	28.7	49.8	10.2	•	3.0	•	16.2	45.3	4.9	13.2	16.2	1.1
Xiphopteris oosora	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
X. serrulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
X. vilosissima	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Total no. of observations	3354														
Other vasc. epiphytes		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Begonia mannii	6	•	•	100.0	•	•	•	•	•	•	16.7	83.3	•	•	•
B. polygonoides	16	•	•	68.7	31.2	•	•	•	•	6.2	62.5	31.2	•	•	•
B. rubro-marginata	70	•	•	35.7	58.6	5.7	•	•	•	2.9	27.1	35.7	1.4	11.4	21.4
Calvoa monticola	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
C. trochainii	2	•	•	50.0	50.0	•	•	•	•	•	50.0	50.0	•	•	•
Medinilla mannii	144	•	1.4	32.6	55.6	10.4	•	•	•	2.1	15.3	19.4	11.8	22.2	29.2
Peperomia fernandopoiana	121	27.3	33.9	26.4	12.4	•	9.1	32.2	2.5	5.0	38.0	9.9	-	0.8	2.5
P. molleri	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. rotundifolia	10	•	•	20.0	70.0	10.0	•	•	•	50.0	•	•	30.0	20.0	•
Preussiella chevalieri	27	•	•	74.1	25.9	•	•	•	•	•	11.1	51.9	•	7.4	29.6
P. kamerunensis	32	•	•	78.1	21.9	•	•	•	•	•	12.5	50.0	•	9.4	28.1
Remusata vivipara	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Rhipsalis baccifera	170	•	•	24.7	58.8	16.5	•	•	•	4.1	21.8	10.0	12.9	32.4	18.8
Total no. of observations	598														

Table 28 b. Total number of records, according to the distance observation method, of orchids in the high forest. (Explanation in Table 27 a.)

	No. of observ.	Section of the phorophytes					Heavy shade			Open shade			Full sun		
		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Orchids															
Aerangis biloba	64	•	•	25.0	32.8	42.2	•	•	•	15.6	21.9	9.4	34.4	15.6	3.1
A. laurentii	19	•	•	•	57.9	42.1	•	•	•	21.1	•	•	73.7	5.3	•
Ancistrochilus rothschildianus	21	•	•	42.9	57.1	•	•	•	•	4.8	85.7	•	9.6	•	•
Ancistrorhynchus capitatus	20	•	20.0	25.0	50.0	5.0	•	•	•	30.0	35.0	5.0	20.0	10.0	•
A. cephalotes	54	•	29.6	24.1	40.7	5.6	•	•	•	35.2	1.9	•	63.0	•	•
A. clandestinus	3	•	•	•	100.0	•	•	•	•	66.7	•	•	33.3	•	•
A. recurvus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Angraecopsis elliptica	8	•	•	100.0	•	•	•	•	•	•	12.5	87.5	•	•	•
Angraecum birrimense	26	•	11.5	84.6	3.8	•	•	•	•	11.5	38.5	46.2	•	•	3.8
A. chevalieri	11	•	•	63.6	36.4	•	•	•	•	27.3	54.5	18.2	•	•	•
A. classensii	2	•	50.0	•	•	50.0	•	•	•	•	•	•	100.0	•	•
A. distichum	59	•	10.2	20.3	64.4	5.1	•	•	•	20.3	15.3	•	45.8	18.6	•
A. podochiloides	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
A. subulatum	4	•	•	•	100.0	•	•	•	•	•	25.0	50.0	•	25.0	•
Ansellia africana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Bolusiella talbotii	76	•	•	•	43.4	56.6	•	•	•	11.8	•	•	72.4	15.8	•
Brachycorytis kalbreveri	3	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
Bulbophyllum barbigerum	6	•	•	•	100.0	•	•	•	•	33.3	•	•	66.7	•	•
B. bifarium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. bufo	189	•	•	41.8	49.7	8.5	•	•	•	13.2	38.1	20.7	5.3	20.1	2.6
B. buntingii	56	•	•	8.9	57.1	34.0	•	•	•	8.9	•	•	76.8	14.3	•
B. calamarium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. cochleatum	72	•	2.8	45.8	51.4	•	•	•	•	20.8	48.6	15.3	2.8	11.1	1.4
B. cocoinum	162	•	•	58.1	38.7	3.2	•	8.1	1.6	•	33.9	45.2	•	4.8	6.5
B. congolanum	19	•	•	•	52.6	47.4	•	•	•	•	•	•	84.2	15.8	•
B. distans	3	•	•	66.7	33.3	•	•	•	•	•	33.3	•	33.3	33.3	•
B. falcatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. flavidum	20	•	•	•	60.0	40.0	•	•	•	•	20.0	•	20.0	60.0	•
B. imbricatum	1	•	•	•	•	100.0	•	•	•	•	100.0	•	•	•	•
B. inflatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. intertextum	74	•	•	•	58.1	41.9	•	•	•	21.6	10.8	•	51.4	16.2	•
B. josephii	5	•	•	20.0	80.0	•	•	•	•	40.0	40.0	•	20.0	•	•
B. linderi	430	•	•	14.2	61.6	24.2	•	•	•	17.0	5.3	•	63.0	14.4	0.2
B. lucifugum	48	•	•	37.5	60.4	2.1	•	•	•	31.2	43.8	•	25.0	•	•
B. lupulinum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. magnibracteatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. maximum	104	•	1.0	13.5	66.3	19.2	•	•	•	26.0	3.8	•	57.7	12.5	•
B. melanorrachis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. nigritianum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. oreonastes	828	•	1.4	11.7	52.4	34.4	•	•	•	16.5	5.8	0.2	53.5	22.2	1.7
B. pavimentatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. phaeopogon	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. recurvum	8	•	•	62.5	37.5	•	•	•	•	37.5	62.5	•	•	•	•
B. rhizophorae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. saltatorium	14	•	7.1	7.1	85.7	•	•	•	•	64.2	7.1	•	28.6	•	•
B. scariosum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. schimperanum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
B. schinzianum	19	•	•	•	73.7	26.3	•	•	•	15.8	5.3	•	63.2	15.8	•
B. winkleri	15	•	20.0	40.0	40.0	•	•	•	•	60.0	6.7	•	33.3	•	•
Calyptrochilum christyanum	70	•	11.4	43.0	41.4	4.3	•	•	•	23.0	14.3	8.6	37.1	17.1	•
C. emarginatum	4	•	25.0	75.0	•	•	•	•	•	•	•	•	100.0	•	•
Chamaeangis vesicata	45	•	6.6	4.4	80.0	8.9	•	•	•	17.8	11.1	•	60.0	11.1	•
Cyrtorchis arcuata	186	•	1.1	52.7	45.2	1.1	•	•	•	24.7	32.3	15.6	15.1	10.8	1.6
C. aschersonii	17	•	11.8	23.6	47.1	17.6	•	•	•	23.6	5.9	•	58.8	11.8	•
C. monteiroae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Diaphananthe bidens	24	•	8.3	37.5	45.8	8.3	•	•	•	8.3	29.2	12.5	37.5	12.5	•
D. densiflora	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
D. pellucida	27	•	14.8	55.6	29.6	•	•	•	•	7.4	66.7	7.4	3.7	11.1	3.7
D. rutila	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eurychone rothschildiana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Genyorchis pumila	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Graphorchis lurida	257	•	0.8	17.9	60.7	20.6	•	•	•	16.0	3.5	•	71.2	8.9	0.4
Habenaria leonensis	2	•	50.0	50.0	•	•	•	•	•	•	•	100.0	•	•	•
H. procera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Liparis caillei	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
L. nervosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Listrostachys pertusa	455	•	5.3	24.6	52.7	17.4	•	•	•	21.1	14.9	0.7	45.1	17.6	0.7
Nephrangis filiformis	306	•	•	7.5	69.3	23.2	•	•	•	18.0	2.0	•	74.2	5.9	•
Plectrelminthus caudatus	20	•	•	•	75.0	25.0	•	•	•	•	5.0	5.0	80.0	10.0	•
Podangis dactyloceras	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Polystachya adansoniae	229	•	•	17.0	50.7	32.3	•	•	•	10.5	23.6	1.7	23.1	39.3	1.7
P. affinis	1	•	100.0	•	•	•	•	•	•	100.0	•	•	•	•	•
P. dalzielii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. elastica	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. galeata	87	•	•	58.6	37.9	3.4	•	•	•	3.4	48.3	20.7	1.1	18.4	8.0
P. laxiflora	10	•	•	80.0	20.0	•	•	•	•	•	50.0	50.0	•	•	•
P. leonensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. microbambusa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. obanensis	6	•	•	50.0	50.0	•	•	•	•	•	100.0	•	•	•	•
P. paniculata	259	•	•	37.1	50.6	12.4	•	•	•	32.8	13.9	0.4	37.8	14.7	0.4
P. pobeguinii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. polychaete	185	•	•	31.9	47.0	21.1	•	•	•	9.2	18.4	22.2	10.3	28.1	11.9
P. pubervla	240	•	•	22.5	54.2	23.3	•	•	•	13.7	33.3	5.0	22.1	23.8	2.1
P. ramulosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. rhodoptera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. saccata	13	•	15.4	•	76.9	7.7	•	•	•	69.2	•	•	30.8	•	•
Polystachya subulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
P. tenuissima	3	•	•	33.3	66.7	•	•	•	•	100.0	•	•	•	•	•
P. tessallata	244	•	0.8	38.1	51.2	9.8	•	•	•	12.7	29.9	23.8	9.0	13.5	11.1
Rangaeris brachyceras	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
R. muscicola	180	•	•	25.0	63.3	11.7	•	•	•	11.7	8.9	13.3	49.4	16.7	•
R. rhipsalisocia	19	•	•	•	63.2	36.8	•	•	•	•	•	•	94.7	5.3	•
Rhipidoglossum paucifolium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Stolzia repens	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Tridactyle anthomaniaca	766	•	•	9.0	50.0	41.0	•	•	•	14.6	6.9	1.3	64.5	11.7	0.9
T. armeniaca	352	•	2.8	53.4	41.8	2.0	•	•	•	20.7	43.8	17.6	7.7	9.9	0.3
T. bicaudata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
T. crassifolia	8	•	•	12.5	75.0	12.5	•	•	•	12.5	•	•	62.5	25.0	•
T. tridactylites	50	•	8.0	52.0	30.0	10.0	•	•	•	10.0	40.0	4.0	16.0	24.0	6.0
T. tridentata	43	•	•	7.0	70.0	23.0	•	•	•	11.6	2.3	•	79.1	7.0	•
Vanilla crenulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Total no. of observations	6551														

The distribution on the phorophytes of the various epiphyte species showed somewhat different results depending on observation method. Compared to the results from the close observation method many species showed a ± marked displacement towards the outer parts of the crown in the distance observation. This could be anticipated since the epiphytes in the distance observation are more easily noticed when growing on the outer parts of the branches.

Large branches from several phorophytes were examined according to the transect technique previously described. A rather clear distribution pattern for most species of epiphytes was obtained (Fig. 79), no matter if there were few or many species present. The distribution pattern also seemed to be similar between various species of phorophytes.

Thus, the transects along the large branches seem to represent a rather fast and informative way to get a good insight into the distribution pattern for the various species. This method may preferably be used when there is a limited number of phorophytes to be examined.

Table 29. Total number of records, according to the occasional observation method, of some epiphytes in the high forest. (Explanation in Table 27 a.)

	No. of observ.	Section of the phorophytes					Heavy shade			Open shade			Full sun		
		I	II	III	IV	V	A	B	C	A	B	C	A	B	C
Pteridophytes															
Arthropteris monocarpa	46	21.7	54.3	15.2	8.7	•	26.1	47.8	•	21.7	4.3	•	•	•	•
A. palisoti	3	•	•	100.0	•	•	•	•	•	•	100.0	•	•	•	•
Asplenium aethiopicum	23	4.3	39.1	52.2	4.3	•	•	•	•	8.7	43.5	26.1	•	8.7	13.0
A. hemitomum	10	20.0	80.0	•	•	•	•	60.0	20.0	•	20.0	•	•	•	•
A. variable v. paucijugum	54	59.3	40.7	•	•	•	•	66.7	25.9	•	7.4	•	•	•	•
Elaphoglossum kuhnii	26	88.5	11.5	•	•	•	•	11.5	76.9	•	11.5	•	•	•	•
Lomariopsis guineensis	19	52.6	47.4	•	•	•	73.6	15.8	5.3	5.3	•	•	•	•	•
Tectaria angelicifolia	36	69.4	30.6	•	•	•	30.6	47.2	22.2	•	•	•	•	•	•
T. fernandensis	35	80.0	20.0	•	•	•	14.3	28.6	57.1	•	•	•	•	•	•
Xiphopteris serrulata	9	•	•	100.0	•	•	•	•	•	•	•	100.0	•	•	•
X. vilosissima	16	•	6.2	62.5	25.0	6.2	•	•	•	6.2	31.3	43.7	•	18.8	•
Orchids															
Ancistrorhynchus clandestinus	8	•	75.0	25.0	•	•	•	•	•	75.0	•	•	25.0	•	•
Angraecum classensii	46	30.4	69.6	•	•	•	•	•	•	54.3	•	•	45.7	•	•
A. podochiloides	37	16.2	78.4	5.4	•	•	•	•	•	10.8	•	•	81.1	8.1	•
Ansellia africana	32	•	9.4	53.1	37.5	•	•	•	•	•	15.6	18.7	6.2	12.5	46.9
Brachycorythis kalbreyeri	65	69.2	15.4	10.8	4.6	•	1.5	35.4	50.8	•	3.1	9.2	•	•	•
Bulbophyllum bifarium	17	•	•	58.8	29.4	11.8	•	•	•	•	70.6	11.8	•	5.9	11.8
B. calamarium	8	•	•	25.0	50.0	25.0	•	•	•	50.0	37.5	•	12.5	•	•
B. falcatum	28	•	7.1	50.0	35.7	7.1	•	•	•	17.9	53.6	14.3	•	14.3	•
B. imbricatum	23	•	4.3	17.4	73.9	4.3	•	•	•	21.7	52.2	•	8.7	17.4	•
B. inflatum	44	9.1	56.8	27.3	6.8	•	20.4	47.7	•	4.5	27.3	•	•	•	•
B. magnibracteatum	11	•	•	36.4	45.4	18.2	•	•	•	18.2	18.2	•	54.5	9.1	•
B. melanorrachis	16	•	62.5	37.5	•	•	•	•	•	•	62.5	•	•	37.5	•
B. nigritianum	17	•	23.5	17.6	58.8	•	•	•	•	11.8	58.8	17.6	•	11.8	•
B. pavimentatum	6	•	•	33.3	66.7	•	•	•	•	83.3	16.7	•	•	•	•
B. recurvum	8	•	•	62.5	37.5	•	•	•	•	37.5	62.5	•	•	•	•
B. rhizophorae	10	•	20.0	20.0	60.0	•	•	•	•	20.0	•	•	10.0	70.0	•
Calyptrochilum emarginatum	40	•	30.0	57.5	7.5	5.0	•	•	•	15.0	2.5	•	77.5	5.0	•
Cyrtorchis monteiroae	7	•	14.3	71.4	14.3	•	•	•	28.6	71.4	•	•	•	•	•
Diaphananthe densiflora	43	48.8	46.5	•	4.7	•	•	•	•	83.7	7.0	•	7.0	2.3	•
D. rutila	120	61.7	33.3	5.0	•	•	•	•	•	23.3	0.8	•	73.3	2.5	•
Eurychone rothschildiana	27	66.7	33.3	•	•	•	•	•	•	59.3	•	•	40.7	•	•
Genyorchis pumila	16	•	25.0	25.0	43.7	6.2	•	•	•	12.5	18.7	•	25.0	37.5	6.2
Habenaria leonensis	13	15.4	84.6	•	•	•	•	•	•	•	7.7	61.5	•	23.1	7.7
H. procera	35	11.4	68.6	17.1	2.9	•	•	•	•	•	22.9	54.3	•	5.7	17.1
Liparis caillei	26	•	76.9	11.5	11.5	•	•	•	•	7.7	69.2	23.1	•	•	•
L. nervosa	29	62.1	31.0	3.4	3.4	•	•	•	•	6.9	48.3	24.1	•	6.9	13.8
Podangis dactyloceras	12	•	•	83.3	16.7	•	•	•	•	33.3	8.3	•	41.7	16.7	•
Polystachya affinis	76	27.6	63.1	6.6	2.6	•	•	•	•	51.3	13.2	•	30.3	5.3	•
P. elastica	3	•	•	•	•	100.0	•	•	•	•	•	•	100.0	•	•
P. microbambusa	21	38.1	57.1	4.8	•	•	•	•	•	14.3	•	•	19.0	66.7	•
P. pobeguinii	33	3.0	24.2	42.4	15.2	15.2	•	•	•	9.1	21.2	•	18.2	48.5	3.0
P. ramulosa	16	62.5	37.5	•	•	•	•	12.5	•	•	18.7	50.0	•	18.7	•
P. rhodoptera	31	74.2	25.8	•	•	•	•	•	•	3.2	22.6	35.5	3.2	9.7	25.8
P. subulata	9	•	•	22.2	55.6	22.2	•	•	•	•	22.2	•	33.3	44.4	•
P. tenuissima	14	•	•	35.7	57.1	7.1	•	•	•	•	28.6	•	21.4	50.0	•
Rangaeris brachyceras	18	•	5.6	22.2	66.7	5.6	•	•	•	•	16.7	•	5.6	50.0	27.8
Rhipidoglossum paucifolium	27	51.9	37.0	11.1	•	•	•	•	•	37.0	11.1	•	37.0	14.8	•
Stolzia repens	15	•	6.7	13.3	60.0	20.0	•	•	•	•	80.0	•	•	20.0	•
Tridactyle bicaudata	57	•	26.3	21.1	47.4	5.3	•	•	22.8	54.4	3.5	3.5	15.8	•	•
Vanilla crenulata	6	83.3	16.7	•	•	•	•	•	33.3	•	•	66.7	•	•	•
Other vasc. epiphytes															
Calyoa monticola	28	85.7	14.3	•	•	•	•	35.7	50.0	•	7.1	7.1	•	•	•
C. trochainii	46	34.8	26.1	39.1	•	•	•	•	•	6.5	54.3	32.6	•	2.2	4.3
Peperomia molleri	25	92.0	8.0	•	•	•	8.0	32.0	44.0	•	8.0	8.0	•	•	•
Remusatia vivipara	32	•	34.4	62.5	3.1	•	•	•	•	•	18.7	53.1	•	9.4	18.7
Total no. of observations	1478														

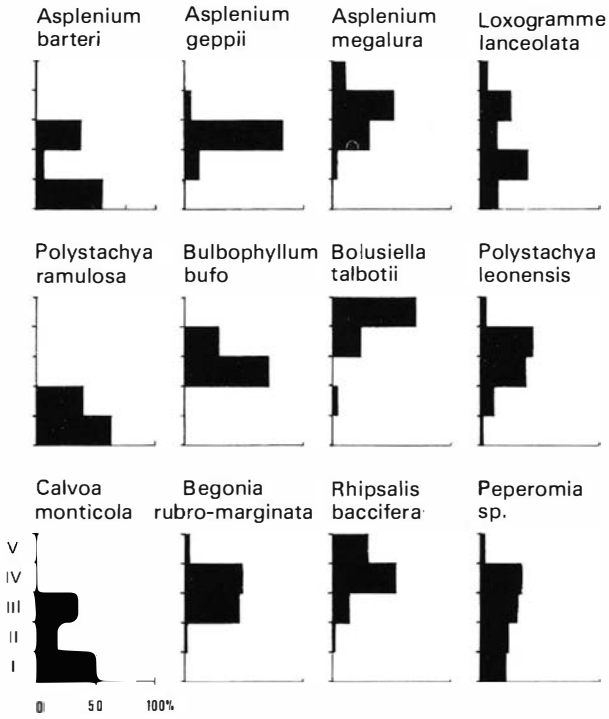


Fig. 78. Occurrence of some epiphytes on the phorophytes distributed among the different sections. (From Table 27, *Polystachya ramulosa* from Table 29.)

Epiphyte communities

Terminology

The frequently observed aggregation of epiphytes ('arboreal gardens' according to Oliver 1930:2) in limited areas on the phorophyte is of interest not only because of the information they provide as to common environmental requirements for various species but also as a source in the analyses of the colonization and development of the epiphytic flora in general. The terminology that has been used in the classification of epiphyte communities is confusing. The terms 'epiphyte societies' (Oliver 1930:16) and 'association' (Went 1940:86) have been used. Epiphytic association and epiphytic sociation were proposed by Omura (1953). Hosokawa (1953, 1954 a, b, c, 1968) has created a new terminology for the community units of epiphytes. From the viewpoint of the ecosystem concept he does not agree with the use of phytocoenosial units for classifying epiphyte communities. Instead he has suggested the terms epies, epilia and epido, for various types of epiphyte communities (Hosokawa 1968:483).

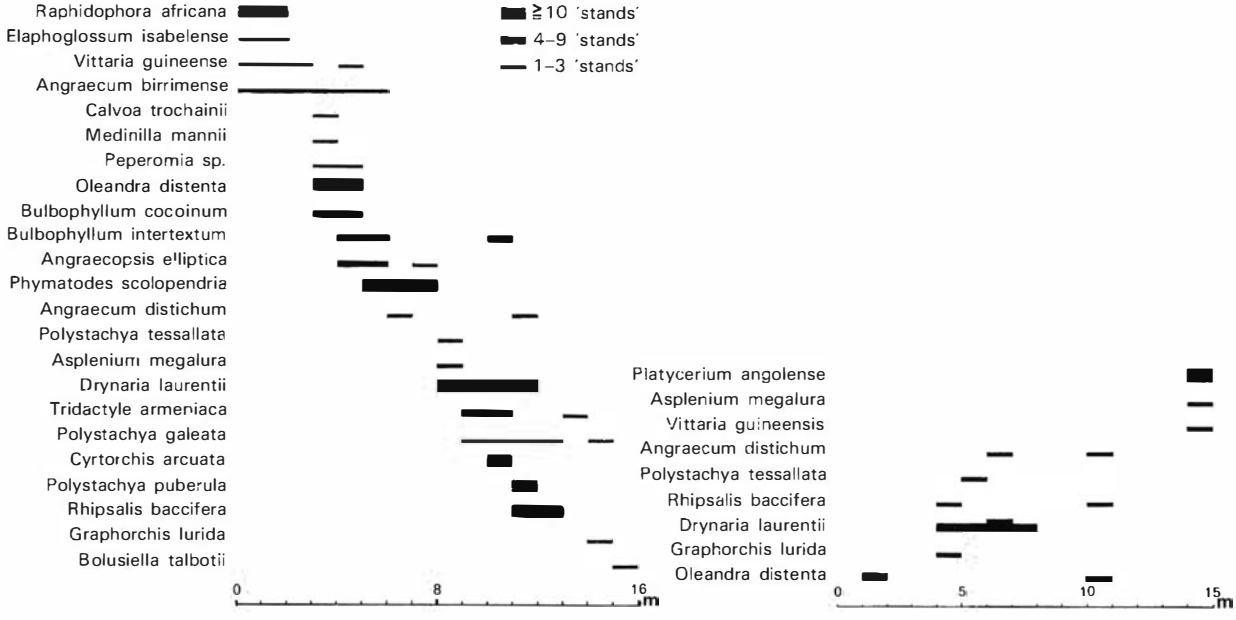


Fig. 79. Number of epiphytes and their distribution along a branch of: Left: *Parinaria excelsa,* illustrated according to the 'transect' technique. Seka Valley 600 m. Right: *Pipptadeniastrun africanum,* illustrated according to the 'transect' technique. Yekepa 500 m.

To avoid adding to the already confusing terminology of epiphyte communities, they will here simply be called epiphyte communities (e.c.). To separate them from each other they are named by the dominant species ('cover') and the most frequently occurring species in the community. This unit should be homologous to the term 'epilia' proposed by Hosokawa.

Methods

The technique used in the investigation and description of terrestrial plant communities is impossible to use under the circumstances of growth and occurrence which the epiphytic plants exhibit. The knowledge of the epiphytic plant communities is based on records from close and distance examinations. The interest has been concentrated on the presence of the various species rather than on their number.

An epiphyte community is considered to exist when a group of three or more species form a unit, and when the distance from two of them does not exceed 0.5 m to the third. The root systems and the stems are often heavily intermixed, to such a degree that the plants often grow on top of each other.

Epiphytes that colonize the vegetative parts of other epiphytes are called hyper-epiphytes by Tixier (1966) and 'secondary' epiphytes by Hosokawa. The delimitation of an epiphyte community in most cases is easy to do, since the grouping of plants is rather distinct (Fig. 79). There are some spectacular exceptions from this rule. *Drynaria laurentii* may often cover stretches of more than five meters' length. This extended distribution will of course connect a larger number of plants to this particular epiphyte. However, most epiphyte communities occur in a limited area with no other plants nearby. This is the case particularly for certain communities formed by epiphytes that are attracted to humus deposits. Seven different epiphyte communities are recognized

Table 30. The number, distribution on the phorophytes and species composition of the epiphyte communities examined. (The distribution is given as a percentage of the total number of communities and the species composition according to close and distance observations.)

Epiphyte community	No of commun.	Distribution on the phorophyte					No. of species								
		Sections					Pterid.		Orchids		Others		Total		Grand total
		I	II	III	IV	V	Cl	Di	Cl	Di	Cl	Di	Cl	Di	
Angraecum birrimense-Raphidophora africana	65	–	43.1	56.9	–	–	13	10	19	15	6	5	38	30	39
Asplenium africanum-Peperomia sp.	13	–	38.5	15.3	46.2	–	3	3	0	1	3	3	6	7	9
Oleandra distenta-Tridactyle armeniaca	104	–	6.8	70.2	23.1	–	13	17	19	20	12	10	44	47	51
Microsorium punctatum-Vittaria guineensis	63	–	6.8	70.2	23.1	–	6	5	13	11	7	5	26	21	29
Drynaria laurentii-Asplenium megalura	190	–	5.3	34.7	48.9	11.1	13	8	37	25	8	8	58	41	62
Platycerium stemaria-Nephrolepis undulata	54	–	7.4	51.8	40.7	–	7	5	9	7	4	3	20	15	22
Platycerium angolense-Nephrolepis undulata	50	–	30.0	12.0	58.0	–	6	4	7	5	3	3	16	12	17
Asplenium dregeanum-Peperomia sp.	42	–	88.1	11.9	–	–	9	–	5	–	5	–	19	–	19
Tridactyle tridactylites-Medinilla mannii	60	–	3.3	76.7	20.0	–	11	8	8	7	5	3	24	18	26
Bulbophyllum scariosum-Polystachya dalzielii	25	–	–	12.0	64.0	24.0	11	8	6	5	3	4	20	17	21

below 1000 m alt. and three more above that altitude.

The investigation includes a total of 666 'community aggregations'. Their distribution on the phorophyte and the total number of species recorded in the various communities are given in Table 30. The ten most frequently occurring species in each community are presented in Table 32.

Abundance

Like epiphytes in general the epiphyte communities are more abundant in older trees. A total of 25 'community aggregations' were found on the 118 trees that were examined in the three sample plots (Tables 14, 15 and 16). In relation to the abundance of the dominant species most communities were scarce. *Oleandra distenta,* however, was found just as frequent in a community formation as in a single state. As would be expected the most common number of species in the individual communities is three, which are the lowest possible according to the definition used (Table 31). There are, however, some exceptions. The *Oleandra distenta - Tridactyle armeniaca* and *Angraecum birrimense - Raphidophora africana* communities, built up by more than five species each, were more common than those with a lesser number of species. The possible explanation to this could be that a more or less simultaneous colonization by several species is taking place when the community forming species has created a suitable environment. Both these communities are found in the lower parts of the phorophyte, and could possibly catch seeds or seedlings washed down by heavy rainfall.

Epiphyte communities at altitudes below 1000 m

Angraecum birrimense-Raphidophora africana e.c. This community is most common around the first ramification on trees which have a rich supply of light in that section. This means that the community will appear mostly in secondary forests or on trees bordering rivers or creeks, or along tracks or roads.

Table 31. The number of species in the different epiphyte communities, expressed as a percentage of the total number of records.

Community	Method of examination	No examined	No. of species			
			3	4	5	> 5
Angraecum birrimense -	Close	36	8.3	9.0	22.0	55.5
Raphidophora africana	Distance	29	13.9	10.3	17.2	58.6
Asplenium africanum -	Close	5	40.0	40.0	20.0	–
Peperomia sp.	Distance	8	50.0	37.5	12.5	–
Oleandra distenta -	Close	26	26.9	19.2	7.7	46.2
Tridactyle armeniaca	Distance	78	25.6	23.1	11.5	39.8
Microsorium punctatum -	Close	27	63.0	18.5	7.4	11.1
Vittaria guineensis	Distance	36	50.0	5.6	22.2	22.2
Drynaria laurentii -	Close	62	45.1	9.7	11.3	33.9
Asplenium megalura	Distance	128	50.8	15.6	14.1	19.5
Platycerium stemaria -	Close	36	55.6	8.3	8.3	27.8
Nephrolepis undulata	Distance	18	50.0	11.1	5.6	33.3
Platycerium angolense -	Close	40	72.5	25.0	2.5	–
Nephrolepis undulata	Distance	10	80.0	20.0	–	–
Asplenium dregeanum -	Close	42	66.6	23.8	4.8	4.8
Peperomia sp.	Distance	–	–	–	–	–
Tridactyle tridactylites -	Close	13	46.1	30.8	23.1	–
Medinilla mannii	Distance	43	60.5	27.9	2.3	9.3
Bulbophyllum scariosum -	Close	7	57.1	28.6	14.3	–
Polystachya dalzielii	Distance	18	50.0	27.8	16.7	5.5

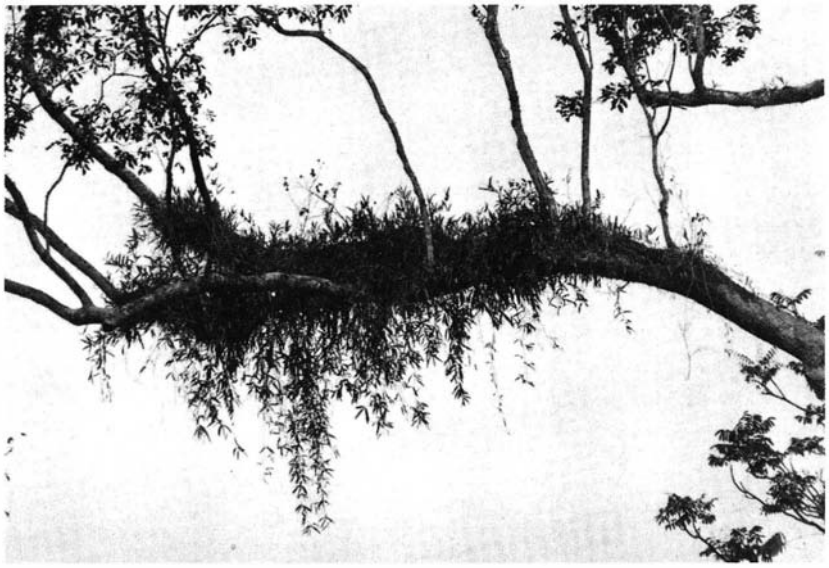


Fig. 80. *Oleandra distenta - Tridactyle armeniaca* epiphyte community. Grassfield 550 m.

It gives an impression of an irregular jumble of herbaceous climbers, lianas and trailing epiphytes.

The community is delicately balanced. An increase in light and evaporation will change this community leaving only the *Diaphanthe* orchids, a decreasing light supply will lead to an overgrowth by the vigorous *Raphidophora africana.*

Asplenium africanum - Peperomia sp. e.c.
Asplenium africanum that is rather uncommon, forms an accumulation of humus around its attachment to the substrate in a similar way as *Microsorium punctatum.* Only 13 communities have been found and examined, 8 with telescope and 5 on felled trees. With so few observations it is of little use to make an analysis of the occurrence of the various species. Worth mentioning is the presence of *Peperomia* sp. in 69.2 % of the communities examined.

Oleandra distenta - Tridactyle armeniaca e.c.
The fern *Oleandra distenta,* that forms the base of this community, is common and easily recognized. It often starts to grow in or around the ramifications of the larger branches in the central part of the crown. It expands in all directions but is mainly found at the basal parts of the branches that are often completely overgrown by thick cushions of this fern and species associated with it. The slender rhizomes often hang down giving this community a characteristic appearance (Fig. 80). In the earlier stages of the development of this community certain orchids may grow between the rhizomes, but later as debris is accumulated they become fewer and fewer.

This community is not subject to the extreme variation in microclimate that exists further out on the branches, and the light intensity is naturally lower. These conditions are also reflected in the composition of the species in the community. A high number of pteridophytes and other vascular epiphytes (non-orchids) are typical. Note that no orchid species except *Tridactyle armeniaca* is found among the 10 most common species (Table 32). This community is composed of a mixture of humus-preferring species and species tolerating different kinds of substrate. Orchids with preference for rich humus and open shade found in this community are, e.g. *Brachycorythis kalbreyeri* and *Habenaria procera.* The majority of orchid species that occasionally occur here normally belong to the central or outer parts of the branches. Also the pteridophytes in this community are a mixture of species of humid habitats such as filmy ferns and *Nephrolepis undulata,* as well as *Drynaria laurentii* and *Microsorium punctatum* of more sunny and drier sections of the crown. *Begonia polygonoides, Remusatia vivipara, Peperomia* sp. as well as more drought resistent species such as *Rhipsalis baccifera* and *Begonia rubro-marginata* are also frequent in this community.

Microsorium punctatum - Vittaria guineensis e.c.
This community has a very limited distribution and

Table 32. The ten most common species in the different epiphyte communities. The occurrence is given as a percentage of the total number of communities examined (Table 30).

Close observation		Distance observation	
Angraecum birrimense - Raphidophora africana e.c.			
Raphidophora africana	79.3	Raphidophora africana	83.3
Vittaria guineensis	48.2	Elaphoglossum barteri	36.1
Elaphoglossum barteri	34.5	Vittaria guineensis	33.3
Calvoa trochainii	34.5	Diaphananthe bidens	27.8
Diaphananthe bidens	24.1	Ancistrorhynchus capitatus	25.0
Microgramma owariensis	20.7	Calvoa trochainii	25.0
Nephrolepis undulata	20.7	Peperomia sp.	19.4
Habenaria procera	13.8	Microgramma owariensis	13.9
Ancistrorhynchus capitatus	6.9	Nephrolepis undulata	11.1
Rhipidoglossum paucifolium	6.9	Diaphananthe rutila	5.6
Asplenium africanum - Peperomia sp. e.c.			
Peperomia sp.	80.0	Peperomia sp.	62.5
Asplenium megalura	40.0	Preussiella sp.	37.5
Calvoa trochainii	40.0	Begonia mannii	25.0
Elaphoglossum barteri	20.0	Arthropteris orientalis	25.0
Nephrolepis undulata	20.0	Nephrolepis undulata	12.5
Begonia mannii	20.0	Asplenium megalura	12.5
		Polystachya tessallata	12.5
Oleandra distenta - Tridactyle armeniaca e.c.			
Tridactyle armeniaca	53.8	Tridactyle armeniaca	41.7
Peperomia sp.	42.3	Drynaria laurentii	30.6
Nephrolepis undulata	34.6	Begonia polygonoides	27.8
Phymatodes scolopendria	30.8	Rhipsalis baccifera	27.8
Begonia polygonoides	26.9	Phymatodes scolopendria	25.0
Calvoa trochainii	23.1	Nephrolepis undulata	19.4
Rhipsalis baccifera	23.1	Nephrolepis biserrata	16.7
Preussiella chevalieri	19.2	Elaphoglossum isabelense	16.7
Asplenium megalura	15.4	Peperomia sp.	13.9
Microsorium punctatum	11.5	Asplenium megalura	12.5
Microsorium punctatum - Vittaria guineensis e.c.			
Vittaria guineensis	51.8	Vittaria guineensis	36.1
Peperomia sp.	44.4	Davallia chaerophylloides	33.3
Davallia chaerophylloides	37.0	Peperomia sp.	30.6
Polystachya tessallata	29.6	Polystachya tessallata	27.8
Diaphananthe bidens	25.9	Asplenium megalura	25.0
Begonia rubro-marginata	22.2	Medinilla mannii	25.0
Nephrolepis undulata	18.5	Diaphananthe bidens	19.4
Oleandra distenta	18.5	Graphorchis lurida	13.9
Medinilla mannii	14.8	Angraecum birrimense	13.9
Bulbophyllum cocoinum	14.8	Nephrolepis biserrata	11.1
Drynaria laurentii- Asplenium megalura e.c.			
Asplenium megalura	53.2	Asplenium megalura	43.7
Tridactyle armeniaca	46.8	Rhipsalis baccifera	29.7
Rhipsalis baccifera	45.1	Tridactyle armeniaca	25.0
Polystachya tessallata	32.3	Graphorchis lurida	25.0
Bulbophyllum linderi	25.8	Bulbophyllum oreonastes	18.7
Ficus kamerunensis	22.6	Angraecum distichum	17.2
Graphorchis lurida	22.6	Cyrtorchis arcuata	14.1
Polystachya galeata	16.1	Polystachya tessallata	14.1
Medinilla mannii	11.3	Phymatodes scolopendria	12.5
Nephrolepis undulata	9.6	Bulbophyllum linderi	11.7
Plathycerium stemaria - Nephrolepis undulata e.c.			
Nephrolepis undulata	58.3	Nephrolepis undulata	66.7
Polystachya tessallata	38.9	Begonia rubro-marginata	50.0
Peperomia sp.	27.8	Polystachya tessallata	38.8
Begonia rubro-marginata	27.8	Davallia chaerophylloides	38.8
Vittaria guineensis	22.2	Diaphananthe bidens	33.3
Lycopodium warneckei	19.4	Rhipsalis baccifera	33.3
Rhipsalis baccifera	16.7	Vittaria guineensis	27.8
Polystachya galeata	13.9	Tridactyle anthomaniaca	22.2
Asplenium megalura	11.1	Peperomida sp.	16.7
Polystachya polychaete	11.1	Asplenium megalura	11.1
Platycerium angolense - Nephrolepis undulata e.c.			
Nephrolepis undulata	47.5	Nephrolepis undulata	60.0
Polystachya tessallata	30.0	Polystachya tessallata	40.0
Peperomia sp.	25.0	Davallia chaerophylloides	30.0
Davallia chaerophylloides	17.5	Begonia rubro-marginata	30.0
Begonia rubro-marginata	15.0	Diaphananthe bidens	30.0
Vittaria guineensis	15.0	Rhipsalis baccifera	30.0
Polystachya galeata	12.5	Tridactyle anthomaniaca	30.0
Lycopodium warneckei	12.5	Vittaria guineensis	20.0
Nephrolepis biserrata	7.5	Chamaeangis vesicata	10.0
Diaphananthe bidens	7.5	Lycopodium warneckei	10.0
Asplenium dregeanum - Peperomia sp. e.c.			
Peperomia sp.	69.0		
Polystachya leonensis	28.6		
Elaphoglossum chevalieri	21.4		
Asplenium barteri	19.0		
Medinilla mannii	16.7		
Arthropteris monocarpa	14.3		
Polystachya laxiflora	14.3		
Asplenium aethiopicum	11.9		
Begonia rubro-marginata	9.5		
Bulbophyllum inflatum	7.1		
Tridactyle tridactylites - Medinilla mannii e.c.			
Medinilla mannii	58.8	Medinilla mannii	53.5
Asplenium dregeanum	41.2	Polystachya laxiflora	27.9
Polystachya leonensis	35.3	Lycopodium mildbraedii	25.6
Vittaria guineensis	35.3	Peperomia sp.	23.3
Asplenium barteri	29.4	Polystachya leonensis	23.3
Polystachya laxiflora	23.5	Asplenium dregeanum	20.9
Polystachya obanensis	23.5	Vittaria guineensis	18.6
Rangaëris muscicola	23.5	Cyrtorchis arcuata	13.9
Peperomia sp.	23.5	Bulbophyllum scariosum	11.6
Elaphoglossum barteri	17.6	Elaphoglossum salicifolium	11.6
Bulbophyllum scariosum - Polystachya dalzielii e.c.			
Xiphopteris oosora	42.9	Polystachya dalzielii	44.4
Polystachya dalzielii	42.9	Lycopodium mildbraedii	27.8
Elaphoglossum salicifolium	28.6	Asplenium megalura	22.2
Bulbophyllum bifarium	28.6	Vittaria guineensis	22.2
Xiphopteris vilosissima	28.6	Tridactyle tridactylites	22.2
Arthropteris monocarpa	14.3	Elaphoglossum salicif.	16.7
Asplenium megalura	14.3	Asplenium geppii	11.1
Lycopodium mildbraedii	14.3	Arthropteris sp.	11.1
Polystachya pobeguinii	14.3	Podangis dactyloceras	11.1
Vittaria guineensis	14.3	Asplenium aethiopicum	11.1

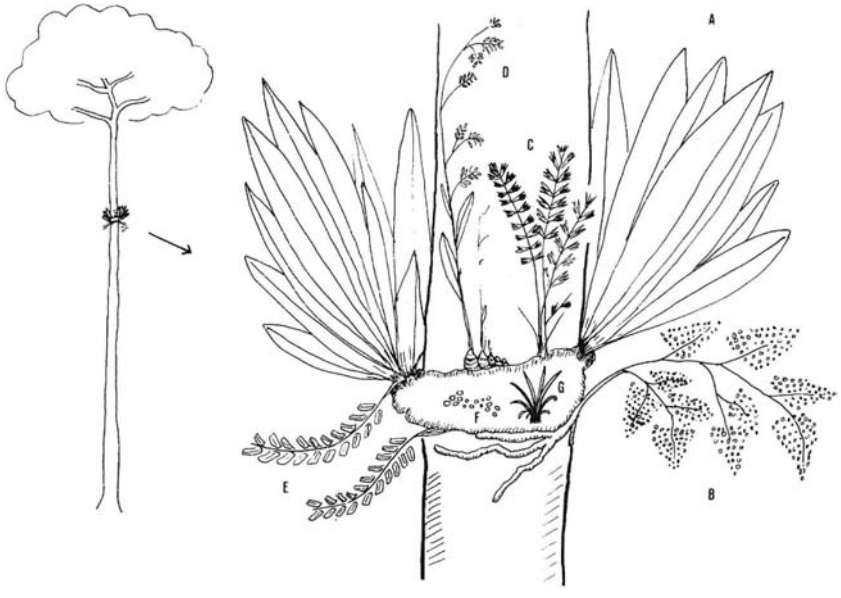


Fig. 81. Simplified drawing of a *Microsorium punctatum* - *Vittaria guineensis* epiphyte community. (A) *Microsorium punctatum,* (B) *Davallia chaerophylloides,* (C) *Asplenium megalura,* (D) *Polystachya tessallata,* (E) *Tridactyle anthomaniaca,* (F) *Peperomia rotundifolia,* (G) *Vittaria guineensis.*

serves as a small refuge for humus-demanding species, particularly if it grows on a smooth barked phorophytes (Fig. 81). Two plants that are often associated with this particular fern are *Vittaria guineensis* and *Davallia chaerophylloides.*

Drynaria laurentii - *Asplenium megalura e.c.*
The *Drynaria* fern is probably the most common species of epiphyte in the investigated area. It is found in sunny habitats mostly in the crowns. It easily gets a foothold on smooth surfaces; it can even be seen growing on vertical concrete walls. This highly specialized fern has two kinds of fronds (Fig. 26). The fertile fronds have long narrow finger-like pinnately arranged lobes. These lobes or segments are articulated from the midrib after maturity. Afterwards the midribs remain in an erect position for many years.

The sterile fronds are thin and papery, somewhat resembling oak leaves, and are held upright and more or less parallel to the substratum. Between these sterile, mostly dead leaves and the substratum a niche is formed in which materials of various kinds are collected. The sterile leaves are persistent and remain in function as 'humus collectors'. When they get older and start to decay, the veins persist forming a delicate net. This species is a very hardy plant that is able to survive severe conditions. A colony that was placed on top of a flat aluminium roof, with no protection whatsoever, showed no sign of discomfort but continued to grow year after year.

Fig. 82. Simplified drawing of a *Drynaria laurentii* - *Asplenium megalura* epiphyte community, 29 m above the ground, on a *Piptadeniastrum africanum.* Yekepa 530 m. (A) *Drynaria laurentii,* (B) *Oleandra distenta,* (C) *Bulbophyllum lupulinum,* (D) *Bulbophyllum bufo,* (E) *Graphorchis lurida,* (F) *Bulbophyllum buntingii,* (G) *Asplenium megalura.*

Fig. 83. *Drynaria volkensii* and *Rhipsalis baccifera*. Usambara Mts 900 m, Tanzania.

Fig. 84. *Platycerium stemaria* - *Nephrolepis undulata* epiphyte community. Nimba Range 700 m. Note the large *Begonia rubro-marginata* in the centre.

The rhizome is thick and hard, covered with a dense insulating layer of scales. Sometimes it branches, particularly when it grows in a vertical direction.

The *Drynaria* community has a wide distribution and passes through several stages in its development. During the colonization stages (Fig. 82) epiphytic orchids, e.g. *Bulbophyllum oreonastes* grow on the open bark surfaces between the rhizomes of the fern. The high total number of orchids, with not less than 38 species registered from this community, are mostly connected to this stage. As the fern grows and takes larger parts of the substrate in possession the orchids become less numerous.

The humus is utilized by several plants. *Rhipsalis baccifera* and *Peperomia sp.* are among the first to settle in this environment (Fig. 83). Among the orchids *Angraecum distichum* and even *Graphorchis lurida* are still present during this stage in development. When more humus has been formed *Asplenium megalura* will be common. In roughly every second community examined this species was present.

In the final stage a wide array of plants that are favoured by a rich supply of humus invade the thick densely overgrown accumulation. Now even terrestrial plants appear as facultative epiphytes. During this stage the *Drynaria* fern itself plays an inferior role, and is in many cases dead or dying. As a matter of fact the presence of rhizomes and old sterile leaves from *Drynaria laurentii* in the bottom parts of many rich accumulations indicate this process.

From the Usambara Mts in Tanzania Moreau (1943) reports: "Somewhat contrary to the expectation orchids do not occur in association with the coarse epiphytic fern *Asplenium nidus* and *Dryopteris laurentii (Drynaria laurentii)* which would seem to offer favourable foothold, but orchids often have their roots closely interwoven with those of smaller ferns and naturally are often more or less embedded in moss and lichens." This is partly true, even if I myself on a brief visit in the same area dis-

Fig. 85. *Chamaeangis vesicata* in a *Platycerium angolense* - *Nephrolepis undulata* epiphyte community. Yekepa 500 m.

covered several ferns and one orchid, *Cirrhopetalum umbellatum* (Forst. f.) Hook. & Arn., associated with *Drynaria volkensii*. Moreau probably refers to the first stages when the *Drynaria* fern seldom has any other epiphytes associated with it.

Platycerium stemaria - *Nephrolepis undulata e.c.* and *Platycerium angolense* - *Nephrolepis undulata e.c.*

Two species of the genus *Platycerium* are common in the Nimba area, *Platycerium angolense* and *P. stemaria* can often be found together in non-limiting environments, but in open or more exposed habitats *Platycerium angolense* dominates. In other parts of Africa they also grow on rocks, e.g. in the Matombo region east of the Uluguru Mts in Tanzania. Both species are widespread in tropical Africa. They inhabit the outermost branches of trees in the primary forest, but in secondary forest or on scattered trees around villages and in farmland they can be found on any part of the tree.

The fertile and sterile leaves are of a different shape (Figs 84, 85). This dimorphism is of a particular function in the life of the plant. The sterile leaves can be divided into two sections. The upper part is open towards the air on both sides, it is thin and pergameneous. Their function is to collect the falling debris to be used in the building of humus. The lower part of the sterile leaves is considerably thicker. This part of the leaf is a deposition area for the debris that has been trapped between the upper part of the leaf and the branch or trunk. The space between the sterile leaves is utilized by roots that clearly can be seen through the lower parts of the newly developed sterile leaves. The fertile leaves are long and pendulous.

The rhizome is short. It is not creeping as in most other epiphytic ferns but is always growing at a 90 degree angle towards its point of attachment.

The occurrence of the *Platycerium* communities in relation to the total presence of these ferns, is low. The low number of epiphytes associated with the *Platycerium* ferns is also surprising. *Platycerium angolense* had 17 species and *P. stemaria* 22 species totally. A look at the species compositions shows that the plants associated with the *Platycerium* ferns commonly appear in other epiphytic communities as well. *Nephrolepis undulata* is the species that most frequent takes advantage of the substrate or perhaps a favourable microclimate caused by the large *Platycerium* leaves. Boyer (1964) reports that *Microgramma owariensis* and *Phymatodes scolopendria* sometimes are associated with *Platycerium* ferns. She also mentions that small plants of cocoa trees and oil palms were found in accumulations of these ferns. Holtum (1960) states that: "*Cymbidiella rhodochila* in Madagascar is invariably found growing in association with a *Platycerium*." The same observation appears in Encyclopedia of Cultivated Orchids (Hawkes 1965:139) with no reference to the source.

Epiphyte communities at altitudes above 1000 m

Asplenium dregeanum—Peperomia sp. e.c.

At the base of trunks (from the ground to roughly 4—5 m height) *Asplenium dregeanum* and *Peperomia*

Fig. 86. *Tridactyle tridactylites - Medinilla mannii* epiphyte community. Mt Gbahm 1300 m.

sp. dominate. They are so common that nearly every tree has at least one of them on its trunk. At these altitudes the filmy ferns are also common and particularly on the trunks, and thus are often associated with the species of this community.

The dominating fern, *Asplenium dregeanum,* multiplies by sending out modified stolon-like fronds which take root and produce a colony of daughter plants, expanding the community in many directions.

Since this community occurs on the trunks relatively close to the ground no distance observations had to be performed.

Tridactyle tridactylites - Medinilla mannii e.c.
In the central part of the crown and especially around the larger ramifications the orchid *Tridactyle tridactylites* forms huge interwoven masses (Fig. 86). Here several plants occur, such as *Polystachya laxiflora, P. leonensis* and *Asplenium dregeanum.* Scattered groups of filmy ferns may occur but very dominant are the mosses that occupy the major part of the branches in and around this community.

Bulbophyllum scariosum - Polystachya dalzielii e.c.
This somewhat less clearly defined community is found in the central or outermost parts of the branches. It includes a number of small sized epiphytes, e.g. *Xiphopteris villosissima,* that are easily overlooked in a distance examination.

Two species of orchids dominate this community: *Bulbophyllum scariosum* which is easily seen, while the more tiny *Polystachya dalzielii* is harder to observe when not in flower. In this section of the crown the lichens cover the branches or hang down (*Usnea* sp.) from the finest twigs.

General observations
Ferns form the base in seven of the ten recognized communities. In all these communities it is the substrate-building capacity of the ferns that seem attractive to the other species. Interaction and antagonism between ferns and orchids, as well as between mosses and liverworths, have been reported by Tixier. He found that the 'stations' rich in orchids has generally no ferns and reciprocally. "Les Fougères présentent une axèmie assez forte vis-à-vis des Orchidées" (Tixier 1966:124). However, *Drynaria rigidula* was found to hold numerous epiphytes. This statement may seem to contradict the observations in the Nimba area, but the statement is more correct for the lower parts of the trunks (a section which was particularly carefully examined by Tixier). It is, however, hard to asess the amount of competition between ferns and orchids. In many cases it is probably the low light intensities close to the ground that limit the presence of orchids, and higher up in the trees the evaporating power of the air often limits the presence of ferns.

Epiphyte succession

As the phorophyte grows it will pass through several 'environmental stages', e.g. it's place in the forest alters, the size and the shape of the crown and the morphology of the bark changes. These are primary changes. Secondary changes, e.g. establishment of new species of epiphytes will effect the competition between the epiphytes. The epiphytic flora itself also participates in the successional processes through active or passive contributions to the formation of humus.

Direct or indirect methods may be employed to estimate the changes. The best method would naturally be to map the epiphytic flora on a number of branches in the crowns of living trees. These branches could then be re-examined after certain time intervals, thus giving a correct picture of the development and eventually changes of the flora. This method would be similar to the 'permanent quadrate' technique used in terrestrial ecology, except for the changes in size of the branch caused by growth or broken off pieces. Unfortunately this method is for practical reasons very difficult to use. The inaccessibility of the tree crowns has previously been discussed. The slow development of many of the epiphytic plants, e.g. the orchids, would also

make it necessary to continue the observations for a very long period of time. Thus the difficulties connected with a detailed study of the epiphytic flora on a phorophyte in situ make this kind of investigation less useful. There are, however, several indirect methods to use. Comparisons of the epiphytic flora between phorophytes in the primary forest and on phorophytes that have become more exposed through changes in their environment may give valuable information on the amount and direction of eventual changes. Analyses of humus deposits may also reveal traces of an earlier epiphytic flora.

Epiphyte succession in Himalayan Quercus forest

The sucessions of epiphytes has been studied by Dudgeon (1923) in a *Quercus incana* forest at Landour, Western Himalayas (1900-2100 m). Since the earliest stages in the colonization of the branches are not dealt with in this study it might be of interest to give an account of his observations.

Six separate stages are distinguished:

1. Crustose lichen stage; starting when the branch is three to four years old.
2. Foliose and fructicose lichen stage; starting almost as early as the crustose lichens, but begins to make a characteristic presence three to four years later.
3. Pioneer moss stage; pioneer mosses gain foothold in favourable spots. Other trailing and erect mosses gradually crowding out the lichens, probably by shading them.
4. Climax moss stage; starting when the thick continuous pads are developed. Under favourable conditions this stage is reached in about 20 years.
5. Fern stage; starts when epiphytic ferns gain footholds in the moss pads. The fern stems and roots collect and hold more dust, forming a soil bed that may attain a thickness of 10 cm.
6. Flowering plant stage; starts with the appearance of other vascular plants apart from the ferns.

Dudgeon summarizes his observations: "Successions shown by epiphytes are considered to be unique, because of (1) the short time required for completion, (2) the unusual clearness of successive stages, (3) the small size of the plants involved, and (4) the adaption of the plants to repeated and prolonged desiccation."

Although Dudgeon's investigation refers to a cooler environment than the rain forest in Nimba, the pattern described could with some exceptions be said to be valid for the rain forest in Nimba as well.

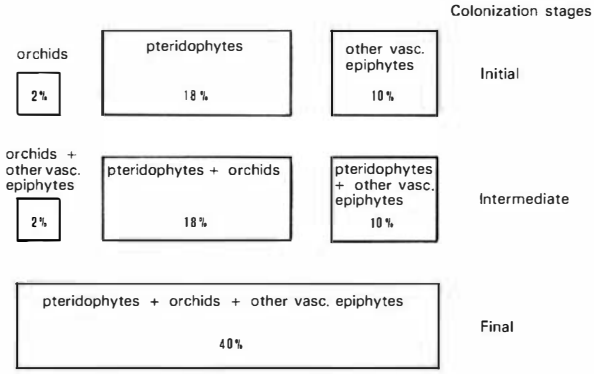


Fig. 87. 'Colonization stages'. The number of phorophytes in sample plots I-III have been split into seven classes based on the presence of different epiphytes. The occurrence of the different classes is given as a percentage of the total number of phorophytes and is also illustrated in blocks proportional to each other.

The moss stages (3 and 4) are non-existent in the rain forest below 1000 m altitude, but become increasingly important at higher altitudes.

Succession indicated by floristic composition

This analyse is built on the assumption that sooner of later species from all of the three major groups of epiphytes, (i.e. the pteridophytes, the orchids and the other vasc. epiphytes), will be represented on the phorophyte. No phorophyte, except the oil palm, *Elaeis guineensis,* has given proof of being rejected by any particular group of epiphytes.

Three stages in the colonization of the phorophytes are recognized, the initial, intermediate and final stage. During the initial stage species from only one of the major groups of epiphytes are represented on the phorophyte. In the intermediate stage species from two groups are present, and in the final stage species of all groups are occurring on the phorophyte. From the three sample plots (Tables 14-16) the occurrence of phorophytes representing the three colonization stages are given in Fig. 87. The colonization seems to start with the pteridophytes or the other vascular epiphytes. This initial stage is succeded by the entry of the orchids. As time passes these phorophytes in the intermediate colonization stage will most likely be colonized by some species from the third group and enter the final stage.

Succession traced by analysis of humus deposits

This technique was used in the attempt to reconstruct the development of the humus deposits

and the plants involved in this process. The nature of these deposits is very heterogeneous. They are built up of material in all stages of decomposition, mostly resembling peat. Occasionally the decomposition has gone so far that a mineralization has begun. Such soil-like deposits can be found at the basal parts on the large branches of old trees. More commonly deposits are built up by material that is partly decomposed. It is rather surprising that parts of dead plants incorporated in the accumulation several years earlier frequently can be identified. This shows either that the plants are very resistent towards decomposition, or that the micro-organisms that are responsible for the break-down process are restrained in their activities by the environment, which is regularly subjected to drought.

Several cross-sections were cut through the accumulations at a right angle to the axis of the phorophyte, with a sharp broadblade knife. This gave a glimpse of the 'stratification' in situ. The content from the bottom layer was sifted through a sieve with a mesh of 10 x 10 mm. Remains of plants, such as old pseudobulbs and rhizomes, could then much easier be discovered. A total of 13 deposits of five different epiphyte communities were examined.

Angraecum birrimense - Raphidophora africana e.c.
Two communities, both occurring on the trunk 3-4 m above the ground on two tall trees, were examined. The humus layer was thin and held in a vertical position by a network of roots. Six species of epiphytes were present: *Angraecum birrimense, Calvoa trochainii, Diaphananthe rutila, Nephrolepis undulata, Polystachya rhodoptera* and *Raphidophora africana,* with the first and last species dominating.

In the bottom layer in one of the communities 3 groups of pseudobulbs from *Polystachya affinis* were discovered.

Drynaria laurentii - Asplenium megalura e.c.
Three humus deposits from this community were examined. Two came from the central part of the crown and one from the outermost part. In one of the deposits from the central part of the crown some old pseudobulbs probably produced by *Bulbophyllum lupulinum* and pseudobulbs and aerial roots of *Graphorchis lurida* were discovered.

Microsorium punctatum - Peperomia sp. and Platycerium stemaria - Nephrolephis undulata e.c.
In two accumulations each of a *Microsorium punctatum* and a *Platycerium stemaria* community no traces of an older epiphytic flora could be found.

Oleandra distenta - Tridactyle armeniaca e.c.
Accumulations from this community proved to be the most rewarding in the search for remains of an earlier flora. Four such accumulations were investigated, two of which held remains that could be identified. In one of them sterile leaves and rhizomes of *Drynaria laurentii* appeared in the bottom layer. The other accumulation was so rich in old plant remains that it will be presented in detail. This community was located at the basal part of a large branch 17 m above the ground on a *Lophira alata* at 600 m altitude. The thickness of the humus layer was not less than 16 cm. In the bottom part of the accumulation the material was partly mineralized. The size of the investigated part was 0.2 x 4.0 m.

The surface vegetation was a dense aggregation of *Oleandra distenta* with the rhizomes hanging down from the branch on both sides. Ten more species were present: *Asplenium megalura, Arthropteris orientalis, Begonia polygonoides, Bulbophyllum cocoinum, Brachycorythis kalbreyeri, Habenaria leonensis, Nephrolepis undulata, Medinilla mannii, Polystachya polychaete* and *Rhipsalis baccifera.* The topmost 10 cm of this accumulation had a felt-like structure, and was composed of living and dead roots and rhizomes. Below this layer large quantities of partly decomposed plant material were found. Sterile leaves and rhizomes of *Drynaria laurentii* were accompanied by leaves and rhizomes from *Phymatodes scolopendria* and pseudobulbs of *Graphorchis lurida* and several unidentified *Bulbophyllum* spp.

Traceable remains of an earlier epiphytic flora were found in 30.7 % of the accumulations examined. It is interesting to note that the species that were overgrown were all able to colonize clean bark surfaces, so called pioneer epiphytes, e.g. *Polystachya affinis, Drynaria laurentii,* and several *Bulbophyllum* spp.

The expansive growth of the *Drynaria* fern will regularly overgrow or surpress other plants of slower growth, e.g. the many *Bulbophyllum* spp. that frequently occur in the same habitat.
In the *Oleandra distenta-Tridactyle armeniaca* community it looks like several other epiphytes also are active in the accumulation of humus, and that *Olean-*

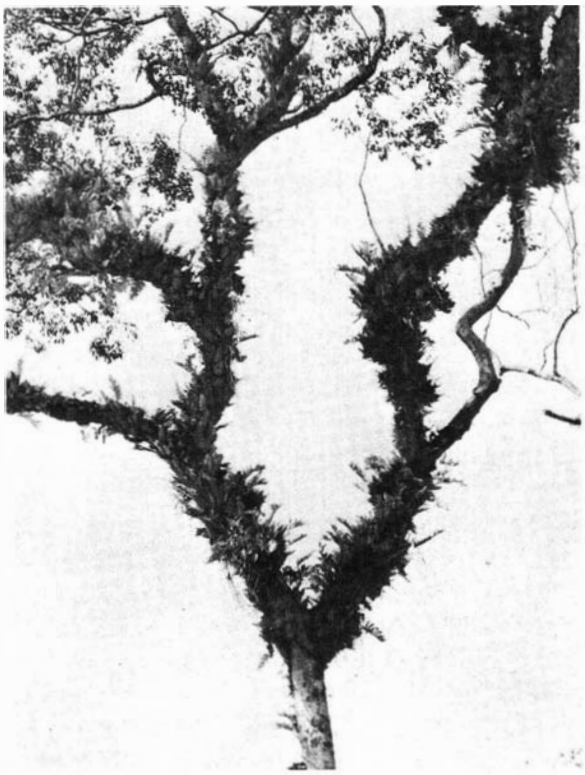


Fig. 88. *Drynaria laurentii* on a phorophyte in secondary forest. Mt Tokadeh 700 m.

Table 33. Epiphytes recorded on three Lophira alata, A, B and C. (See text.)

Epiphyte	Phorophyte		
	A	B	C
Asplenium megalura	+	+	
Drynaria laurentii	+	+	+
Elaphoglossum isabelense	+	+	
Elaphoglossum salicifolium		+	
Oleandra distenta	+		
Phymatodes scolopendria	+		
Vittaria guineensis	+		
Aërangis laurentii		+	
Angraecum birrimense	+		
Angraecum distichum	+		
Angraecum subulatum			+
Bulbophyllum distans		+	+
Bulbophyllum linderi	+	+	+
Bulbophyllum maximum	+		
Bulbophyllum oreonastes	+	+	+
Bulbophyllum phaeopogon	+		
Bulbophyllum saltatorium			+
Bulbophyllum schimperanum			+
Bulbophyllum schinzianum			+
Chamaeangis vesicata			+
Cyrtorchis arcuata		+	
Graphorchis lurida		+	
Listrostachys pertusa	+	+	+
Plectrelminthus caudatus			+
Polystachya polychaete	+	+	
Polystachya saccata	+	+	
Tridactyle anthomaniaca	+	+	+
Tridactyle armeniaca	+	+	
Tridactyle crassifolia		+	
Medinilla mannii	+	+	
Peperomia rotundifolia		+	
Rhipsalis baccifera	+		
Total no. of species	20	18	12

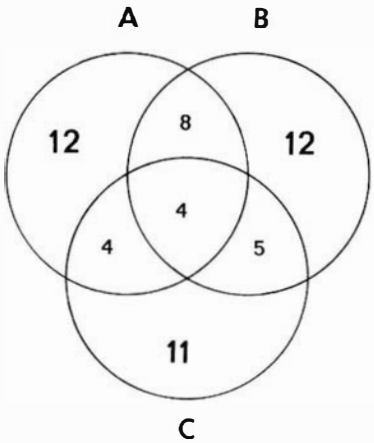


Fig. 89. Number of orchid species on three *Lophira alata:* A, B and C. (See text and Table 33.) The figures in the overlapping areas give the number of species in common.

dra distenta under certain conditions can utilize this substrate. The fact that this community is restricted to the basal area of the crown indicates that a large accumulation of humus is not enough to promote a successful colonization by *Oleandra distenta.*

Effects of environmental changes

The direction of the colonization process may be reversed or changed if the phorophyte is subjected to an environmental change. Such changes occur frequently when the forest is affected by human activities. Here and there isolated trees will be left for one reason or another.

A telescopic survey of twelve large isolated trees in Yekepa revealed that the ratio between species of pteridophytes and orchids was roughly 1:3 (12:39),

which may be compared to the ratio in the dense forest that was exactly 1:2 (19:38, Table 17). This is hardly surprising, since the higher light intensities will favour the orchids which also are able to withstand the much drier environment of more exposed trees. *Drynaria laurentii* is the only fern that can take advantages of these changes in the environment, and occurs here in sizes and numbers never found in the dense forest (Fig. 88). *Rhipsalis cassytha* is the only species of the other vascular epiphyte group that seems to thrive on these exposed phorophytes.

Comparison of the epiphytic flora on three phorophytes of the same species (*Lophira alata)* of approximately the same sizes, from the same altitude but growing in three different habitats, may exemplify the effect of the environment in more detail.

One phorophyte (A) was 42 m in size and grew in a high forest surrounded by several other trees of the same size. The second phorophyte (B) was 40 m and was left in a forest subjected to logging operations that had created a rather broken canopy. The third phorophyte (C) was 39 m and grew in a very exposed environment with several dead trees around it.

A total of 32 species of epiphytes were recorded from these three phorophytes (Table 33). A more open environment seems mainly to limit the presence of non-orchid epiphytes. The number of orchid species was about the same on all of the phorophytes (12, 12 and 11), but it should be noticed that the phorophyte (C) in the most exposed environment had only four orchid species (36.3%) in common with the phorophyte from the most protected environment (A) (Fig. 89). This may indicate that most of the orchids are adapted to rather narrow environmental conditions, which also could explain their richness in species.

The study of the changes during a two years period in the epiphytic flora on a branch that had fallen down from a large tree may serve as an example of changes that occur when the environment becomes darker and more humid. The branch had fallen down over a small creek and was lying about 2 m above the small stream. A stretch of six meters was examined, in November 1967 and re-examined at the same time during the years 1968 and 1969 (Table 34).

One must remember when analyzing the changes in the flora on this branch that it does not represent the same substrate as a living branch. The effect of the decomposition of the bark remains unknown. Anyway, the changes may give an idea of the tolerance or adaptability of the various species involved.

The original species composition shows a number of sun-demanding orchids, pteridophytes and other vascular epiphytes. Only after some months the leaves of the orchids started to turn yellow. After one year the *Bulbophyllum* species were dead and so were the *Angraecum distichum* and *Polystachya saccata* specimens. After one year three species of

Table 34. Changes in the epiphytic flora on a dead branch during a two years period. (See text.)

1967	1968	1969
Orchids	*Orchids*	*Orchids*
Angraecum distichum	Graphorchis lurida	Brachycorythis kalbreyeri
Bulbophyllum intertextum	Listrostachys pertusa	Tridactyle armeniâca
Bulbophyllum oreonastes	Tridactyle armeniaca	
Graphorchis lurida		*Pteridophytes*
Listrostachys pertusa	*Pteridophytes*	Arthropteris monocarpa
Polystachya saccata	Arthropteris monocarpa	Asplenium barteri
Tridactyle armeniaca	Asplenium megalura	Asplenium megalura
	Nephrolepis undulata	Asplenium paucijugum
Pteridophytes	Oleandra distenta	Elaphoglossum kuhnii
Asplenium megalura		Oleandra distenta
Drynaria laurentii	*Other vasc. epiphytes*	Vittaria guineensis
Lycopodium warneckei	Begonia polygonoides	
Nephrolepis undulata	Peperomia sp.	*Other vasc. epiphytes*
Vittaria guineensis	Remusatia vivipara	Begonia mannii
	Raphidophora africana	Begonia polygonoides
Other vasc. epiphytes		Calvoa monticola
Rhipsalis baccifera		Remusatia vivipara
		Raphidophora africana

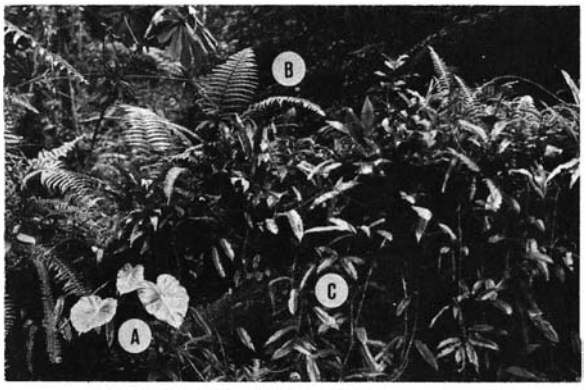


Fig. 90. Epiphytes on a dead branch (see text). (A) *Remusatia vivipara,* (B) *Nephrolepis biserrata,* (C) *Oleandra distenta.*

orchids were still alive, but the *Graphorchis lurida* plants had developed very elongated leaves and the plant did not flower later in the season. The few *Tridactyle armeniaca* and *Listrostachys pertusa* specimens were also in poor shape. The *Drynaria* plants had been overgrown by *Nephrolepis undulata,* and *Raphidophora africana* seedlings could be seen in large numbers.

After two years the branch was completely overgrown by epiphytes. *Nephrolepis undulata* and *Raphidophora africana* dominated the picture (Fig. 90). Only one species of the original group of orchids was still alive, but some small seedlings of *Brachycorythis kalbreyeri* were discovered.

Effects of the epiphytes on the phorophytes

According to the definition of an epiphyte, it should not affect the phorophyte in a direct way, e.g. draw water of nutrients from its living tissues.

EARLIER OBSERVATIONS

Indirect effects

Epiphytes may affect the phorophyte in a more indirect way. There are many opinions concerning the effect of cryptogamic epiphytes on the phorophytes, as related by Barkman (1958:18-19) and Ruinen (1953:101). It has generally been recognized that epiphytic growth is richer on dead than on living trees, but without experimental proof it is difficult to say whether the epiphytes are the direct cause of death of the phorophyte, or only infest sick trees, eventually accelerating their death. The presence of a

Fig. 91. Very extensive epiphytic growth on a tall tree. Nimba Range 800 m.

rich moss or lichen flora may indirectly contribute to a higher humidity in the bark which would favour development of numerous fungi that saprophytically or parasitically could endanger the existence of the phorophyte. Bacteria and insects may also take advantage of the humid environment.

The vascular epiphytes have generally been considered harmless and at most troublesome due to overgrowing (Fig. 91) and thus strangling the hosts on which they live, e.g. Richards (1964:110): "Through epiphytes are wholly dependent on other plants, they in their turn have little effect on their supports."

Coffee growers in Java suspect that the common epiphyte *Cyclophorus nummularifolius* kills the coffee trees as reported by Went (1940:92). The latter thinks this is only an illusion since these epiphytes are most common on the upper dead branches and twigs. When the dead branches fall the roots and rhizomes keep them hanging around the

tree instead of falling down to the ground. This creates the impression that the trees carrying this epiphyte have more dead branches than others.

Direct effects

Cook-Melville (1926) considers the epiphytic orchids to be parasites on citrus trees in Puerto Rico.

The generally accepted belief that epiphytes as a whole are limited to a non-parasitic life has been carefully examined by Ruinen (1953), whose opinion and interesting results will be summarized here. She states that the typical epiphytes preferably develop on young, living tissue and that plants declining in health usually recover, if the epiphytes are removed. Contrary to Went, Ruinen confirms the observation by planters on Java that cleaning their coffee, tea and citrus trees from epiphytes causes the trees to become healthier subsequent to this treatment.

The early symptoms of decline under epiphytic growth are difficult to define. They suggest a general deficiency, an aspect of ill-health, of failing. The leaves are no longer lush, still green but less so than usual, not as turgescent as the non-infested branches, but nevertheless not wilted. In this stage the developing buds are slightly smaller. The leaf fall is premature, therefore the vegetative period is shortened. The noxious effect is localized at first to the parts directly under the epiphyte, the other parts are only secondarily affected, viz. show the influence at a later date.

The phenomenon, which is termed *epiphytosis,* may be described as a slow exhaustion of all partners of the biocoenosis one after the other (Ruinen 1953:108). As the epiphytes are known to be mycotrophic, the most simple form in which the biocoenosis in its relations and deterioration might be represented is illustrated in Fig. 92.

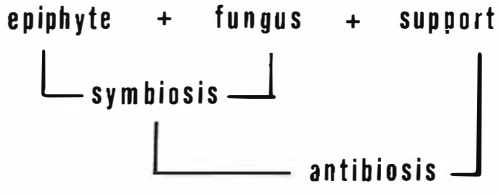


Fig. 92. Interactions between epiphyte, fungus and support. (From Ruinen 1953.)

The prompt recovery of the host plant when the epiphytes are removed was experimentally proved. Plants artificially infected with the fern *Drymoglossum* showed a rapid decline within a year. An anatomical investigation revealed that in the infested branches the vessels were partly blocked by gum and fungus and the cortex contained many hyphae. The resultant deficient nutrient and water supply would amply account for the inhibitory effect.

The invading hyphae were traced microscopically to the place of exit from the epiphyte in which it formed a mycorrhiza. The inference drawn from this is that the mycorrhizal fungus of the epiphyte is potentially parasitic on the supporting trees. It depends on the constitutional conditions presented by the supporting tree, whether or not it will appear as such.

It would seem hardly possible to speak of a symbiosis between epiphyte and supporting plant, were it not for the failures in cultivating some orchids, e.g. *Taeniophyllum* sp. on inorganic substrate and, moreover, for the marked preference shown by epiphytes for some definite phorophytes under otherwise identical environmental conditions. These conditions are undoubtedly inherent in the supporting plant itself, which obviously offers favourable symbiotic relations with the epiphytes, and therefore, from the point of the support the symbioses should be qualified as antagonistic.

Ruinen concludes that the generally accepted belief that epiphytes as a whole are limited to a saprophytic habit, seems not only open to discussion but as such has been proved to be actually erroneous. (Cf. Harvais & Hadley 1967.)

In a study of structural connections between epiphytes and host plants, Furman (1959:127) has made observations similar to those of Ruinen. In a Honduran cloud forest the interpenetration of root hairs or root mycelium with host tissues was examined. Vascular epiphytes, chiefly orchids, bromeliads and ferns, were found to penetrate living hosts' stem tissues with root hairs, or share a common fungus mycelium with them. Frequently the host tree stems had very thin, lightly suberized bark. Schimper (1935:311) have earlier stressed the fact that many epiphytes belong to those families known for their mycorrhiza, e.g. Orchidaceae, Ericaceae, Melastomaceae and 'perhaps' even other ones and that the fungus might play an important role in the metabolism of the epiphyte.

AUTHOR'S OBSERVATIONS

Any direct effect by the epiphytes on their phorophytes has not been noticed. However, certain species of phorophytes, e.g. *Mitragyna ciliata* and *Parinari excelsa* (Fig. 18) with a rich epiphytic flora often give the impression of suffering from 'epiphytosis' as described by Ruinen.

The 'preference' of certain epiphytes for a substrate of young bark or living tissues, as reported by Ruinen and Furman, should be reflected in the distribution pattern. Species with such preferences would have their main location in the outermost parts of the crown, on the youngest branches and twigs. Only one species, *Bolusiella talbotii*, shows such a distribution pattern (Fig. 78).

There are, however, certain species of orchids that seldom appear on the tall trees, but seem to prefer younger ones and even shrubs. Such habitats are found around creeks and small rivers, or in 'farmlands'. Five species are ±restricted to these habitats: *Angraecum classensii, Diaphananthe densiflora, D. rutila, Eurychone rothschildiana* and *Rhipidoglossum paucifolium.*

The leafless orchids

Brief observations of the leafless orchid *Microcoelia exilis* Lindl., (Fig. 93), in Tanzania may contribute to the picture of the relationship between epiphyte and phorophyte.

Along the Great Ruaha river in the vicinity of Kidatu at 400 m altitude the *Microcoelia* plants were very common on certain trees in the riverine forest. They generally occurred on the topmost branches in very exposed positions, and on twigs or branches of small trees (Fig. 94). Very frequently the section of the branch on which the orchid occurred was dead or dying.

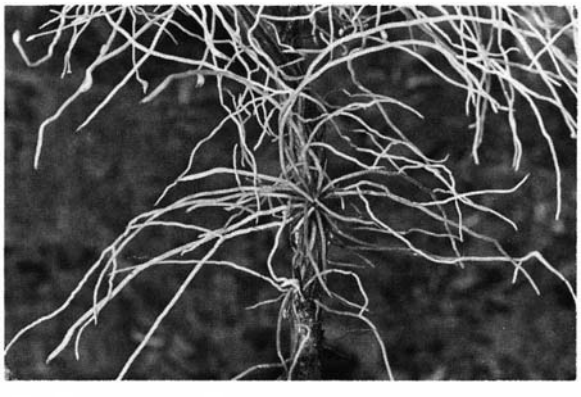


Fig. 93. *Microcoelia exilis.* The young roots grow horizontally and freely probably to increase photosynthesis and water uptake. Kidatu 400 m, Tanzania.

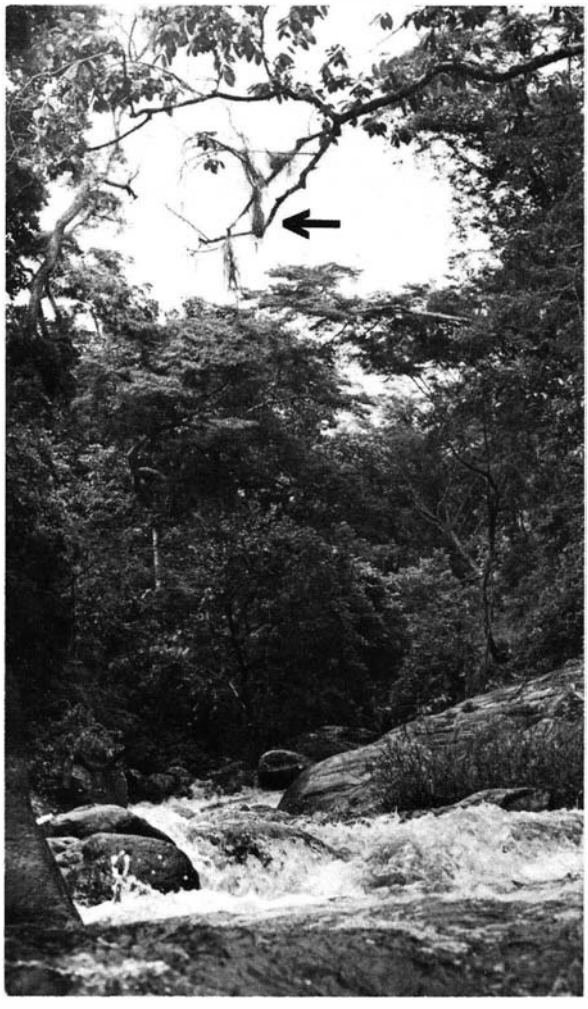


Fig. 94. *Microcoelia exilis* (see arrow) in a typical habitat. Kidatu 400 m, Tanzania.

Morris (1970:88) reports that *Microcoelia exilis* occurs "mainly on smooth barked trees and . . . mainly on the outer branches". Several species of *Microcoelia* are reported to grow on the outermost twigs or thin branches of large trees, or amongst bushes and young trees (Stewart 1973:802-803). Leafless orchids of the genus *Taeniophyllum* were observed to cause deficiency symptoms in the phorophyte (Ruinen 1953:105) and were preferably attached to the living epidermis of the younger branches, twigs or stems. *Taeniophyllum* shows optimum growth at surprisingly low light intensities; 1/8-1/5 of the outside light (Wiesner 1897). This may indicate that it is not primarily the need of light that is responsible for its occurrence in the outermost

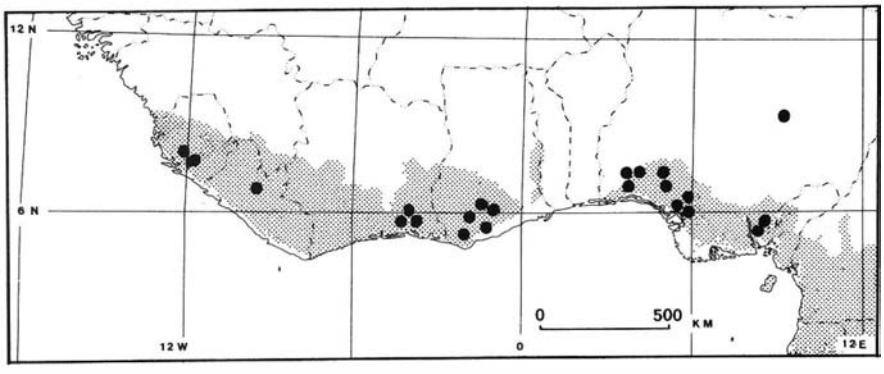


Fig. 95. Records of *Microcoelia* species in West Africa. (From F.W.T.A. 3 (1) 1968.)

parts of the branches. It has generally been assumed that the photosynthesis taking place in the roots of the leafless orchids is sufficient for the needs of the plant (Dycus & Knudson 1957). However, there seems to be no experimental proof of this assumption. The rate of photosynthesis in roots of orchids with green leaves (Erickson 1957, Dycus & Knudson 1957) clearly shows that these roots do not even produce material that can support their own respiration. Difficulties for leafless orchids growing on dead substrate (Kerr 1972:307) (Teuscher 1972:497) or when transplanted (Stewart, 1970:90, 1973:803) can be used as argument that these orchids to a certain extent are dependent on living tissues.

The reduction of leaves that occur in several genera of orchids throughout the world has generally been considered to be an adaptation for preventing water losses through the leaves (Kerr 1972:307, Teuscher 1972:497).

If one looks upon the distribution of the species among e.g. the West African leafless orchid genus *Microcoelia* Lindl., they all appear in areas with considerable amounts of rain and with such minor climatic disadvantages for epiphytes that a very large number of leaf carrying epiphytic orchids with green leaves occur in the very same area (Fig. 95). The possibility that the leaves have become obsolete due to a partly parasitic life, should be carefully examined.

V. Environmental influence

Environmental influences can be referred to three main groups: climatic factors, substrate and biotic factors. Although environmental influences result from a combination of these factors, they will be examined separately. Their possible combined effect will be considered later (Chapter VI).

Climate

Macroclimate

The large altitudinal differences that exist in the investigated area will naturally give rise to a number of different macroclimates. For reasons of simplicity the epiphyte flora of the highest parts (1000-1300 m) will be compared with the one occurring at lower altitudes (500-700). Comparisons will also be made with the epiphytic flora at altitudes higher than those in the investigated area, as observed on the high mountains in East Africa. From Tanzania, the epiphytic flora in dry environments will exemplify climatic influences not represented in the investigated area.

Fig. 96. *Parinari excelsa* densely overgrown by epiphytes. Nimba Range, 1350 m.

Nimba Mountains

The epiphytic flora in the highest parts of the Nimba Mountains has few similarities to the one at lower altitudes. The abundance of mosses, lichens, and pteridophytes is very obvious (Fig. 96). Several species of pteridophytes and orchids are ± restricted to the higher altitudes e.g.: *Elaphoglossum chevalieri, Lycopodium mildbraedii, Xiphopteris oosora* and *X. villosissima, Bulbophyllum bifarium, B. inflatum, B. scariosum, Podangis dactyloceras, Polystachya dalzielii, P. leonensis, Rangaëris brachyceras* and *Tridactyle tridactylites.*

Few species from lower altitudes are present, exceptions being *Asplenium dregeanum* and *Medinilla mannii.*

The proportion between the number of species of epiphytic pteridophytes and orchids respectively is also altered with altitude (Table 35).

East African Mountains

During a brief study tour to several of the high East African mountains similar changes were observed in the composition of the epiphytic flora. On Mount Kenya, the trees near the forest boundary (at approximately 3200 m) were devoid of orchids but ex-

Table 35. Number of epiphytic pteridophyte and orchid species in the foothills (500-700 m) and at the crest (1000-1300 m) of the Nimba Range.

Altitude (m)	Pteridophytes	Orchids	Pteridophytes: orchids
500-700	33	94	1:3
1000-1300	28	27	1:1

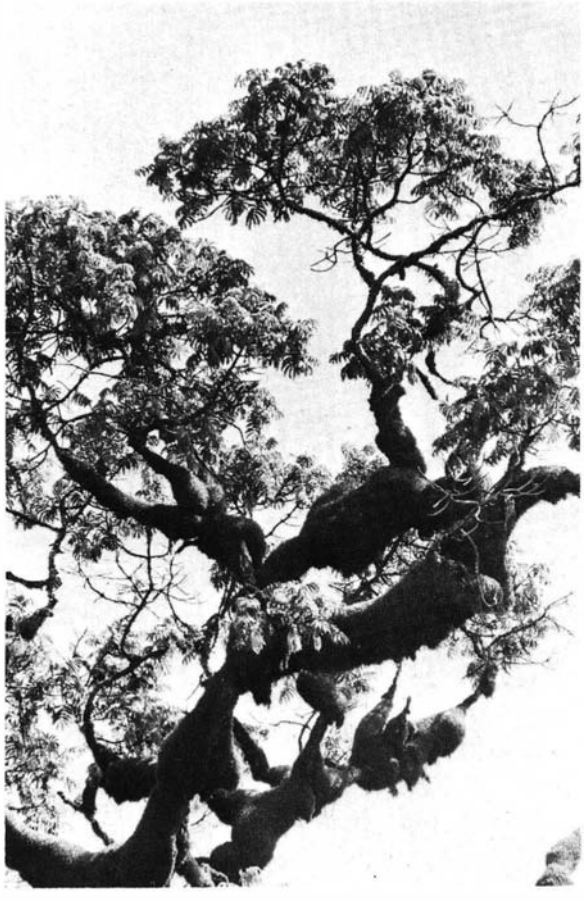


Fig. 97. Moss-covered branches of *Hagenia abyssinica* (Bruce) J.F. Gmel. (Rosaceae). Mt Kenya 3100 m, Kenya.

hibited a few pteridophytes, e.g.: *Asplenium kassnerii* Hieron., *Xiphopteris flabelliformis* (Poir.) Schelpe and *Pleopeltis excavata* (Bory) Sledge (Fig. 97). Pteridophyte nomenclature follow Schelpe 1970.

At 3000 m in the bamboo zone a small *Polystachya* sp. (probably *P. campyloglossa* Rolfe), was observed, and at 2600 m several species of orchids were present such as *Tridactyle scottelii* (Rendle) Schltr., *Polystachya cultriformis* (Thou.) Spreng., and *P. campyloglossa.*

On the eastern slope of Mount Meru in Tanzania, at 2600-2700 m altitude, only one orchid, *Polystachya campyloglossa,* was observed. However, several pteridophytes, e.g. *Asplenium aethiopicum, A. friesiorum* C. Chr. and *A. loxoscapoides* Bak. were abundant.

At 2500 m the pteridophytes were very abundant, e.g. *Asplenium aethiopicum, Pleopeltis macrocarpa* (Willd.) Kaulf., and *Elaphoglossum acrostichoides* (Hook. & Grev.) Schelpe. Only two orchid species were observed: *Polystachya nigrescens* Rendle and *Ypsilopus* sp.

Table 36. Epiphytes recorded in the Kiwira forest, Mt Rungwe 2200 m, Tanzania.

Pteridophytes
Arthropteris monocarpa
Asplenium aethiopicum
Asplenium barteri
Asplenium geppii
Asplenium monanthes L. Mant.
Asplenium rutifolium (Berg.) Kunze var. bipinnatum (Forsk.) Schelpe
Asplenium theciferum (Kunth) Mett. var. concinnum (Schrad.) Schelpe
Asplenium erectum Bory var. usambarense (Hieron.) Schelpe
Drynaria volkensii Hieron.
Loxogramme lanceolata
Lycopodium ophioglossoides Lam.
Oleandra distenta
Pleopeltis excavata (Bory) Sledge
Pleopeltis macrocarpa (Bory) Kaulf.
Orchids
Bulbophyllum stolzii Schltr.
Polystachya zambesiaca Rolfe
Stolzia nyassana Schltr.
Other vascular epiphytes
Peperomia tetraphylla (Forst.) Hook. & Am.

At 1950 m several orchids were common, e.g. *Bulbophyllum* spp., *Polystachya campyloglossa, P. cultriformis, Tridactyle* spp. Among the pteridophytes *Drynaria volkensii* Hieron. and *Pleopeltis macrocarpa* (Bory) Kaulf. were noticed.

At 2250 m altitude in the Kiwira forest, at Mount Rungwe in southern Tanzania, the ratio between the species of orchids and pteridophytes was roughly one to five (Table 36).

At lower altitudes as in the Usambara Mountains in Tanzania the number of orchid species outnumber the pteridophytes. At Amani, 950 m, 14 species of orchids and 12 species of pteridophytes were counted on one *Parinari* tree (Table 37). On another tree at the same place 11 orchids and 6 pteridophytes were observed.

Epiphytes disappear, according to Tixier (1966:21) in tropical humid montane forests, at 3500 m in the Himalayas and Africa, and at 4000 m in the Columbian Andees and maybe in New Guinea.

From Tanzania Moreau (1943:8) reports: "On the whole, epiphytic orchids seem most plentiful, in both individuals and species, between 3000 ft and 5000 ft

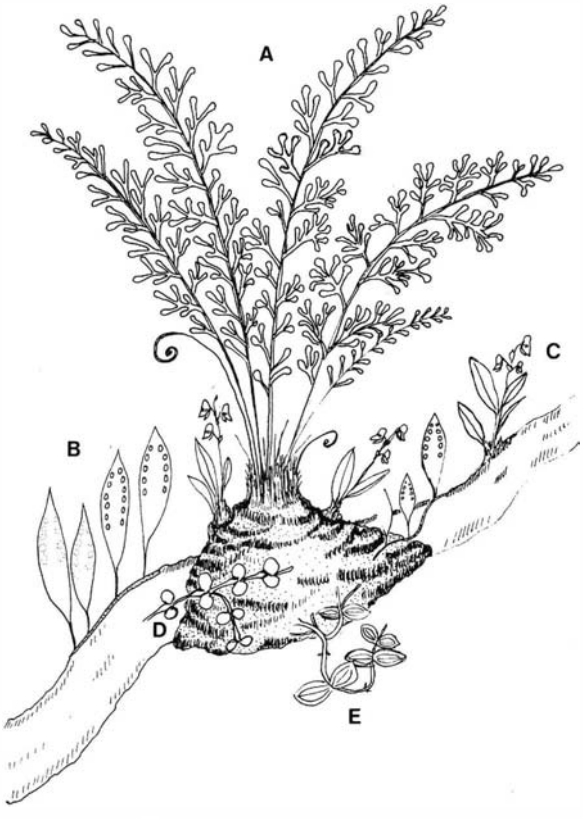


Fig. 98. Simplified drawing showing the epiphytes utilizing the humus held by the root system of *Asplenium theciferum* on a *Nuxia congesta* R.Br. (Loganiaceae). Ngong Hills 2400 m, Kenya. (A) *Asplenium theciferum,* (B) *Elaphoglossum macrocarpum,* (C) *Polystachya campyloglossa,* (D) *Stolzia repens,* (E) *Peperomia sthulmannii.*

in rain forest... Above 5000 ft in Usambara, species became less numerous again with the genus *Polystachya* predominating."

Possible influences of altitude

The effect of the altitude on the epiphytes has been compared with either the water balance, e.g. drought correlated to low temperatures (Went 1940:94, Tixier 1966:36) or the temperature.

The lower the temperature (Table 2) the higher the relative humidity (Fig. 9) and the presence of local cloud systems or mist, at the highest parts of the Nimba Range (Fig. 11), will naturally influence the evapotranspiration and favour less drought resistant species such as filmy ferns, and certain pteridophytes. Mosses and lichens are also favoured by the higher light intensities that exist at all levels in the more open forest type at the crest of the range.

Table 37. Occurrence of epiphytes in different sections of a 32 m tall Parinari excelsa, Amani 950 m, Usambara Mts, Tanzania.

I No epiphytes

II Asplenium nidus L.

III

Pteridophytes

Asplenium pellucidum Lam. subsp. pseudoporrectium (Hieron.) Schelpe
Asplenium megalura
Drynaria volkensii
Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe
Elaphoglossum lastii (Bak.) C. Chr.
Lycopodium warneckei
Microgramma owariensis
Oleandra distenta
Vittaria ensiformis Swartz

Orchids

Ancistrorhynchus refractus Kraenzl.
Bulbophyllum plathyrachis Schltr.
Cirrhopetalum umbellatum (Forst.f.) Hook. & Arn.
Oberonia disticha (Lam.) Schltr.
Polystachya adansoniae
Rangaëris muscicola
Tridactyle anthomaniaca
Tridactyle bicaudata

IV

Pteridophytes

Drynaria volkensii
Microgramma owariensis

Orchids

Ancistrorhynchus refractus Kraenzl.
Bulbophyllum bequaertii De Wild
Bulbophyllum encephalodes Summerh.
Bulbophyllum plathyrachis
Diaphananthe subsimplex Summerh.
Polystachya adansoniae
Tridactyle teretifolia Schltr.

Other vascular epiphytes

Rhipsalis baccifera

V *Orchids*

Bolusiella iridifolia (Rolfe) Schltr.
Tridactyle anthomaniaca

Temperature influence on the occurrence of orchids has been stressed by Rupp (1969:1): "The epiphytes reach their greatest development in the tropics, decreasing in numbers towards cooler

regions. This fact is well illustrated in Eastern Australia, where Queensland has approximately 100 known species of epiphytes, New South Wales 52, Victoria 5, and Tasmania 2."

There are diverging opinions about the ability of orchids to survive frost. Piers (1968:5) states that epiphytic orchids can not survive frost, while Stewart (1970:54) reports that *Bolusiella iridifolia* "may even withstand frost on the coldest nights of the year".

Generally speaking, it is hard to believe that the pteridophytes, which as a group are poorly adapted to desiccation, would dominate over the epiphytic orchids with their advanced technique to survive dry periods, if drought was a main limiting factor on the occurrence of epiphytes at higher altitudes.

Kidatu

A thorough study of the epiphytes in the Kidatu area (7° 40' S, 36° 59' E) in Tanzania was performed in April-June 1971.

The slopes of the Great Ruaha River Valley, east of Kidatu, are covered with patches of forest. The annual rainfall is around 1000-1400 mm (Atlas of Tanzania 1967:6), with a long dry season of 4-5 months. Close to the stream bed a riverine forest occur with a rather large number of tree-forming species, e.g. *Burkea africana* Hook., *Cassia* sp., *Combretum* sp., *Diplorynchus condylocarpon* (Müll. Arg.) Pichon, *Ficus sycomorus* L., *Lonchocarpus bussei* Harms, *Markhamia obtusifolia* (Baker) Sprague, *Milletia bussei* Harms, *Piliostigma thonningii* (Schumach.) Milne-Redhead, *Pterocarpus* sp., *Stereospermum kunthianum* Cham., *Sterculia quinqueloba* K. Schum., *Xeroderris stuhlmannii* (Taub.) Medonca & E.P. Sousa, *Vitex doniana* Sweet.

A total of eight species of epiphytes were recorded in the riverine forest: *Aërangis flabellifolia* Rchb. f., *Aërangis kotschyana* (Rchb. f.) Schltr., *Bulbophyllum* sp., *Ansellia gigantea* Rchb. f. var. *nilotica* (Baker) Summerh., *Cyrtorchis arcuata* subsp. *variabilis* and *C. arcuata* subsp. *whytei* (Rolfe) Summerh., *Microcoelia exilis* Lindl., *Polystachya tessallata*. The only epiphytic fern was *Phymatodes scolopendria* (one 'stand'), which was partly growing on some wet rocks in a shady habitat.

Trees along two parallel strips 50 m long and 10 m wide were examined ('distance' method) (Table 38). The first strip was situated in the riparian forest 10 m from the shore of the Great Ruaha River, parallel to the river. The second strip was 50 m away from the river 10 m higher on the slope in a grassland with scattered trees (wooded grassland).

Table 38. Occurrence of epiphytes in two different forest types. (Trees < 5 m are excluded). Great Ruaha River 400 m, Kidatu, Tanzania.

Habitat	No. of trees examined	% of trees with epiphytes	Max. no. of species on a single tree
Riparian forest	20	60.0	2
Wooded grassland	24	8.3	1

The two species that occurred in the riparian forest were *Cyrtorchis arcuata* subsp. *variabilis* and *Microcoelia exilis*, which were also the only two common species in this area. In the wooded

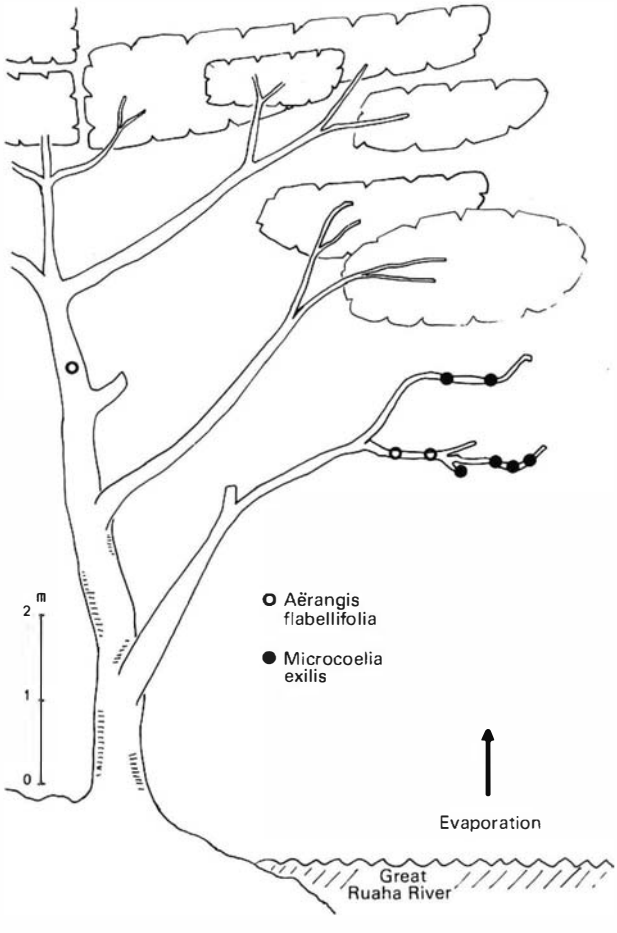


Fig. 99. Simplified drawing showing the distribution of epiphytes on a *Combretum* tree close to the Great Ruaha River. Kidatu 390 m, Tanzania.

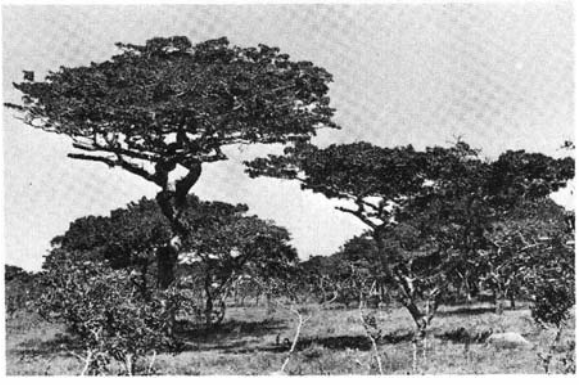


Fig. 100. *Brachystegia* woodland ('Miombo'). Makumbako 1900 m, Tanzania.

grassland *Aërangis flabellifolia* was the only species with a total of three 'stands'. The relative 'richness' of epiphytes in the riparian forest can probably be correlated to a favourable climatic effect which was also indicated by a kind of 'reversed' distribution pattern of the epiphytes on several phorophytes (Fig. 99).

Growing sites close to water are according to Teuscher (1972:497) a general habitat for leafless orchids. Stewart (1973), however, has pointed out that a number of *Microcoelia* species are adapted to different habitats.

Makumbako

In the Southern Highland, near Makumbako (8° 56' S, 34° 52' E) at approximately 1900 m altitude, large areas are covered with a *Brachystegia* woodland (so-called 'Miombo', Fig. 100). The yearly rainfall is 800-1000 mm (Atlas of Tanzania 1967:6), and the dry season lasts for 5-6 months. Fifty trees selected at random, four meters or higher, were examined for epiphytes.

Two orchid species were observed, *Tridactyle tricuspis* (Bolus) Schltr. (Fig. 101), and a *Polystachya* sp. of which only the old inflorescences

Table 39. Occurrence and abundance of epiphytes on 50 trees in a Brachystegia woodland ('miombo'). (Trees < 4 m are excluded.) Classes of abundance explained in the text. Makumbako 1900 m, Tanzania.

Species	% of trees with epiph.	Abundance		
		1	2	3
Tridactyle sp. + Polystachya sp.	100.0			
Tridactyle tricuspis (alone)	98.0	22.0	64.0	12.0
Polystachya sp. (alone)	98.0	48.0	48.0	2.0

Fig. 101. *Tridactyle tricuspis.* Makumbako 1900 m, Tanzania.

and pseudobulbs remained. The occurrence and total number of each species were estimated (Table 39). Three frequences of abundance were used: (1) less than five 'stands', (2) 5-25 'stands', (3) more than 25 'stands'. The *Polystachya* species were very hard to discover when the old inflorescences were absent. The leafless pseudobulbs were more or less covered with lichens. Therefore, the frequence of the *Polystachya* species are probably too low in this estimation.

Every tree examined had at least one species of epiphyte. Also surprising is the very high number of individuals, particularly *Tridactyle tricuspis.* Sixty-four per cent of the trees had 5-25 'stands' of this species. The presence of such a large number of individuals indicates that they are well adapted to this environment.

The climatic influence in these two areas in Tanzania obviously limits the number of epiphytic species although the abundance of certain species is surprising.

Brief observations in even drier areas of Tanzania in the Iringa and Dodoma districts (600-800 mm yearly rainfall) revealed that *Ansellia gigantea* var. *nilotica* (Fig. 102) was locally rather common, often on *Adansonia digitata* L. and *Hyphaene thebacia* (L.) Mart. In those very dry areas two species of the

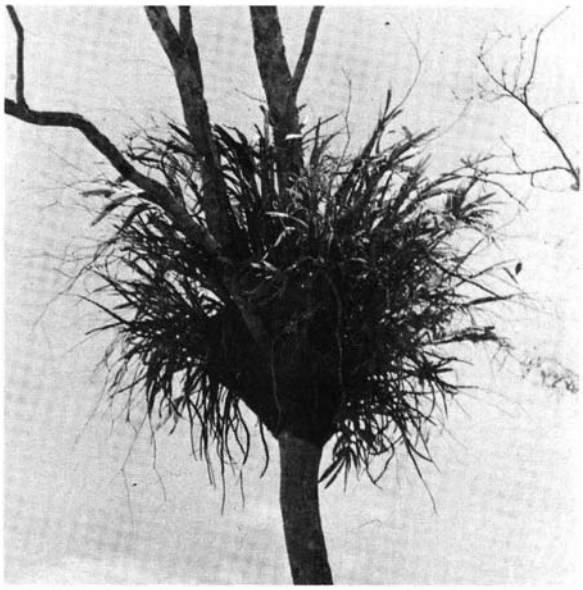


Fig. 102. *Ansellia gigantea.* A large orchid of rather dry areas in East Africa. Kidatu 400 m.

family Crassulaceae, *Kalanchoe lanceolata* (Forsk.) Pers., and *K. pilosa* Bak., occur as epiphytes. The latter species has also been recorded (J.B. Gillett, 15123 K) as an epiphyte in the Marsabit area, Kenya (780 mm yearly rainfall).

Rainfall importance

The rainfall may not only be of importance for the water economy of the epiphytes but also serve as a source of nutrients. It has been clearly shown that rainfall nutrients play an important part in the nutrient cycle of ecosystems on oligotropic sites (Allen et al. 1968:497). Analyses of the nutritional content of rainwater are available from two countries in West Africa (Table 40). Jones (1960:432) remarks that his nitrogen, potassium and sodium figures are the highest so far recorded in rainwater.

The origin of the nutrients in rainwater has been subject to various explanations. Commenting on his figures, Jones states: "generally the figures to date point to the ocean as the main source of rainwater nutrients" since "the low nitrate figures eliminate the possibility of large contributions from dust and electric storms". In Uganda, Visser (1964:35) observed that the heavier the shower the more nitrate-N was precipitated, and therefore states that storms preceding heavy rains take a lot of dust into the atmosphere from which NO_3^- and other nutrients are later washed.

A similar view is presented by Thornton (1965:1025) who found in Gambia that the highest values for potassium and calcium were obtained at the beginning of the rains which indicate that the elements are either washed from or fall in the form of dust present in the atmosphere. No matter what origin the nutrients in the rainwater should represent, a valuable addition to the nutrients of the substrate is made.

Table 40. Annual total nutrients (kg/ha) in rain according to records from West Africa (from Gore 1968).

Location	Rainfall (mm)	Inorg. N	P	Na	K	Ca	Mg
N. Nigeria (Jones, 1960)							
	1067	54.7	2.58	60.3	36.76	1.01	2.91
Gambia (Thornton, 1965)							
Yundum	1054	47.1	0.31	9.5	5.94	4.37	–
Jenoi	1006	44.9	0.61	8.9	4.26	2.69	–
Yoroberi K.	709	14.2	0.27	5.8	2.80	1.68	–

Microclimate

The microclimate in a rain forest is of course dependent on the structure and density of the vegetation and is thus very complex. There is a ±continuous vertical climatic gradient from the ground to the highest treetops.

Since none of the strata are uniform in density there are also variations in microclimate from place to place at the same horizontal level. Furthermore, the microclimate in the crowns will vary according to the species and age of the tree.

In a study like this the largest interest is connected with the variation of the microclimate in various strata of the forest, but no such investigation has been possible to perform. For reasons easy to understand there are in fact few and limited reports of the microclimate in the higher strata of the rain forest.

From the Shasha Forest Reserve in Southern Nigeria Evans (1939) has published results of investigations at the ground level and at 24 m level. A more detailed study has been carried out in the lowland rain forest at Banco in the Southern Ivory Coast by Cachan (1963). By help of a 46 m high tower, recordings from four different levels were obtained. The results from these investigations quoted here cannot be simply transferred to the Nimba area. However, some of the general observations can probably also be applied to the situation within the forests in Nimba.

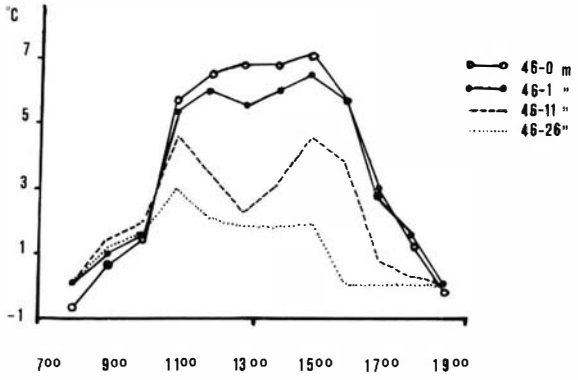


Fig. 103. Daily temperature differences between different levels in a tropical rain forest (from Cachan 1963).

Temperature

Evans found that the temperature showed a smaller range of variation in the undergrowth than at the upper levels of the forest. In the dry season the maximum temperature is about the same. In the wet season the differences are much more accentuated and the minimum temperatures in the undergrowth are in every case from one to two degrees higher than in the treetops.

The vertical temperature gradient shows, in the middle of the day, a fairly steady decrease from the canopy down to the undergrowth. The temperature is 2-3 degrees higher at 24 m than at ground level. At nighttime the undergrowth at 0.7 m was always warmer than the air 24 m above the ground.

Cachan noted a similar temperature pattern in the Ivory Coast. The daily variations of the differences between the temperature at four levels is shown in Fig. 103.

Humidity

The humidity of the air can be expressed in three ways: relative humidity, saturation deficit and vapour pressure. In general, the minimum relative humidity and the maximum temperature are simultaneous, the daily variation of these elements are inversed. The variation of the saturation deficit is inversed to that of the relative humidity, while the vapour pressure shows a double, daily oscillation with a maximum in the morning and also in the afternoon (Cachan 1963:152).

The humidity of the air determined from the relative humidity, the saturation deficit, and the duration of periods with a relative humidity of less than 95 %, are usually identical between the 46 m level on a humid day and the 1 m level on a dry day (Cachan 1963:152). The following characteristics were observed for a dry resp. a wet period (Table 41).

Table 41. Humidity of the air during dry and wet seasons at two levels in an Ivory Coast rain forest (from Cachan 1963).

	Level	Dry period	Wet period
Minimum relative humidity	46 m	50-70 %	60-80 %
	1 m	60-80 %	90-100 %
Saturation deficit	46 m	12-16 mm	6-12 mm
	1 m	6-10 mm	0-4 mm
Hours with rel. humidity less than 95 %	46 m	10-14 hrs	8-12 hrs
	1m	10-12 hrs	0-2hrs

The rate of evaporation at various levels in a rain forest, given as a percentage of the value obtained at 46 m level (above the canopy), showed a steady decrease from the canopy level towards the ground. At 26 m the value was 58 %, at 11 m 35 %, and at 1 m 21 % of that at 46 m (Cachan 1963:149).

Light intensities

In the undergrowth

The instrument used was a photoelectric cell of unknown spectral range. The cell itself was connected to a galvanometer with a 3 m long cable. The light cell was placed on top of a 1.3 m high stick, that was pushed into the ground during the recordings. Lower down on the stick two waterlevel instruments were attached to ensure that the stick and the light cell were held in an absolute vertical position at each measuring point. The recording was done along three parallel strips at 5 m distance from each other, at every 5 m of the 100 m long strips. Three recordings during one minute at each recording spot were taken and the median value chosen. The investigation was done at noon on a sunny day at two plots, one at 600 m (Nov. 2, 1969) and another at 1300 m (Nov. 12, 1969) Table 42. The samples from 600 m were

Table 42. Light intensities in the undergrowth at two different altitudes, given as a percentage of the light in the open.

Altitude	No. of records	Light intensity Max.	Min.	Mean
600 m	61	0.70	0.17	0.36
1300 m	63	17.24	2.59	6.55

taken in a high forest with the canopy around 40 m above the ground in the Seka Valley. Common species of trees in this forest were: *Parinari excelsa, Heritiera utilis, Calpocalyx aubrevillei* and *Chidlowia sanguinea.* The ground was covered with dead leaves and the herb flora was sparsely represented, e.g.: *Selaginella vogelii* Spring and *Selaginella versicolor* Spring. On the lower parts of the trunks a few ferns were noticed, *Hymenophyllum kuhnii* and *Asplenium barteri.*

At 1300 m the samples were taken at the crest of the main ridge 300 m SW of the point where the borders of Liberia, Guinea and the Ivory Coast meet. The forest in this locality almost exclusively consisted of *Parinari excelsa* with a somewhat broken canopy at 10-12 m level above the ground which was irregularly covered with herbs.

The high light intensities in the montane forest is remarkable, but judging from the abundance of plants on the ground it was not totally unexpected. In a montane forest in Ecuador, Whitmore (1968:238) found that the canopy was more transparent than in a lowland forest.

Particular interest has been paid to the illumination of the undergrowth and the effect of the sunflecks on the forest floor, e.g. Evans (1939) in Nigeria, Gusinde & Lauscher (1941) in Congo, Eidmann (1941) on Fernando Po, Evans et al. 1960 and Cachan (1963) in the Ivory Coast. The shade illumination was found by all of them to be 1 % or less of the outside light. The light intensity in the sunflecks in British Guiana varied between 10.4 and 72 % (Carter 1934). The spectral composition of the light reaching the forest floor as examined by Evans (1939) showed approximately 40 % portion of the wave-lengths above 7000 A (infra-red light). Similar observations have been reported from Puerto Rico (Johnson & Atwood 1970). This indicates a considerable increase in the transmission of the forest canopy just beyond the red end of the visible spectrum. The effect of this portion of light on the plants is unknown but it can probably not be used in the photosynthesis, since it is outside the range of chlorophyll's absorption. As the forest became denser a decrease in the proportion of blue light was also noticed.

At the growing sites of the epiphytes

The same photoelectric cell as described earlier was used. The recording equipment stood on the ground and was managed by an assistant. The recording was performed by holding the cell at the growing site of the plant to be investigated. To reach the plants growing in more inaccessible places, the light cell was attached to a four m long aluminium pipe. At the end of the pipe, where the light cell was attached at a 90-degree angle towards the pipe, a V-shaped metal piece was connected to a ball bearing on the pipe. When the metal piece with its open end was held against the substrate, the whole pipe could be turned around on its axis, and thus moving the light cell at the same time. By placing the light cell at the actual growing site of the epiphyte, and then turning it, the maximum light intensity was found.

The tree chosen was a *Parinari excelsa* growing in a typical section of the forest that covers the narrow crest of the main ridge at 1300 m altitude from the mark of the three national borders down to the mining area. The canopy in this single dominant *Parinari* forest was at 10-15 m above the ground and partly open. There were a few trees and shrubs of smaller dimensions. e.g. *Ochna membranacea* Oliv., reaching up to the lower parts of the crowns of the emergent trees. The tree investigated had a size of 23 m and a circumference of the trunk at breast-height of 162 cm and was heavily branched, with the first ramification starting 3.5 m above the ground. The foliage was concentrated to the outermost branches which made movements easier in the central part of the crown. At the basal part of the trunk the cover of epiphytic mosses and filmy ferns was 100 %. Higher up on the trunk (1-3.5 m) the epiphytes were more or less concentrated to one side (S), with the plants appearing in small patches with clean bark surface in between. In the basal parts of the crown *Tridactyle tridactylites* formed dense, untidy 'stands'. In the central part of the branches the mosses e.g. *Porothamnion hildebrandtii* (C.M.) Fleisch. were very abundant, forming large cushions. In the apical part of the branches the lichen cover was pronounced especially on the twigs, where an *Usnea* sp. with hanging growth habit was noticed. *Bulbophyllum scariosum* and *Polystachya dalzielii* were also abundant.

A total of 15 species of epiphytes were growing on the tree, 7 pteridophytes, 5 orchids and 3 other vascular epiphytes. Thus the pteridophyte/orchid ratio was 1.4:1. A total of 119 recordings, which were estimated to cover 80 % of the plants present, were performed during a 3 hours period in the mid-

Table 43. Light intensities as a percentage of the light in the open at the growing sites of epiphytes on a Parinari excelsa. Nimba Ridge, 1300 m.

Epiphytes	No. of records	Light intensity Mean	Light intensity Max. - Min.
I + II			
Asplenium dregeanum	9	14.2	16.8 - 12.6
Begonia rubro-marginata	2	17.7	23.2 - 11.9
Bulbophyllum inflatum	5	13.5	19.7 - 7.1
Elaphoglossum chevalieri	6	15.2	24.5 - 7.1
Medinilla mannii	5	13.2	17.4 - 9.4
Peperomia sp.	8	16.1	23.2 - 10.3
Polystachya leonensis	6	14.2	18.4 - 9.0
III			
Asplenium dregeanum	5	26.8	29.3 - 23.2
Lycopodium mildbraedii	4	20.0	26.8 - 9.3
Medinilla mannii	6	25.5	29.7 - 16.8
Peperomia sp.	3	21.6	28.4 - 16.4
Tridactyle tridactylites	7	21.6	29.7 - 15.8
IV			
Asplenium aethiopicum	2	24.5	25.1 - 23.9
Asplenium megalura	4	28.4	36.8 - 19.0
Bulbophyllum scariosum	6	27.7	36.4 - 16.4
Begonia rubro-marginata	2	26.4	28.7 - 23.9
Elaphoglossum isabelense	3	21.0	23.9 - 18.7
Polystachya dalzielii	8	29.3	37.1 - 24.5
Tridactyle tridactylites	5	22.3	27.2 - 18.4
Xiphopteris vilosissima	4	17.7	22.6 - 13.9
V			
Bulbophyllum scariosum	11	37.4	43.2 - 28.1
Polystachya dalzielii	7	37.7	45.5 - 32.9
Usnea sp.	7	42.6	58.7 - 30.0

dle of the day. An additional 7 recordings of the light intensities at the more exposed positions of the typical *Usnea* lichens were also included for comparison (Table 43).

It is interesting to note that the arbitrary division of the trees into 5 sections that has been used throughout this study, was in this tree not correlated to the light intensities (Table 44).

No marked difference in the light intensities could be found between the basal and middle parts of the branches. The very wide variation in the values between maximum and minimum intensities should be noted with caution, since sun-flecks with a very short duration may be responsible for the high figures.

Table 44. Light intensities in the five sections of a Parinari excelsa at 1300 m. Based on the mean light intensity in each section (Table 43).

Section	I + II	III	IV	V
Light intensity	14.9	23.1	24.7	37.6

At various levels above the ground

The general knowledge of light conditions in the crowns of the trees in the tropics is very scanty. The need for the erection of large structures to reach the upper parts of, or preferably above, the canopy has naturally been difficult to overcome. There are actually only a few such investigations (Allee 1926, Dirmhirn 1961 and Cachan 1963). The decrease in the light intensity from the canopy towards the ground is by no means a gradual process, but rather abrupt changes occurring at various levels, depending on the structure of the forest (Richards 1939:30). Cachan (1963:93) reports on the vertical variation of the light intensity from a tropical rain forest in the Ivory Coast. The emergent trees in this forest reach a height of little more than 40 m, e.g. *Combretodendron africanum, Piptadeniastrum africanum, Guarea thomsonii* Sprague & Hutch. and *Turraeanthus africanus* (Welw. ex DC.) Pellegr. The light intensity above the canopy varies continuously, since the sky is more or less hazy. Values above 100,000 Lux were exceeded during rather short periods. The daily variation in the light intensity at 44 m and 33 m above the ground, is presented in Fig. 104. Wide variation in the light intensity occurs in the middle of the day at 46 m, where the daily

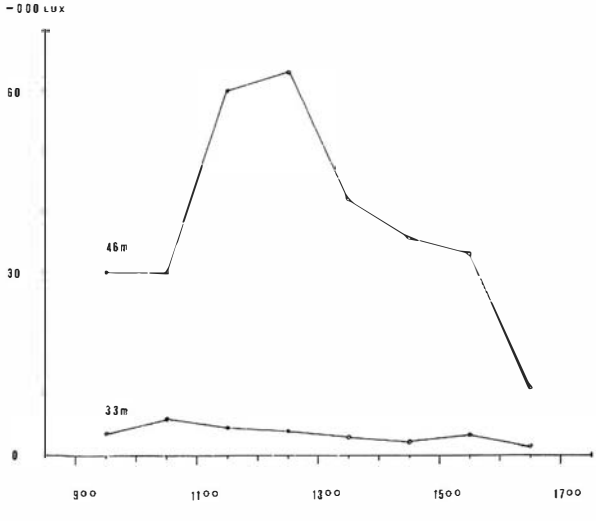


Fig. 104. Variations in daily light intensity above the canopy (46 m above the ground) and at 33 m in a tropical rain forest in the Ivory Coast (from Cachan 1963).

Fig. 105. Daily variation of light intensity measured by a light cell at the growing site of a *Diaphananthe pellucida* four meters above the ground (see text).

average was 38,000 Lux. The average light intensity at 33 m level is less than 10 % (3082-38,000 Lux) of the intensity above the canopy. Observe that in such a short vertical distance as 11 m a 90 % reduction of the light intensity has already taken place. At ground level, the light intensity never reached above 1 % of the light above the canopy.

Daily variations in light intensity

Through a special 'writing unit' the daily continuous changes in light intensity were recorded. The same light cell as previously described was simply connected to the 'writing unit' through a cable.

The light cell was placed at the growing site of the epiphyte to be investigated pointing in the direction of the supposed main light influx, which in most cases meant a vertical direction (Fig. 105). The graphs obtained with this equipment should only be compared with each other, since the spectral range of the light cell was unknown. No extra instruments that could be used for simultaneous recordings in the open were available. Therefore, all the curves shown are from different days, which of course include a source of error. To reduce the error the comparisons shown are all taken from cloudfree days. The seasonal effects must also be considered, since the recordings are from different times of the year with different solstices. The aim of these recordings was to find out if there were differences between various species of epiphytes in their light climates over a longer period, and to get an idea of the frequence and duration of direct light (sun-flecks). The light intensities of three species of epiphytes, *Diaphananthe pellucida, Vanilla crenulata, Arthropteris monocarpa,* from the lowest parts of a high forest (Seka Valley 600 m) compared with the light outside the forest is given in Fig. 106. The *Diaphananthe* specimen was growing on a liana, four meters above the ground (Fig. 105), and the *Vanilla* vine on the rotten stump of a large tree at about 1.5 meters height, while the *Arthropteris monocarpa* specimen occupied the basal part of the trunk of a large tree.

The daily variation of the light intensity in the open on a clear day shows a fairly even rise and decline with the maximum in the middle of the day.

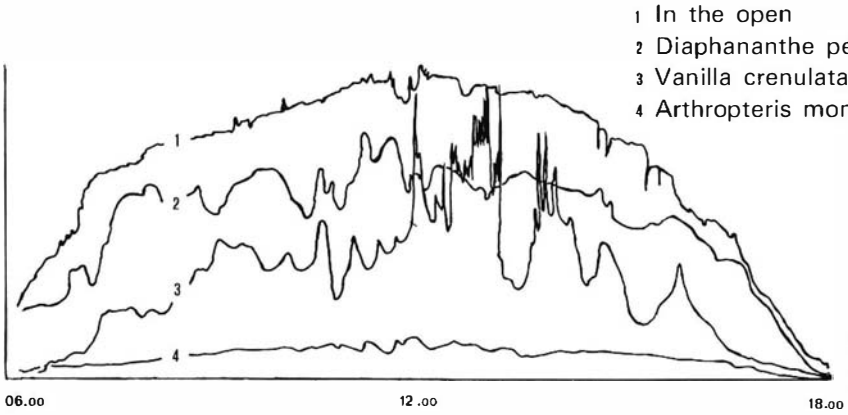


Fig. 107. Daily variations in light intensity at the growing site of a *Bulbophyllum inflatum.* Nimba Range 1300 m.

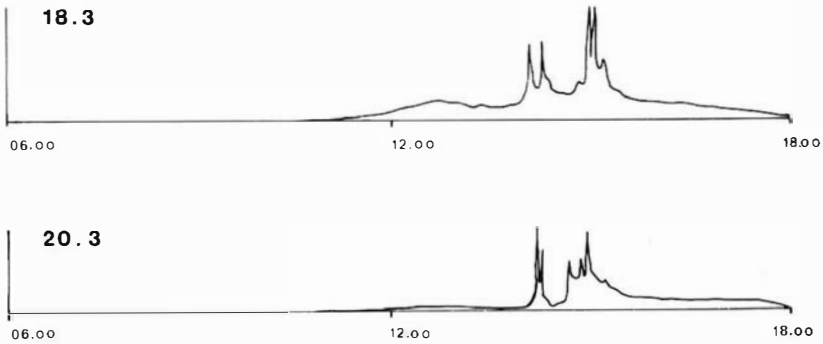


Fig. 107. Daily variations in light intensity at the growing site of a *Bulbophyllum inflatum*. Nimba Range 1300 m.

The minor variations that can be observed throughout the day are probably caused by haze. The more gentle peaks in the curve for *Diaphananthe pellucida* probably indicate that this species recieves a more indirect type of light. The series of distinct peaks with a very short duration that occur between 12^{00}-14^{00} on the *Vanilla* curve is a result of direct sunlight that has been able to penetrate down to this level. In denser shade closer to the ground the penetration of direct light is less likely. The light level tends to be more uniform throughout the day as can be seen for *Arthropteris monocarpa*.

In the montane forest the light regularly penetrates the lower parts of the vegetation. The curves for *Bulbophyllum inflatum*, growing on a trunk 1.5 m above the ground at 1300 m altitude, give the variation in light intensities for the orchid which grows in the most shady habitat of all the orchids in the Nimba area (Fig. 107). These two curves can also serve as an example of the 'micro light climate' that probably is of great importance for the epiphytes. Note the similarity between the two curves of March 18 and 20, 1970 (March 19 was a cloudy and rainy day) when the light that was registered reached the plant between 14^{00}-15^{30}. For many plants that live in a superficially dark environment these short periods of higher light intensities may be of critical importance in their survival. It may also influence the occurrence of small groups of several species that com-

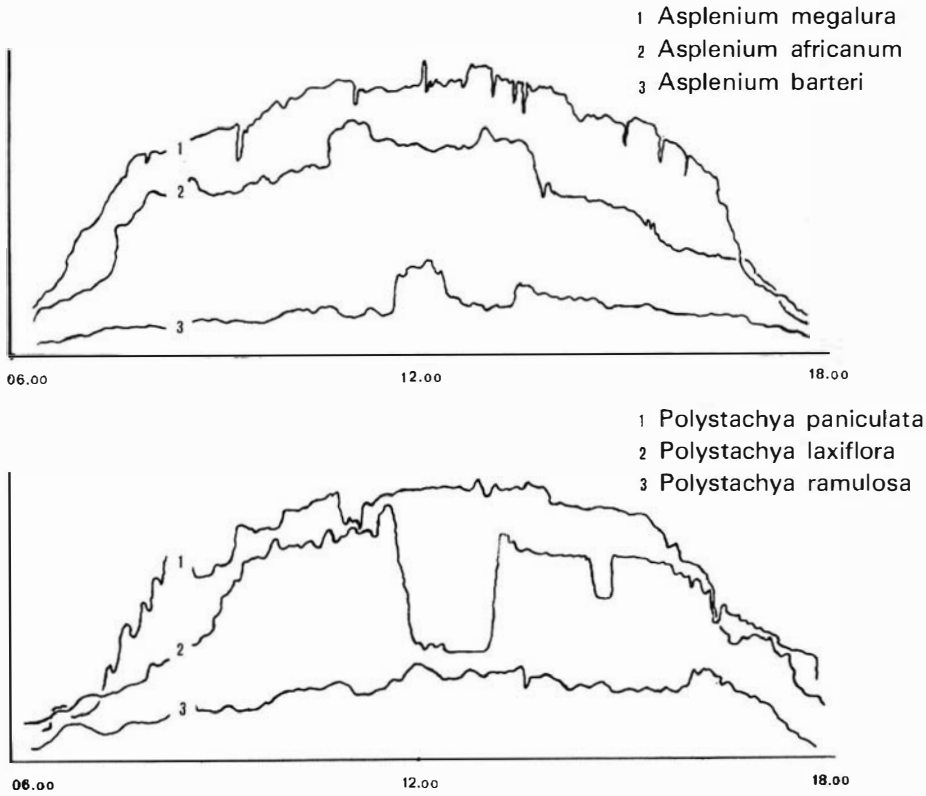


Fig. 108. Daily variations in light intensity at the growing sites of (A) three pteridophyte species, (B) three orchid species. Nimba Range 600 m.

monly are found in patches of small and restricted range. To find out if there are any correlation between the observed stratification of the epiphytes and the light-intensities, three species in each of the genera *Asplenium* and *Polystachya* were chosen for study. One species in each genera represented a specific level in the rain forest. The lowest level (section I) was represented by *Asplenium barteri* and *Polystachya ramulosa,* the intermediate level (II) of *Asplenium africanum* and *Polystachya laxiflora,* and the crown stratum (III + IV) of *Asplenium megalura* and *Polystachya paniculata.*

Two different phorophytes that each carried these three plants of the same genus were selected for the study. The light cell was then applied in the same way as earlier described. The result is presented in Fig. 108. The differences in light intensities as observed for certain species with the aid of recording instruments (short or long period recordings) seem to confirm the estimations made in the field.

A limitation to one or rarely two of the particular light groups that are recognized was common among the species in all major groups of epiphytes (Fig. 109). The majority of pteridophytes, however, occur in diffuse light while the orchids are more evenly divided between habitats with diffuse or bright light (Table 46).

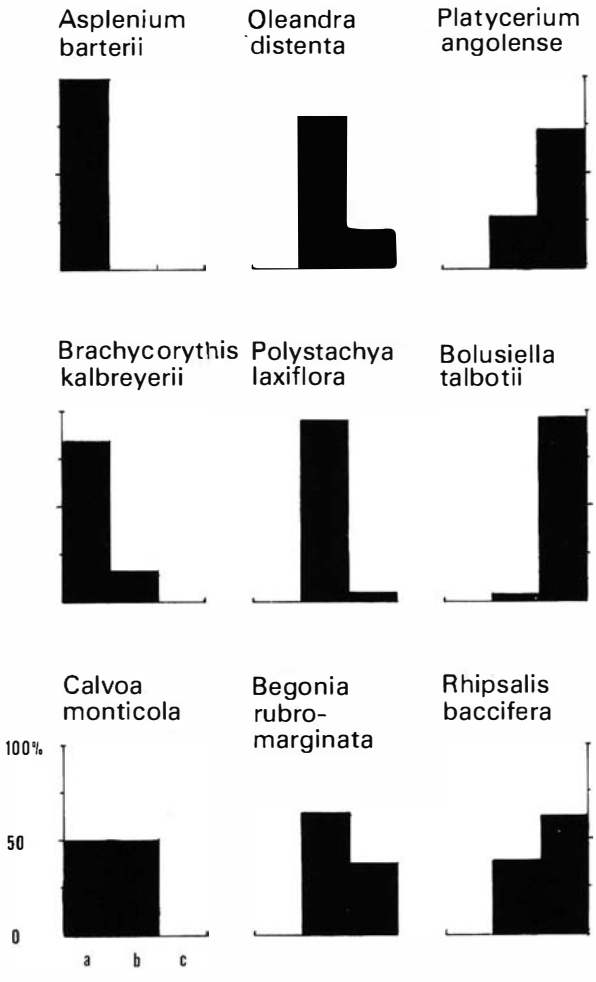


Fig. 109. Records of epiphytes distributed between the different light classes (from Table 27, *Brachycorythis kalbreyeri* from Table 29). (A) heavy shade, (B) open shade, (C) full sun.

Substrate

PROPERTIES OF THE SUBSTRATE AND THEIR INFLUENCE ON THE EPIPHYTES

The bark

The properties of the bark affect the epiphytes in several ways, e.g. through (1) relief and growth habit (2) structure or porosity, and (3) chemical composition. When comparing the relief of bark between various species of trees one must remember that the bark by no means is uniform over the entire tree but varies with age.

(1) The importance of the bark's relief can be suspected to be connected with the establishment of the seedlings. A deeply fissured bark could provide both a suitable microclimate for the germination of seeds and spores, and also more easily prevent the young seedlings from being washed away.

In the Nimba area a clear correlation has been established between the size of the tree (which in most cases is proportional to the age and roughness of the bark) and the number of epiphytic species (Fig. 69). On trees 10-15 m in size, e.g. *Lophira alata, Triplochiton scleroxylon, Ceiba pentandra,* there are seldom any epiphytes, although these species when older are very rich in epiphytes. This refers to trees of the primary forest as well as those in more open environments. However, several species of epiphytes seem to have a marked 'preference' for smooth bark surfaces, e.g. *Ancistrorhynchus cephalotes* (Fig. 110), *Angraecum podochiloides,* and *Polystachya affinis.*

From other parts of the world observations of a rich epiphytic flora on trees with rough bark are frequent (Oliver 1930:14, Eggeling 1947:56). Went (1940:95) observed that phorophytes with a poor

Fig. 110. *Ancistrorhynchus cephalotes* (lower down) and *Graphorchis lurida* (above) are two epiphytes which often occur on bark without humus deposits. Seka Valley 700 m.

epiphytic flora frequently were found among species with smooth or hard bark, and fast growing species.

Boyer (1964) concluded that it probably was the smooth nature of the bark that was the cause of the absence of *Platycerium* ferns on *Musanga Smithii*. In the Nimba area trees with a defoliating bark (e.g. *Distemonanthus benthamianus*), seem to be very difficult for the epiphytes to colonize. This has also been observed elsewhere (Dudgeon 1923, Pessin 1925:34, Oliver 1930:14, Went 1940:95, Rupp 1969:XI). Voorhoeve (1965:200), however, states that colonization of flaking bark does occur, and in some cases the epiphytes even prevent the shedding of the bark, e.g. on *Gilbertiodendron preussii*. The absence of epiphytic orchids on the oil palm is hard to correlate to any morphological characteristics of the phorophyte, but may possible be attributed to germination difficulties of the orchid seeds. When full-grown epiphytic orchids are transplanted on oil palms they readily attach themselves and seem to thrive.

Sulit (1950:8) even states that the 'palm trees' are especially suitable for growing orchids on.

(2) The structure or porosity of the bark will naturally effect its water capacity.

The absorbation ability of the bark varies naturally from tree to tree, depending on age, species and inclination (Freise 1936:303, Voth 1939). The subsequent water content of the bark is also dependent on the amount and type of rainfall, and the rate of evaporation, and thus varies with weather conditions and the season. Another fact to consider is that water does not flow evenly over the bark surface but is concentrated into so-called rain tracks or drainage channels (Richards 1964:118, Yarranton 1967).

The water content of the bark is thus dependent on a large number of variable factors. Measurements must therefore be carried out during a long period and involve samples from different sections of the trees. This study does not include measurements of the water capacity or the water content of the bark. Water capacity of bark have been investigated in various parts of the world with different methods. The results, however, show large variation between trees of the same species (Barkman 1958:75-76).

(3) No analyses of the chemical composition of bark have been undertaken, but pH measurements of bark samples in water suspension were performed.

Bark pH and the epiphytic flora

The samples were taken from representative areas in the vicinity of epiphytes in various sections of the phorophyte. They were all taken from trees felled the same day, except for a living *Parinari excelsa* tree at 1300 m altitude which was climbed. The bark pieces used in the survey had a size of 6-10 cm^2. They were pulverized and dried in 24 hrs in 55 % relative humidity. Distilled water twice the dry weight of the sample was added. The measurements were performed 24 hrs later on an electric pH-instrument. The sampling procedure, e.g. cutting a piece of bark, involves a great deal of subjectivity, since the actual choice of bark pieces may influence the result. It was found that dead, corky pieces gave higher pH values than living bark, a fact that is well known. There are also difficulties in utilizing a completely identical method of sampling due to the variation in the bark morphology. Some species have a thick easily

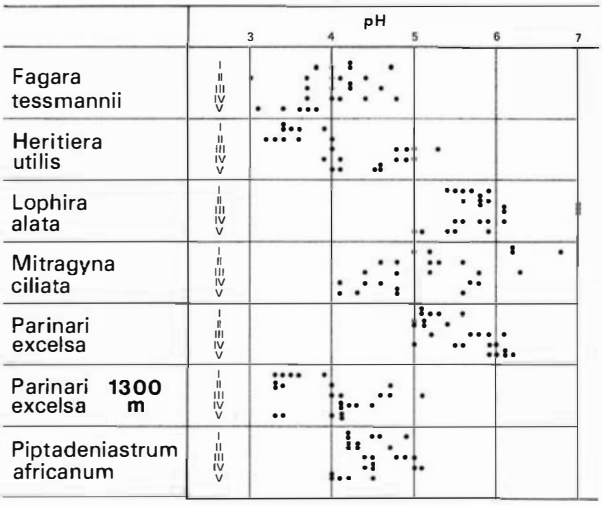


Fig. 111. pH in water extracts of bark from different phorophytes. Yekepa.

detachable bark while others have a thin flaky, corky or deeply fissured one. Differences in pH value for samples of large and small pieces of bark have also been reported (Sjögren 1961:102).

The pH values exhibit a ± significant pattern within the phorophytes (Fig. 111). The lowest values were obtained from the upper part of the main trunk and the outer branches.

The pH of the bark has been studied by many authors using various methods. It has been observed that the pH values decrease from the bases of the trees and upward, probably due to decreasing dust content. The pH has also been found to vary according to the time of day (Pessin 1925:34).

Du Rietz (1945:198-199) distinguishes three groups of bark based on the pH values, 'rikbark' (rich bark) pH 5-7, 'övergångs-fattigbark' (intermediate bark) pH 4-5 and 'extrem fattigbark' (extremely poor bark) pH <4. When trying to evaluate the influence of the pH value of the bark on the epiphytic flora one should remember that the pH value might have changed since the time when the seedlings were established. The long span from germination to a fully developed plant exemplified by the orchids emphasizes this problem.

The epiphytes themselves influence, in a complex and imperfectly known way, the acidity in their environment. This can be done by collecting dust and forming humus, through photosynthesis, by release of lichen acids and exchange of ions (Kolkwitz 1932, Skye 1968:107). The acidity also regulates the nitrification since this process is strongly pH dependent (Barkman 1958:103). The acidity may influence the germination of spores and seeds, or affect the growth of established plants. Pessin (1925:24), however, remarks: "It appears that the acidity or alkalinity of the substratum does not influence the occurrence and distribution of *Polypodium polypodioides*."

Exudates

"Orchids seem to dislike trees which exude a latex juice such as most *Ficus* species and tree *Euphorbias*." (Piers 1968:4).

In the Nimba area several species of phorophytes which exude a latex juice have a rather rich epiphyte flora, e.g. *Chlorophora regia, Uapaca guineensis* and even the rubber tree, *Hevea brasiliensis,* while others show an opposite tendency, e.g. the figs.

The toxic effect of certain exudates must also be considered. Barkman (1958:134) suspects the 'robin' in the bark of the *Robinia* tree to be the cause of the poverty of non-vascular epiphytes of this tree.

Large differences in the presence of orchids between various species of trees of the genus *Quercus* were observed by Frei (1973a:311-312) in a cloud forest in Mexico. Two species in the genus had only a few species of orchids, two others carried many orchids, and one was never observed with any orchids whatsoever.

When analyzed, the bark from the species with many orchids showed no presence of inhibitory substances. The bark from the phorophytes devoid of orchids, contained gallic and egallic acids, which are known to be growth inhibitory substances (hydrolyzable tannins). (See also Frei 1973b:701-708.)

Bark from several tropical species of trees e.g. *Ficus pumila* contain strong growth inhibitors (Bovey & Diaz-Colon 1959:256).

The importance of the leaching of growth-regulating substances from the vegetation has also been stressed by Tukey Jr (1970:160).

Went (1940:90) assumed that the rich epiphytic flora on *Castanopsis argentea* could be connected to the high amounts of tannin in the water on the bark surface. The excretion of water-soluble substances by the bark or the leaves has seldom been measured. Schweitzer (quoted from Ruinen 1953:151) found that a total leaf surface area of one sq. m of coffea leaves, leached in distilled water during one hour, yielded 21-35 mg mineral substances, *Erythrina*

33.8 mg, *Hevea* 55 mg. In many instances sugar could be detected in rainwater dripping from the leaves. Rain wash in a mature forest in Ghana carried the following amounts of nutrients out of the vegetation, in lb/acre: N 11, P 3, K 196, Ca 26, Mg 16 (Greendale & Nye 1964:248). See also Eaton et al. (1973). Ruinen (1953:151) states that germination and settlement of the epiphytes are possible even in a milieu with minimal nutrient value, because of the rich substrate offered by the living tissues and their excretions.

An efficient adaptation to intercept leachates from the overhead canopy is shown by certain bromeliads. It has been shown experimentally that metabolites fall in the well (formed by the diverging leaf bases) from which they are absorbed and utilized in growth (Tukey Jr 1970:155-160).

Humus deposits

Origin and composition

The accumulation of humus starts with the decomposition of the outer layers of the bark. The bark is continuously renewed from within, so that it automatically provides a steady supply of new material for decomposition. This is mainly carried out by fungi, which in many cases are connected to the roots of the epiphytes.

To the material from the bark external material is added. Dead leaves, twigs, small branches, etc., from the phorophyte itself can be assumed to form the bulk of the deposits. In this more or less accidental process the growth habit of the phorophyte and structure of its bark are of importance. The root systems of the epiphytes also help to catch debris in the many niches they form. Certain epiphytes play a more active role in the catching of falling debris. Usually a niche between the plant itself and the substrate is formed in which debris from above can be caught, e.g. *Drynaria laurentii, Platycerium* spp. (Fig. 112). The term 'sole epiphytique' has been used by Boyer (1964) for the humus collected by *Platycerium* ferns. She is of the opinion that these accumulations of organic material can hardly be compared to the soil in its proper sense. These accumulations have attracted the interest of several authors, e.g. Miehe (1911), Paulian (1945) and Klinge (1963).

In the Ivory Coast Boyer (1964) found that in the humus of the 'leaf basket' of *Platycerium angolense* and *P. stemaria* 63.4-90.9 % of the dry weight was

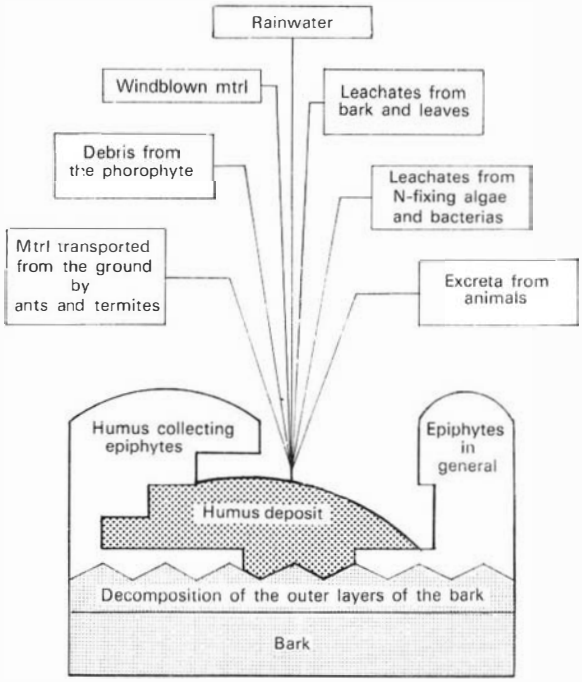


Fig. 112. Origin of substrate and nutrients of importance for the epiphytic flora.

organic in origin. This can be compared to the soil under the trees containing 3.0-3.9 % of organic matter. 10-23 % of the material belonged to a fraction less than 2 mm in diam. The rest consisted of living, or dead and more or less decomposed parts of leaves and roots.

The accumulation of organic material through wind, animals, and water running along branches and stem amounted to 5-10 % of the total weight. The bulk of the organic material was derived from the tissues of the fern itself. The addition of organic material from sources outside the fern was considered to play a minor role in the nutritional supply for this epiphyte.

The formation of the humus was slow. It was estimated that it takes 10 years to form a layer of 10 cm thickness. It was also noticed that the material that was incorporated was only slowly decomposed despite the rich microflora. The external contribution to the assemblage of humus may be small in volume but important in its nutritional effect on the epiphytic flora.

Dust carried by the winds may be of considerable importance in certain areas. Every year in the winter months the Harmattan winds fill the air with a fine dust in vast regions of West Africa. It is easily observed that trees close to dusty roads often show a

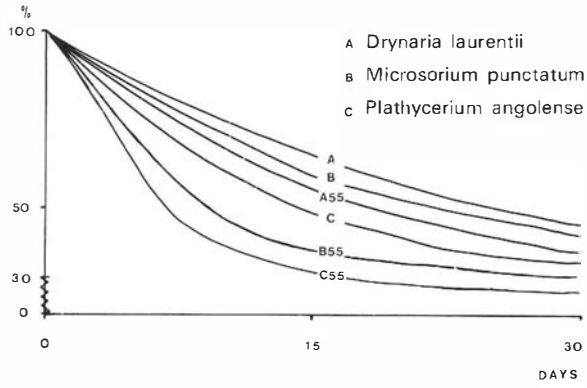


Fig. 113. Water holding capacity of humus from different epiphyte communities, in % of the wet weight.

luxuriant growth of epiphytes (Thorold 1952:139, Richards 1964:114). Ants and termites carry material of inorganic as well as organic origin up into the trees. Termite nests built from earth, and the earth-covered tracks of these insects are common on the trees. Richards (1964:111) states that the roots of flowering epiphytic plants and ferns are one of the chief nesting places for arboreal ants. Adamson (1943) suggested that certain epiphytes in the rain forest of Trinidad may be at least partly dependent on soil carried up into the trees by termites. In an analysis of the mineral content in the humus from a *Platycerium* fern in the Nimba Mountains Schnell (1952:58) found that 38 % of the mineral content had a granular size of gritty sand and 68 % was of lesser sizes. The mineral particles appeared as grains of quartz, hematite, and loam. Schnell did not elaborate on the origin of the larger sized particles that can hardly be transported by the wind, but it can be mentioned that the earth in this particular region is very rich in hematite.

Water holding capacity

Pieces of humus of roughly the same volume (1.5 dm^3) (100 x 100 x 150 mm) were cut out from a humus deposit in a *Drynaria laurentii,* a *Microsorium punctatum* and a *Platycerium angolense* epiphyte community. Four samples from each type of humus were taken. The pieces were placed in baskets of 'chicken wire' and then saturated with water for 3 hours. The water was allowed to drip off, and when no more water was given off, the weight of the twelve samples were taken. The samples were divided in two groups, one was placed in an air-conditioned room at 55 % relative humidity, the other placed outdoors but prevented from contact with rainwater. The weight of the samples were taken every second day during a 30-day-period. The water holding capacity for the humus is shown in Fig. 113. It is obvious that the humus deposits may serve as a water reservoir. The ability of rapid water absorption during a shorter rainfall and the slow release of it is naturally of great importance for the epiphytes.

pH of humus deposits

Thirteen different humus deposits utilized by epiphytes were examined. The methods used in these determinations are the same as described in the investigation of the bark, i.e. the bark piece has simply been replaced by a piece of humus (50 g dry weight).

Rather high pH values were obtained, considerably higher than those of the bark, Table 45.

Schnell (1952:58-59) gives the pH in the humus of a *Bulbophyllum* sp. as 4.8 and for a *Listrostachys* sp. to 5.7. Boyer (1964) reports the pH of humus from *Platycerium stemaria* as 4.6-6.4 (6.0 for *P. angolense*).

Correlation between substrate and epiphytic flora

Many epiphytes show a high frequence in the recor-

Table 45. pH in water extracts from humus deposits with growing epiphytes. Median value of five samples.

Phorophyte	Section	pH	Epiph. utilizing the humus
Heritiera utilis	IV	6.6	Drynaria laurentii Nephrolepis undulata
Heritiera utilis	V	6.0	Drynaria laurentii Nephrolepis undulata
Lophira alata	III	5.8	Vittaria guineensis
Lophira alata	IV	7.0	Oleandra distenta Tridactyle armeniaca
Lophira alata	V	6.8	Drynaria laurentii Polystachya polychaete
Parinari excelsa	III	6.0	Oleandra distenta Arthropteris orientalis
Parinari excelsa	IV	5.6	Drynaria laurentii Microsorium punctatum
Parinari excelsa	III	6.8	Asplenium megalura Peperomia sp.
Parinari excelsa	IV	6.1	Asplenium dregeanum Polystachya leonensis
Piptadeniastrum africanum	III	6.2	Asplenium geppii Begonia polygonoides
Piptadeniastrum africanum	IV	6.3	Oleandra distenta Microsorium punctatum
Triplochiton scleroxylon	IV	5.5	Platycerium angolense
Triplochiton scleroxylon	IV	4.8	Platycerium stemaria

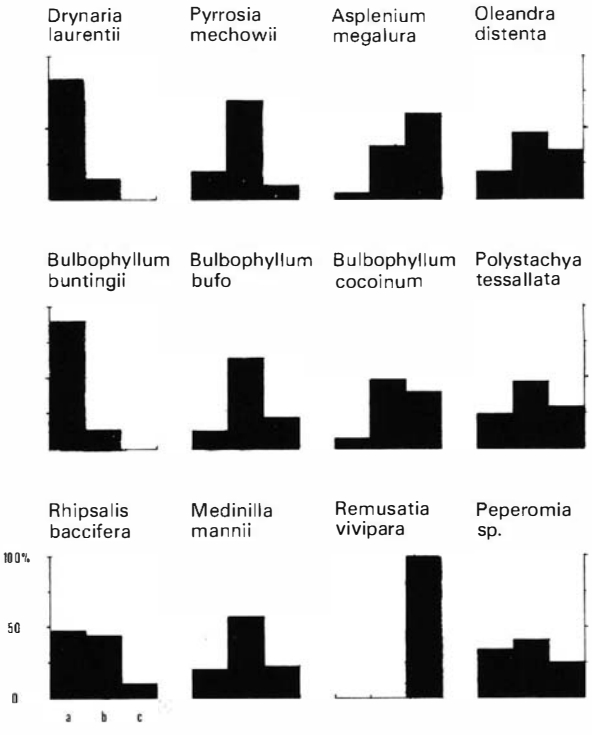


Fig. 114. Records of epiphytes distributed between the different humus classes (from Table 27). (a) bark, (b) minor humus deposits, (c) large humus deposits.

dings from only one substrate class (of the three that are recognized), as can be assessed from Tables 27-29. Less frequently an even distribution between the substrate classes is observed. This 'preference' for a particular type of substrate occurs among all the major groups of epiphytes (Fig. 114).

Most pteridophyte species (51 %) grow in minor humus deposits. The orchid species occurred on bark (50 %). The other vascular epiphytes were found in large humus deposits (54 %) (Table 46).

Regarding the interrelationship between epiphytes and phorophytes three case may be distinguished in the area studied (denoted A, B and C below).

A. Phorophytes with an abundance of epiphytes

In the Nimba area a 'preference' by epiphytes for colonizing certain species of phorophytes is easily observed, but somewhat more difficult to express. The abundance can be expressed as previously described, either by the number of species of epiphytes on a certain species of phorophyte or the number of 'stands' of epiphytes on the individual phorophyte. Since the results from these two methods correlate for the most part, the first method

Table 46. Most frequent light-substrate class at the growing sites of each epiphyte species. Given as a percentage of the total number of species in each of the three groups. Based on Table 27 a and b, for species with 10 records or more. For species with less records the sum of records from Table 27 a and b, and Table 28 a and b are used if it reach 10 or more. For the remaining species the sum of records from Tables 27 a and b, 28 a and b and 29 are used.

Substrate	Light			Total, substrate
	Heavy shade	Open shade	Full sun	
The Pteridophytes (39 spp.)				
Large humus deposits	7.7	10.3	2.6	20.6
Minor humus deposits	10.3	38.5	2.6	51.4
Bark	5.1	5.1	17.9	28.1
Total, light	23.1	53.9	23.1	100.1
The orchids (101 spp.)				
Large humus deposits	1.0	7.9	1.0	9.9
Minor humus deposits	1.0	25.7	12.9	39.6
Bark	—	15.8	34.7	50.5
Total, light	2.0	49.4	48.6	100.0
The other vascular epiphytes (13 spp.)				
Large humus deposits	15.4	38.5	—	53.9
Minor humus deposits	—	30.8	7.7	38.5
Bark	—	7.7	—	7.7
Total, light	15.4	77.0	7.7	100.1

will be used (Table 47). Phorophytes with a high number of species of epiphytes are:

Amphimas pterocarpoides
Anthonotha fragans
Calpocalyx aubrevillei
Canarium schweinfurthii
Ceiba pentandra
Chlorophora regia
Combretodendron macrocarpum
Coula edulis
Cryptosepalum tetraphyllum
Entandrophragma utile
Heritiera utilis
Lophira alata
Mitragyna ciliata
Parinari excelsa
Piptadeniastrum africanum
Triplochiton scleroxylon

An often striking difference in the abundance and floristic composition of the epiphyte vegetation depending on the species of phorophyte is well documented from various parts of the world.

In the Phillippines the 'preference' for certain phorophytes that the orchids exemplify, has even led

Table 47 a. Records of pteridophytes and other vascular epiphytes growing on different phorophytes in the Nimba area.

	Phorophytes of the high forest	Albizia glaberrima	Albizia zygia	Alstonia boonei	Amphimas pterocarpoides	Anthocleista nobilis	Anthonotha fragans	Antiaris toxicaria	Bertinia contusa	Bombax buonopozense	Bussea occidentalis	Calpocalyx aubrevillei	Canarium schweinfurthii	Ceiba pentandra	Chidlowia sanguinea	Chlorophora regia	Chrysophyllum perpulchrum	Combretodendron macrocarpum	Coula edulis	Cryptosepalum tetraphyllum	Daniellia ogea	Distemonanthus benthamianus	Entandrophragma utile	Erythrophleum ivorense	Fagara tessmannii	Guarea cedrata	Hertiera utilis	Khaya antholheca	Lophira alata	Lovoa trichilioides	Mammea africana	Mitragyna ciliata	Nauclea diderrichii	Parinari aubrevillei	Parinari excelsa	Parinari glabra	Parkia bicolor	Pentaclethra macrophylla	Pentadesma butyracea	Piptadeniastrum africanum	Pycnanthus angolensis	Rhodognaphalon brevicuspe	Sacoglottis gabonensis	Terminalia ivorensis	Terminalia superba	Triplochiton scleroxylon	Uapaca guineensis	Vitex micrantha	Total no. of phorophyte spp.	Phorophytes outside the high forest	Cola nitida	Cussonia barteri	Hevea brasiliensis	Musanga cecropioides	Dead trees	Elaeis guineensis	Total no. of phorophyte spp.
Pteridophytes																																																												
Antrophyum immersum		+	·	·	·	·	·	·	x	·	+	x	·	o	·	o	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	10		+	·	·	·	·	·	·	1
A. manniamum		·	·	·	·	·	·	x	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	x	·	·	·	·	o	+	·	o	·	·	x	·	·	·	·	·	·	·	·	·	·	·	·	7		·	·	·	·	·	·	·	–
Arthropteris monocarpa		·	·	·	+	x	+	·	·	+	·	+	+	·	·	·	·	+	·	+	·	·	+	·	+	+	+	+	x	·	x	·	+	·	·	·	·	·	·	·	·	·	+	·	·	·	+	+	+	20		+	·	·	·	·	·	·	1
A. orientalis		·	+	+	+	·	x	·	+	·	+	+	·	o	+	+	·	+	x	+	·	·	+	x	·	·	x	·	x	·	+	x	x	+	o	·	·	+	x	+	·	+	·	·	·	+	+	+	29		·	+	+	·	·	+	·	3
A. palisoti		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1		·	·	·	·	·	·	·	–
Asplenium aethiopicum		·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	4		·	·	·	·	·	·	·	–
A. africanum		·	·	·	+	·	+	·	x	+	·	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	x	o	·	·	x	·	·	o	·	·	·	·	o	·	·	x	·	·	·	·	·	x	14		+	+	·	·	·	+	·	3
A. barteri		·	+	+	·	+	·	·	+	+	x	·	·	·	x	+	·	·	+	·	·	x	·	·	·	+	+	+	·	+	·	+	·	·	+	x	·	·	o	·	·	+	·	·	·	·	·	x	·	20		·	·	·	·	·	·	·	–
A. dregeanum		·	·	·	·	·	+	·	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·	x	·	·	·	·	·	·	·	·	·	·	·	·	x	·	7		·	·	·	·	·	·	·	–
A. geppii		·	+	x	+	·	o	·	+	·	·	x	·	+	·	·	+	·	x	o	·	·	o	·	·	·	o	·	+	·	o	x	+	·	x	+	·	·	x	·	·	o	·	x	o	+	·	23		+	·	·	·	·	·	+	2
A. hemitomum		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	·	+	·	·	·	+	·	·	o	·	·	·	·	·	·	·	4		·	·	·	·	·	·	·	–
A. megalura		+	·	x	o	·	x	x	x	·	·	x	o	o	·	x	x	x	x	x	·	·	x	x	·	·	x	x	x	x	·	x	x	+	x	·	x	o	+	x	x	o	x	·	·	x	x	+	34		+	·	+	·	·	+	+	4
A. variable var. paucijugum		·	·	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	o	·	·	·	·	o	·	·	·	·	·	·	·	+	·	6		·	·	·	·	·	·	·	–
Davallia chaerophylloides		x	·	·	x	·	o	·	·	+	·	·	+	o	·	o	·	x	·	+	·	·	x	x	·	·	x	·	+	+	·	o	·	·	+	·	x	·	·	o	·	o	·	·	·	x	·	·	21		+	·	·	+	·	+	+	4
Drynaria laurentii		x	x	x	·	+	x	x	x	+	·	x	x	x	o	x	x	x	x	x	x	·	x	x	·	o	x	x	x	x	x	x	x	x	x	+	x	x	x	x	x	x	x	x	+	+	x	+	+	43		+	+	+	+	+	+	·	5
Elaphoglossum barteri		·	·	+	·	·	·	·	·	·	·	x	·	·	+	+	x	·	·	·	·	·	+	·	·	·	x	·	·	·	·	x	·	·	o	·	·	·	·	·	·	·	·	·	·	·	·	+	·	10		·	·	·	·	·	·	·	–
E. chevalieri		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	x	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	x	·	4		·	·	·	·	·	·	·	–
E. isabelense		·	·	x	+	·	+	·	x	x	·	x	+	o	·	+	·	+	o	x	+	·	x	x	·	x	x	+	x	x	·	x	x	x	●	·	·	·	·	x	·	·	·	·	x	+	·	+	28		+	+	·	·	·	+	3
E. kuhnii		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	2		·	·	·	·	·	·	·	–
E. salicifolium		·	·	·	+	·	+	·	x	+	+	·	o	+	o	+	o	o	x	x	·	x	x	x	·	x	·	x	x	·	+	·	+	x	·	+	+	·	x	·	x	·	+	+	·	x	+	+	32		+	·	·	·	·	+	·	2
Lomariopsis guineensis		·	·	·	·	·	·	·	·	·	·	x	·	·	·	·	·	·	o	·	·	+	·	·	·	+	·	·	·	·	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	8		·	·	+	·	·	·	·	1
Loxogramme lanceolata		·	+	·	o	x	o	·	·	x	x	+	·	x	x	·	·	·	+	·	+	·	+	+	·	x	+	·	+	·	·	x	x	·	x	+	o	·	·	+	·	+	x	·	·	+	x	o	27		+	·	+	·	·	+	3
Lycopodium mildbraedii		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	+	·	·	·	·	·	·	·	·	·	·	·	·	2		·	·	·	·	·	·	·	–
L. warneckei		+	·	·	x	·	o	·	x	+	·	·	o	+	·	o	o	x	x	x	x	·	x	x	·	●	o	o	x	x	o	x	·	+	o	·	o	+	·	o	+	o	x	·	·	o	x	+	33		+	·	+	·	·	+	+	4
Microgramma owariensis		·	x	·	x	x	·	·	x	·	x	x	o	o	o	o	·	·	·	o	+	·	x	x	·	·	+	·	x	x	·	x	+	·	o	+	·	·	+	o	x	x	x	+	·	+	o	x	30		+	+	+	·	·	+	4
Microsorium punctatum		·	x	x	o	x	o	x	x	x	·	x	o	o	x	x	x	x	·	o	o	·	x	x	+	x	x	x	x	x	x	x	x	x	x	x	·	x	·	x	·	·	x	·	x	x	x	o	38		+	+	+	·	·	+	+	5
Nephrolepis biserrata		·	x	·	o	+	·	x	x	·	·	·	+	x	·	o	·	x	+	+	·	+	+	·	·	·	x	·	o	·	·	x	·	+	o	·	+	·	·	o	x	+	·	·	·	x	·	+	24		+	·	+	·	·	+	+	3
N. undulata		·	o	x	x	·	x	+	x	·	+	x	o	o	x	x	x	x	x	x	x	·	x	x	+	x	x	x	x	x	x	x	x	x	x	·	x	·	·	o	·	x	x	·	o	x	o	x	38		+	·	·	·	·	+	+	3
Oleandra distenta		+	x	x	o	+	x	·	x	·	·	x	x	x	·	o	x	+	+	+	+	·	x	x	·	o	x	o	x	x	·	x	·	+	o	x	·	+	x	x	x	·	x	·	·	x	+	·	34		+	·	+	·	·	+	+	4
Phymatodes scolopendria		·	·	x	x	·	x	x	·	+	·	x	o	x	o	·	+	·	+	x	+	·	x	x	·	x	+	·	x	o	·	x	·	x	x	·	·	x	x	x	·	+	x	·	·	x	x	+	30		+	+	+	·	·	+	+	5
Platycerium angolense		x	·	·	x	·	·	x	·	+	·	·	o	x	·	x	·	x	·	o	·	·	x	·	·	·	·	·	·	·	·	x	x	·	·	·	x	·	·	x	o	·	·	·	·	x	·	·	17		+	+	+	·	·	+	·	4
P. stemaria		+	+	·	x	·	x	x	·	·	·	·	o	x	·	x	x	x	·	o	·	·	x	x	·	·	·	·	·	·	·	x	·	+	o	·	x	·	·	x	·	x	x	·	o	x	·	x	23		+	+	·	·	·	+	3
Pyrrosia mechowii		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	·	+	·	·	·	·	·	·	·	·	·	·	·	+	·	3		+	+	·	·	·	·	·	2
Tectaria angelicifolia		+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	x	·	6		·	·	·	·	·	·	·	–
T. fernandensis		·	·	·	+	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	5		·	·	·	·	·	·	·	–
Vittaria guineensis		+	o	·	x	+	x	+	x	x	x	x	+	x	x	x	x	+	+	x	+	x	x	x	x	+	x	+	x	x	x	x	x	·	x	x	·	x	+	x	x	x	·	·	+	x	o	x	42		+	+	·	+	+	+	5
Xiphopteris oosora		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	·	·	·	·	·	·	·	·	·	·	·	·	2		·	·	·	·	·	·	·	–
X. serrulata		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	2		·	·	·	·	·	·	·	–
X. villosissima		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	x	·	·	·	·	·	·	·	·	·	·	·	·	·	1		·	·	·	·	·	·	·	–
Total no. of pteridophyte spp.		10	14	12	19	10	18	10	16	13	10	21	15	19	13	19	12	14	14	20	12	3	22	15	4	13	21	14	21	17	9	29	11	13	36	8	11	11	8	21	8	13	16	3	7	19	24	16		21	11	13	2	12	15		
Other vasc. epiphytes																																																												
Begonia mannii		·	·	·	·	·	·	·	·	·	+	+	x	·	·	·	·	·	·	·	·	·	+	·	·	·	x	·	·	·	·	x	·	·	o	·	·	·	·	·	·	·	·	·	·	·	·	·	7		·	·	·	·	·	·	·	–
B. polygonoides		·	·	+	o	·	+	·	x	·	·	·	+	o	o	o	·	·	o	·	·	·	o	·	·	·	o	+	+	x	·	o	·	·	+	·	·	·	x	·	o	·	·	·	o	·	+	20		·	·	·	·	·	·	·	1
B. rubro-marginata		·	·	x	x	·	o	·	·	+	·	·	o	o	+	o	x	x	·	x	·	·	x	x	·	·	x	·	o	o	·	x	·	·	x	x	x	o	●	x	x	·	o	+	·	x	·	x	28		+	·	·	·	·	·	·	1
Calvoa monticola		·	·	·	·	+	·	+	·	·	·	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	6		·	·	·	·	+	·	1
C. trochainii		·	·	·	+	·	+	·	·	·	·	+	+	·	+	+	·	+	x	+	+	·	·	+	o	·	o	·	·	o	·	·	x	x	+	·	·	x	+	x	·	·	·	x	·	·	·	22		·	·	·	·	·	·	·	–
Medinilla mannii		·	·	x	+	·	·	·	+	·	·	x	x	o	·	·	+	o	o	x	·	·	x	x	·	·	o	·	x	·	x	·	·	x	x	x	·	o	+	o	o	·	·	·	·	x	+	·	24		+	+	·	·	·	+	·	3
Peperomia fernandopoiana		·	+	+	+	·	·	+	·	·	·	+	x	+	·	+	·	·	·	·	x	+	+	·	x	+	x	·	+	·	·	+	x	·	x	·	·	·	·	·	+	·	+	·	x	+	+	23		+	·	·	·	·	+	·	2
P. molleri		+	+	·	·	+	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	7		·	·	·	·	·	·	·	–
P. rotundifolia		·	x	·	x	·	+	·	+	·	·	·	+	·	·	·	●	+	x	·	·	x	+	·	·	x	·	x	x	·	+	·	o	·	+	+	·	+	+	·	+	·	+	·	·	+	·	+	23		+	·	·	·	·	·	·	1
Preussiella chevalieri		+	·	·	+	·	·	·	+	·	·	+	+	o	·	·	+	·	·	x	x	·	+	·	·	·	·	+	·	·	·	x	·	·	+	·	·	·	+	+	·	·	·	·	o	·	·	16		·	·	+	·	+	+	3
P. kamerunensis		·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	1		·	·	·	·	·	·	·	–
Remusatia vivipara		·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	x	·	·	·	x	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	+	·	·	7		·	·	·	·	·	·	·	–
Rhipsalis baccifera		+	+	o	●	+	o	·	x	x	·	+	o	o	+	·	x	x	o	o	o	·	x	+	·	·	x	x	x	·	·	x	·	·	x	x	·	o	o	x	x	·	x	·	·	x	x	·	32		+	+	+	·	+	·	4
Total no. of other vasc. epiphyte spp.		3	4	5	8	3	5	2	5	2	3	7	8	7	6	4	4	5	5	6	4	1	9	5	1	2	9	2	9	3	1	9	1	3	8	8	3	4	3	7	6	3	3	2	–	9	5	4		5	2	3	–	5	1		

x = close observation, o = distance observation, + = occasional observation. Only one kind of record is given, i.e. when a close observation record occur, distance and occasional observations are excluded. If a distance observation is given no close record exist and only when close and distance records are lacking, occasional records are shown.

Table 47 b. Records of orchids growing on different phorophytes in the Nimba area.

Phorophytes of the high forest	Albizia glaberrima	Albizia zygia	Alstonia boonei	Amphimas pterocarpoides	Anthocleista nobilis	Anthonotha fragans	Antiaris toxicaria	Berlinia confusa	Bombax buonopozense	Bussea occidentalis	Calpocalyx brevipilosus	Canarium schweinfurthii	Celtis pentandra	Chidlowia sanguinea	Chlorophora regia	Chrysophyllum perpulchrum	Combretodendron macrocarpum	Coula edulis	Cryptosepalum tetraphyllum	Daniellia ogea	Distemonanthus benthamianus	Entandrophragma utile	Erythrophleum ivorense	Fagara tessmannii	Guarea cedrata	Heritiera utilis	Klainedoxa gabonensis	Lophira alata	Lovoa trichilioides	Mitragyna ciliata	Nauclea diderrichii	Parinari anbrevillei	Parinari excelsa	Parinari glabra	Parkia bicolor	Pentaclethra macrophylla	Pentadesma butyracea	Piptadeniastrum africanum	Pycnanthus angolensis	Rhodognaphalon brevicuspe	Sacoglottis gabonensis	Terminalia ivorensis	Terminalia superba	Triplochiton scleroxylon	Capaca guineensis	Vitex micrantha	Total no. of phorophyte spp
Afrangis biloba	•	•	•	•	o	•	•	•	•	+	o	•	x	•	•	o	•	•	•	•	•	•	•	o	•	•	x	•	x	•	•	•	•	•	•	x	•	•	•	•	x	•	•	•	•	•	•	•	22
A. laurentii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	x	•	•	•	•	•	•	o	•	x	•	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	8
Ancistrochilus rothschildianus	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	8
Ancistrorhynchus capitatus	•	•	•	•	•	•	•	•	•	•	•	x	x	•	•	•	•	•	•	•	•	•	•	•	•	x	x	•	•	•	•	x	x	•	•	•	•	•	•	x	x	•	•	•	•	•	•	•	20
A. cephalotes	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	o	•	x	•	•	•	•	•	x	o	•	•	•	•	•	x	x	x	•	•	•	o	•	•	x	•	•	•	x	x	•	•	•	23
A. clandestinus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
A. recurvus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	-
Angraecopsis elliptica	•	•	•	•	•	•	•	•	•	x	•	•	x	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	6
Angraecum birrimense	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	x	•	x	•	x	x	•	x	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	15
A. chevalieri	•	•	•	•	•	•	•	•	•	x	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
A. classensii	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
A. distichum	•	•	•	•	•	•	x	•	•	•	•	•	•	o	•	x	x	x	o	x	•	•	•	•	x	o	•	x	x	x	•	x	x	•	x	•	o	x	•	•	•	•	•	•	•	•	•	o	31
A. podochiloides	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
A. subulatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	x	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	4
Ansellia africana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
Bolusiella talbotii	•	•	•	•	•	•	•	•	x	x	•	•	o	•	x	•	•	o	o	•	•	•	•	•	o	•	•	•	•	x	•	x	x	•	x	x	•	x	•	•	•	•	•	•	•	•	x	•	17
Brachycorytis kalbreyeri	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	+	•	+	•	+	o	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	8
Bulbophyllum barbigerum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	x	•	•	x	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
B. bifarium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
B. bufo	•	•	x	x	•	•	x	•	•	•	o	o	•	•	o	•	o	•	x	x	•	•	•	o	+	x	x	x	•	o	•	•	•	x	o	•	•	x	•	•	•	x	+	•	•	•	•	•	27
B. buntingii	•	•	•	x	•	•	•	•	•	•	•	x	•	x	•	•	•	•	x	•	x	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	x	•	x	•	•	•	•	•	•	12
B. calamarium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	4
B. cochleatum	•	•	•	o	•	•	•	•	•	x	•	x	x	x	•	o	•	•	•	•	x	x	•	•	o	•	•	•	•	o	x	•	x	•	•	•	o	•	•	x	•	•	•	•	•	•	•	•	19
B. cocoinum	•	•	x	•	•	•	•	•	x	•	•	o	x	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	o	•	x	x	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	20
B. congolanum	•	•	•	•	•	•	•	•	•	•	•	o	o	•	•	•	o	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	x	•	•	•	•	•	•	x	11
B. distans	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	x	x	x	•	•	x	•	•	x	•	•	x	•	•	x	•	•	•	•	•	o	•	•	•	12
B. falcatum	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	o	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	10
B. flavidum	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	o	•	•	x	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
B. imbricatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
B. inflatum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
B. intertextum	•	•	•	•	•	o	•	x	•	+	x	x	o	x	o	•	o	o	o	•	•	o	•	•	x	•	o	•	•	o	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	26
B. josephii	•	•	•	•	•	o	•	•	•	•	•	x	•	o	x	•	•	•	•	•	•	x	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	11
B. linderi	•	•	•	•	•	•	x	x	•	•	•	•	+	o	•	x	•	x	x	o	x	•	•	x	•	x	•	x	x	x	•	•	•	•	o	x	•	•	x	x	•	•	•	•	•	•	•	x	28
B. lucifugum	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	4
B. lupulinum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	7
B. magnibracteatum	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
B. maximum	•	•	•	+	•	o	•	+	•	o	+	o	•	o	•	o	•	+	x	•	•	•	•	•	+	•	x	•	+	+	•	•	•	•	•	+	o	•	•	•	•	+	+	x	•	•	•	x	24
B. melanorrachis	•	•	•	•	•	•	•	•	o	•	•	+	•	•	o	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	o	•	8
B. nigritianum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	o	•	2
B. oreonasies	+	•	+	•	•	x	x	x	+	x	o	x	o	x	x	x	x	o	•	x	+	x	+	x	x	x	x	x	x	+	x	•	x	x	•	x	x	•	x	x	x	x	x	•	x	x	•	•	39
B. pavimentatum	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
B. phacopogon	•	•	•	x	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	10
B. recurvum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
B. rhizophorae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
B. saltatorium	•	•	•	•	•	o	•	•	•	•	o	•	x	•	•	•	x	•	•	•	+	•	•	x	•	x	•	•	•	•	•	x	+	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	14
B. scariosum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
B. schimperanum	•	•	•	•	•	o	•	•	•	•	•	•	•	•	x	•	o	•	o	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
B. schinzianum	•	•	•	•	•	•	•	•	•	•	•	o	•	o	•	x	x	•	•	•	x	•	x	•	x	x	•	•	•	•	x	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	19
B. winkleri	•	•	o	•	•	•	•	•	•	•	•	•	•	•	x	•	o	x	•	•	•	•	x	•	o	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	x	18
Calyptrochilum christyanum	•	•	•	•	•	•	•	•	•	•	•	o	•	x	•	o	•	x	•	•	x	•	•	x	•	•	•	•	•	•	x	•	•	•	o	•	•	x	•	•	x	•	o	•	•	•	•	•	16
C. emarginatum	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	4
Chamaeangis vesicata	•	•	•	x	•	•	•	x	x	•	+	•	•	x	•	x	•	•	•	x	x	•	+	o	•	x	•	x	•	x	+	•	•	•	•	o	•	•	x	•	•	•	•	•	•	•	•	•	23
Cyrtorchis arcuata	•	•	x	•	•	•	x	x	•	•	•	•	•	x	x	o	o	x	•	•	x	•	•	x	x	x	x	•	x	•	•	x	•	•	x	•	x	o	•	•	•	•	•	•	x	o	•	•	27
C. aschersonii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	o	o	•	•	•	•	•	o	x	•	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	•	•	10
C. monteiroae	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
Diaphananthe bidens	•	+	x	•	•	o	•	•	•	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	o	•	•	•	x	•	+	•	•	•	•	•	o	•	•	•	•	x	•	•	•	•	•	•	19
D. densiflora	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
D. pellucida	•	•	•	•	•	•	•	•	•	x	•	•	o	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	x	•	+	o	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	22
D. rutila	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	7
Eurychone rothschildiana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
Genyorchis pumila	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
Graphorchis lurida	•	•	o	x	•	x	x	x	•	x	•	•	x	•	o	x	x	x	•	+	x	•	+	•	x	x	x	x	+	x	x	•	x	•	x	•	x	•	x	•	x	x	•	o	•	•	•	•	34
Habenaria leonensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
H. procera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
Liparis caillei	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
L. nervosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
Listrostachys pertusa	•	•	•	•	•	x	•	x	+	•	+	•	•	•	x	x	x	x	x	•	x	•	+	•	x	x	x	•	x	+	o	•	x	+	•	x	•	x	x	•	o	x	o	•	28	+	•	•	+	•	2
Nephrangis filiformis	x	•	•	•	•	o	x	•	•	•	•	•	x	•	x	+	o	o	x	x	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	13
Plectrelminthus caudatus	•	•	•	x	•	•	•	•	•	•	•	+	•	•	•	+	o	•	•	+	•	x	•	•	•	•	x	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	o	•	9
Podangis dactyloceras	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
Polystachya adansoniae	•	•	•	•	•	•	o	•	•	•	•	•	•	•	x	•	o	•	•	•	•	•	•	•	•	•	•	•	•	x	+	•	x	•	•	•	+	•	•	•	•	•	x	•	x	•	•	•	15
P. affinis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	6
P. dalzielii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
P. elastica	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
P. galeata	•	x	x	•	•	o	o	x	•	•	+	+	o	o	•	•	o	•	•	•	o	x	•	o	+	o	•	x	x	x	x	x	o	•	+	o	•	x	•	•	•	•	•	•	•	•	x	•	27
P. laxiflora	•	•	x	•	•	+	•	•	•	x	x	•	o	o	x	•	•	•	•	•	+	•	•	x	o	•	•	•	x	•	+	+	•	•	•	•	•	x	•	•	x	•	•	•	•	•	•	•	17
P. leonensis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
P. microhambusa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
P. obanensis	•	•	x	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	o	•	•	•	•	+	+	o	•	•	x	+	x	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	11
P. paniculata	•	•	•	•	•	•	•	•	x	•	•	x	•	x	•	o	o	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	o	•	•	•	•	•	x	•	x	•	•	•	•	•	13
P. pobeguinii	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	6
P. polychaete	•	•	x	•	•	•	•	•	•	•	•	o	•	o	•	o	o	x	•	•	•	•	•	x	•	x	•	x	•	x	x	+	•	+	•	o	•	•	x	•	•	•	•	•	•	•	o	•	25
P. puberula	•	•	•	x	•	•	•	•	•	•	•	o	•	o	•	o	•	•	•	x	x	•	•	•	•	•	•	x	•	•	•	•	•	•	o	•	•	•	x	x	•	•	•	•	•	•	o	•	14
P. ramulosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	5
P. rhodoptera	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	7
P. saccata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	x	•	x	x	x	•	o	•	•	x	•	x	•	•	•	x	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	12
Polystachya subulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	3
P. tenuissima	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	o	•	•	•	5
P. tessallata	•	o	x	x	o	o	•	•	x	•	+	+	o	•	•	x	x	x	x	o	•	x	•	•	x	x	x	x	x	x	x	•	x	x	x	x	+	x	x	x	+	o	x	x	x	•	•	•	39
Rangaeris brachycras	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
R. muscicola	•	•	•	•	•	•	o	•	•	•	•	x	•	x	x	x	x	x	x	•	x	•	•	x	•	•	•	o	•	•	•	x	•	x	x	•	x	•	x	x	•	•	•	•	•	•	•	•	27
R. rhipsalisocia	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	o	•	•	•	•	•	•	•	•	•	•	o	7
Rhipidoglossum pancifolium	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
Stolzia repens	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
Tridactyle anthomaniaca	•	•	o	x	•	x	x	•	x	•	x	x	•	o	x	•	•	x	•	x	x	x	•	x	•	x	x	o	o	+	x	•	•	•	•	x	o	x	x	•	+	x	•	x	x	•	•	•	32
T. armeniaca	•	•	x	x	x	+	o	x	x	•	•	+	x	x	•	x	x	x	•	x	+	x	x	x	x	x	x	o	x	•	x	x	•	x	x	•	x	•	x	x	•	x	•	x	x	x	x	•	32
T. bicaudata	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	6
T. crassifolia	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	x	o	•	•	•	•	x	•	x	•	•	•	•	•	x	•	•	•	x	•	x	•	•	•	•	•	•	•	•	•	•	8
T. tridactylites	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	2
T. tridentata	•	•	o	•	•	o	•	•	•	•	•	•	o	x	x	o	x	x	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	x	•	•	•	•	•	•	•	•	•	•	•	•	o	13
Vanilla crenulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1
Total no. of orchid spp.	9	5	10	6	30	24	22	16	16	23	29	42	15	44	26	29	45	24	27	31	39	16	15	56	21	52	22	19	47	23	16	57	13	12	20	14	47	3	20	25	9	9	41	26	25		39	25	10	1	31	1	

x close observation, o distance observation, + occasional observation. Only one kind of record is given, i.e. when a close observation record occur, distance and occasional observations are excluded. If a distance observation is given no close record exist and only when close and distance records are lacking, occasional records are shown.

to the construction of a list of favourite 'host trees' for certain popular orchids, for aiding the collector in field-work (Sulit 1950:6-8). Morris (1970:5) uses the term 'orchid-prone' for trees that are attractive to epiphytic orchids. The following species of phorophytes have been reported to carry an abundance of epiphytes:

Liberia: *Cola nitida* (Harley 1955:71), *Mitragyna ciliata* (Voorhoeve 1965:324), *Parinari excelsa* (Voorhoeve 1965:319)

West Africa: *Parinari excelsa* (Jaeger et al. 1968:270, *Schnell* 1970:309)

Malawi: *Brachystegia spiciformis, Bridelia micranta, Ilex mitis, Parinari mobola, Podocarpus milanjuanus, Syzygium cordatum, Uapaca kiekiana* (Morris 1970:5)

Java: *Castanea argentea, C. javanica* (Went 1940)

West Borneo: *Vitex* sp. (Schuitemaker, in Went 1940:95)

Florida, U.S.A.: *Annona glabra* L., *Taxodium distichum* L. (Frei 1973b:701)

Haiti: *Eugenia jambos* L. (Curtis 1946), *Euphorbia lactera* Haw. (Curtis 1947)

S. America: *Crescentia cujete* (Schimper 1888:95)

B. Phorophytes with few epiphytes

In the Nimba area epiphytes are poorly represented on a number of species of phorophytes (Table 47), in particular on *Fagara tessmannii, Terminalia ivorensis,* T. *superba* and *Musanga cecropioides,* considering the abundance of full-grown individuals of these phorophytes. Less frequent phorophytes with a sparse epiphytic flora are e.g. *Albizia glaberrima, A. zygia.*

The absence of epiphytic orchids on the trunks of *Elaeis guineensis* is obvious. However, they support a rich pteridophyte flora (Fig. 71). Only two epiphytic orchid species have been observed on this palm: *Graphorchis lurida* and *Habenaria procera.* (The Kew Herbarium has 26 collections of the latter species. The growth habitat is given for fifteen of them. Eighty per cent of these were epiphytes, all of them on *Elaeis guineensis.)*

In a study of the epiphytes on *Elaeis guineensis* in the former Belgian Congo (Zaire), Van Oye (1924) did not mention any orchids, but several pteridophytes and figs. In the Philippines it is even stated that "Orchids will choose any other tree in the wild than the palm" (Sulit 1950:8).

Ruinen (1953:102) has suggested the term 'axeny' for this condition of general inhospitality of trees which never or only occasionally bear epiphytes. Trees belonging to this group have been reported from all over the world. Piers (1968:4) reports that *Acacia* and *Ficus* trees are avoided by most epiphytic orchids. The same applies to tree Euphorbias, exotic conifers and *Eucalyptys* trees. Moreau (1943:8), however, remarks that conifers such as *Juniperus bermudiana* are colonized by orchids with a surprising frequency.

From Australia Rupp (1969:XI) confirms that *Eucalyptys* trees are usually barren of orchids. The absence of epiphytes on figs has been observed by several authors. Schnell (1970:309) mentions that *Ficus mucuso* lacks epiphytes and Went (1940) notes that humus epiphytes are lacking on *Ficus involucrata* Bl.

C. Specific relationships between phorophyte and epiphyte

In the Nimba area, no specific relationship between phorophyte and epiphyte has been observed, even if the total dominance of *Parinari excelsa* at the highest parts of the mountains has resulted in a nearly absolute correlation between this tree and some epiphytes naturally occurring at these altitudes (Table 47).

There are several reports of a relationship between a particular species of phorophyte and a particular species of epiphyte. Piers (1968:4) states: "Some epiphytes have marked idiosyncrasies regarding their host tree, e.g. *Ansellia nilotica* has a strong preference for the Doum Palm (*Hyphaene thebaica*), the Baobab tree *(Adansonia digitata)* is the typical host of *Angraecum dives* and *Polystachya adansoniae,* while *Aërangis thomsonii* attaches itself almost exclusively to the rugged stems of the gigant ceder (*Juniperus procera*) of the Kenya highlands." Rupp (1969:XI) gives a similar observation:"one or two of the ironbark eucalypts are favoured by *Dendrobium aemulum,* which for this reason is often callen 'Ironbark Orchid' ". More examples of this kind are listed by Richards (1964:119). Morris (1970:5) found few specific host/orchid relationship in Malawi, but observed: "There are however a few orchids which would appear to associate with specific hosts . . . *Bulbophyllum intertextum* on *Newtonia buchananii, Polystachya johnstonii* on *Vellozia spendens* come to mind."

Moreau (1943:8) is a little more hesitant: "there is little evidence of specific relation between orchid and tree host, except that certain aberrant *Polystachyas* that are otherwise terrestrial also grow on the curios-

ly looking fibrous stem of *Vellozias,* but no other host." (See also Richards 1957:568.)

Boyer (1964) states that the occurrence of the epiphytic ferns *Platycerium stemaria* and *P. angloense* on various phorophytes in the Ivory Coast, does not permit any conclusions regarding their preference for particular species of phorophytes.

Whether a relation between a certain species of phorophyte and epiphyte really exist is doubtful. In many cases the epiphytes have for various reasons a very limited choice of host trees. Given the opportunity, many of these epiphytes now occurring on a specific host tree, might very well thrive on other trees. Another fact that favours the theory of a specific relation between host and epiphyte is the poor knowledge of the presence of the epiphytes. Increasing information on the ecology and presence of the epiphytes will probably decrease the number of 'specific relationships'.

Biotic factors

Several of the biotic factors have already been presented and discussed in Chapter III.

Human influence

The human influence on the rain forest effects the epiphytes indirectly. In the Nimba area patches of scattered trees that remain after forest destructions are the particular growing sites of several orchid species. These are species of the deciduous forest, e.g. *Ansellia africana, Plectrelminthus caudatus, Polystachya paniculata, P. puberula* and *Rangaëris rhipsalisocia.*

Animal influence

Direct effects, as judged by signs of being eaten or used by animals, on the epiphytes is very seldom observed. Some species, however, show signs of frequently being eaten (probably by insects), e.g. *Pyrrosia mechowii, Ancistrochilus rothschildianus, Angraecopsis elliptica* and *Polystachya ramulosa.*

Effects on the leaves by herbivores or other agents, as can be judged by holes in the falling leaves, seem to be of minor importance for the rain forest species in general (Odum 1970 b). Voute (1946, 1964) states that insect outbreaks do not occur in tropical forests because of the stability of checks and buffers that act on any species that becomes overabundant.

Nutritional importance of animals and micro-organisms

The presence of a rich fauna in the crown of the rain forest trees naturally influences the nutritional supply of the epiphytes through excreta from mammals, birds, snakes, lizards, frogs and insects. The effect of bird excreta was early recognized. Sernander (1912) coined the term 'ornithocoprophily' for such plants that were favoured by bird excrement (or rather their nitrogen content). Du Rietz (1932) showed that bird excrements also increased the pH of the substrate. Trees with nesting birds, edible berries, as well as those used as sleeping trees and observation posts, are known to attract nitrophytic lichens. It is impossible to even try to estimate the total effect of nutrition provided by the animals in the diversified rain forest. It should at least be kept in mind during the analysing process.

The role of the microorganisms in the nutritional balance is unknown, but Ruinen (1956) found bacteria of the genus *Beijerincka* on leaves on nearly all trees and shrubs tested in Java and Sumatra. These nitrogen-fixing bacteria obtain their minerals and some organic material from substances excreted by the leaves. Blue-green algae of several kinds are always abundant on the bark of trees in the wet tropics but their nitrogen-fixing capacity is unknown. (cf. Ruinen 1961).

Bond (1959) reports: "There are also nitrogen-fixing micro-organisms present on leaves and branches of trees, which doubtless adds to the nitrogen available to the roots of epiphytes, as similar microorganisms do in the soil."

The high amounts of nitrogen in the humus from *Polypodium polypodioides* puzzled Pessin (1925:32): "It is indeed remarkable that the nitrogen of the humus on the bark of the tree is frequently as high and at times even higher than that of the most fertile soils."

VI. Distribution on the phorophytes

General pattern

At the same time as it is possible to recognize a distribution pattern on the phorophyte according to the occurrence of a particular species of epiphyte, one can also distinguish a pattern for whole groups of epiphytes (Table 48).

Although lichens, climbers, filmy ferns and mosses were not consistently recorded, their presence was noted. Generally speaking, each of the five zones of the phorophyte are characterized by a particular group or groups of epiphytes (Fig. 115).

Specific patterns

Species seldom observed on tall phorophytes

Certain species of orchids are very rarely observed on tall phorophytes, instead they frequently occur on smaller trees and even shrubs that often border small rivers and streams, or are found along tracks in the forest. *Angraecum classensii, Diaphananthe densiflora, D. rutila, Eurychone rothschildiana* and *Rhipidoglossum paucifolium* exhibit this pattern.

Species normally restricted to the basal part of the trunk

This section of the tall phorophytes is occupied by a number of species very rarely found in any other section. Among the pteridophytes *Asplenium barteri* is the most common, but several others e.g. *Elaphoglossum kuhnii, Lomariopsis guineensis* (Fig. 116), *Tectaria angelicifolia* and *T. fernandensis* are frequent. The orchids are represented by *Polystachya ramulosa* and *P. rhodoptera* which are almost exclusively located in this section.

Also *Brachycorythis kalbreyeri, Habenaria procera, Liparis nervosa* and *Vanilla crenulata* belong to this section, being epiphytes which grow in large humus deposits. The group of other vascular epiphytes is represented by *Calvoa monticola* and more seldom *C. trochainii.*

Species normally located on the main trunk

Several species may appear in this section, e.g. *Ancistrorhynchus cephalotes, Asplenium africanum, Diaphananthe bidens, D. pellucida.* However, there are rather few species that are restricted to this vertical section, which is mostly devoid of humus

Table 48. General distribution pattern (section) on the phorophyte of the pteridophytes, the orchids and the other vascular epiphytes. Based on the most frequent growing site (section) of each species (Tables 27 a + b, 28 a + b, 29). The result is presented as a percentage of the total number of species in each group.

Group	Total no. of spp.	Section				
		I	II	III	IV	V
Pteridophytes	39	15.4	15.4	48.7	20.5	–
Orchids	101	8.9	10.9	27.7	48.5	4.0
Other vasc. ep.	13	7.7	–	61.5	30.8	–

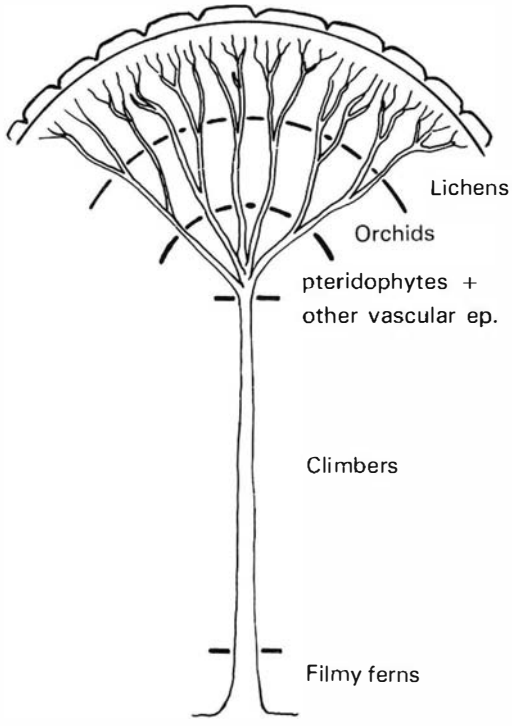


Fig. 115. General distribution of epiphytes on tall phorophytes.

Fig. 116. *Lomariopsis guineensis* normally occurs on the lowest parts of the trunks. Nimba Range 700 m.

deposits. Two species of ferns and two orchids can be considered to have the center of their distribution in this section: *Antrophyum immersum, Elaphoglossum chevalieri, Polystachya saccata* and *Tridactyle crassifolia.* Two species with a climbing habit, *Culcasia angolense* and *Raphidophora africana* (Fig. 117), which are included among the facultative epiphytes, play an important role through their substrate holding capacity.

Species of the crowns

In this analysis the results from the close observations for species with at least 20 separate records from the crowns have been used. For species with fewer observations the results from the distance observations are added and then used, if the total sum is at least 20 observations. It might seem hazardous to use such a low number of observations as a base for a detailed distribution pattern. However, in most cases the information obtained with these rather accurate methods are checked against the more numerous but ecologically not as well-documented, so-called occasional observations. When there are uncertainties in the distribution pattern, e.g. differences in the results between the various observation methods used, the discrepancies are discussed in the text.

Since the absolute majority of the records of species belonging to this group are located in the crown, the records from other sections of the phorophyte have simply been omitted in this analysis.

The distribution pattern of the individual species can be divided into six major patterns (A-F). The first three, A, B and C are represented by species that are ± restricted to only one section of the branches, (A, for species in section III, B, for species in section IV and C, for species in section V). The

Fig. 117. *Raphidophora africana* and *Culcasia angolense* are common climbers on the trunks of tall trees. Yekepa.

fourth and fifth pattern, D and E, are formed by species that occur in almost equal numbers in two sections with very few individuals in the third, (D, for species in sections III + IV and E for species in sections IV + V). The last pattern, F, is formed by species that occur more or less evenly in the various sections of the large branches (III + IV + V).

Species exhibiting the various distribution patterns are:

A (III)

Asplenium africanum
A. dregeanum
A. geppii
Arthropteris monocarpa
A. orientalis
Elaphoglossum salicifolium
Microgramma owariensis
Nephrolepis biserrata
N. undulata
Vittaria guineensis
Xiphopteris oosora

Ancistrochilus rothschildianus
Ancistrorhynchus capitatus
Angraecum chevalieri
Bulbophyllum bufo
B. falcatum
B. josephii
B. saltatorium
B. winkleri
Calyptrochilum christyanum
Diaphananthe pellucida
Polystachya laxiflora

Begonia mannii
B. polygonoides

B (IV)

Asplenium megalura
Elaphoglossum isabelense
Lycopodium mildbraedii
L. warneckei
Platycerium angolense
P. stemaria

Ancistrorhynchus clandestinus
Angraecum distichum
Bulbophyllum barbigerum
B. buntingii
B. intertextum
B. maximum
B. oreonastes
B. schinzianum
B. schimperanum
Chamaeangis vesicata
Cyrtorchis aschersonii
Diaphananthe bidens
Graphorchis lurida
Nephrangis filiformis
Polystachya galeata
P. paniculata
P. puberula
Rangaëris muscicola
R. rhipsalisocia
Tridactyle anthomaniaca
T. crassifolia
T. tridentata

Medinilla mannii
Peperomia rotundifolia
Rhipsalis baccifera

C(V) Only one species exhibits this pattern, *Bolusiella talbotii* (Fig. 118).

D (III + IV)

Drynaria laurentii
Microsorium punctatum
Phymatodes scolopendria

Aërangis biloba
Angraecopsis elliptica
Angraecum birrimense
Bulbophyllum cochleatum
B. cocoinum
B. distans
B. linderi
B. lucifugum
Cyrtorchis arcuata subsp. variabilis
Polystachya leonensis
P. polychaete
P. tessallata

B. rubro-marginata

Bulbophyllum linderi exhibit an A-pattern in the distance examinations. *Aërangis biloba* shows a C-pattern in the distance observations and in the occasional records it appears in all sections of the phorophytes.

E (IV + V) Only orchid species exhibit this distribution pattern: *Bulbophyllum scariosum, Polystachya adansoniae, P. dalzielii.*

F (III + IV + V) Species representing this pattern are very rare, a fact that suggest that each of the epiphytic species is confined to restricted habitats. *Aërangis laurentii* and *Tridactyle tridactylites* seem to follow this pattern, but it should be noted that these two species deviate from this distribution in the distance observations where *A. laurentii* shows an E- and *T. tridactylites* and A-pattern.

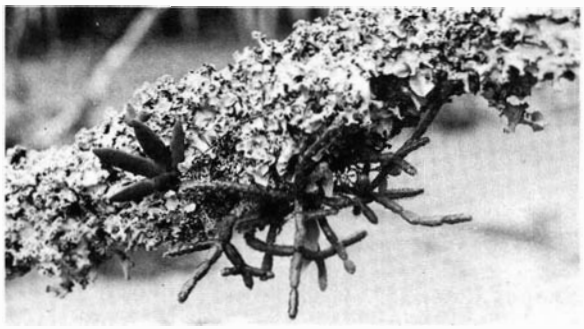


Fig. 118. *Bolusiella talbotii* normally occurs on the outer parts of large branches among lichens. A small *Rhipsalis baccifera* has also established itself.

Species distribution and environment gradients along large branches

In the absence of data about the most important environmental factors concerning the changes along the branches a theoretical discussion may throw some light on this problem.

The environmental changes that occur are listed here in two main groups, i.e. factors that decrease respectively increase towards the outer parts of the branches. In the first group the roughness of the substrate, humus deposits, nutritional content of the substrate, humidity of the substrate and the relative humidity of the air can be mentioned. In the second group the temperature, light intensity and wind velocity are important.

In Fig. 119, the decreasing and increasing factors are each represented by a straight line. The steepness and irregularities of these gradients are naturally dependent on a number of variable factors, e.g. species of phorophyte and the physiognomy of the forest.

The distribution pattern of six species of epiphytes, each representing one of the major patterns that previously were described, are also illustrated with the decreasing and increasing factors shown as dotted lines.

A. This pattern follows the decreasing gradient. The proportionally large number of pteridophytes, but also some orchids that belong to this group, seem to be primarily limited in their distribution by the decreasing factors.

B. This pattern seems to arise from the interaction of the increasing and decreasing gradients. In the basal parts of the branch the increasing gradient, and in the outer parts the decreasing gradient limit the presence of epiphytes. A large number of orchids exhibit this pattern which probably can simply be described as a delicate balance between the need of light and the influence of evapotranspiration.

C. This pattern follows the increasing gradient. It is probably the higher light intensities that favour the only species that exemplifies this pattern.

D. This is a modified A-pattern where the influence of the increasing gradient effects the pattern in the basal parts of the branch.

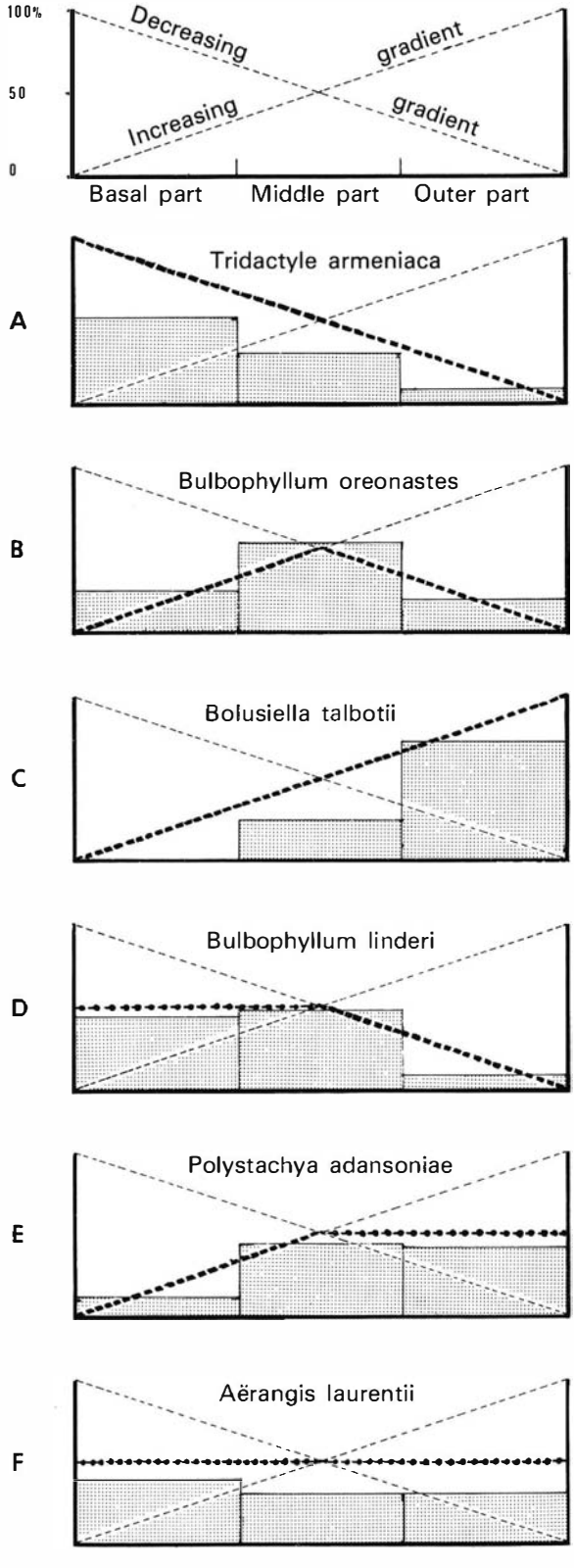


Fig 119. A theoretical model presenting a possible explanation for the different distribution patterns of epiphytes on the large branches (see text).

E. This is a modified C-pattern. The effect of the decreasing gradient is noticed at the outer part of the branch. Only three orchids show this pattern. The evapotranspiration in these more exposed parts of branches represents a severe drawback for the survival of epiphytes. Therefore it is interesting to note that two of the orchid species, *Bulbophyllum scariosum* and *Polystachya dalzielii,* only occur in high altitudes where low temperatures and mist surpress the evapotranspiration. The third species, *Polystachya adansoniae,* is adapted to dry environments with a geographical distribution in rather dry areas over large parts of Africa.

F. This pattern is the average of the increasing and decreasing gradients, suggesting a wide tolerance towards environmental influence. However, *Aërangis laurentii* and *Tridactyle tridactylites,* both show a different pattern in the records from the distance observations which may indicate that this pattern is less distinct than the others.

The importance of any single factor in the total environment is naturally very hard to estimate. In a detailed study of the epiphytic fern *Polypodium polypodioides* the following statement was presented: "It is safe to conclude from the results obtained that neither the light, the relative humidity of the air, the temperature of the air nor the substratum temperature exert any direct influence on the occurrence and distribution of *Polypodium polypodioides* nor on the epiphytes associated with it. It is the sum of the total of the effects of the first three conditions on the evaporating power of the air, in the immediate vicinity of each station on the tree, which is responsible for the particular epiphytic flora at the given station" (Pessin 1925:31).

The evaporating power normally increases from the base of the large branches towards the outer part through influences previously described.

Most pteridophytes in the area investigated show a distribution pattern on the branches that is reversed compared to a possible increase in evaporating power.

For most of the orchids the distribution pattern seems to be a result of a need for high light intensities and the tolerance of the evaporating power of the air, while the composition of the substrate can be considered of secondary importance.

To make the distribution solely dependent on the evaporating power of the air without any considera-

tion of light intensity and substrate composition is not accurate for the majority of epiphytes. This investigation showed that the different epiphytes often have a marked preference for a certain kind of substrate and light intensity. The almost total absence of epiphytes from the crowns of the trees in the lower strata of the forest cannot be satisfactorily explained with differences in the evaporating power of the air. It is more probable that low light intensities are the limiting factor since substrates of similar composition and evaporating power of the air equal to the conditions in the crowns also exist at various places in the lower parts of the forest.

Résumé

Ecologie des épiphytes vasculaires dans la forêt dense humide d'Afrique occidentale

La superficie examinée

Cette étude est centrée sur l'écologie des épiphytes vasculaires dans la partie libérienne des Monts Nimba et superficies adjacentes (Fig. 2). La flore d'ensemble de cette même région a été décrite par Schnell (1952) et Adam (1971).

Dans l'aire examinée, la haute forêt (dont la strate arborescente supérieure est à 30 m ou plus au-dessus du sol) occupe de petites surfaces. Ce sont les forêts à différents étages de régénération et les surfaces agraires qui dominent le paysage. La partie la plus haute de la région est couverte d'une forêt vierge Parinari excelsa.

Composition de la flore épiphytique

L'étude porte sur 153 espèces au total (39 ptéridophytes, 101 orchidées et 13 autres épiphytes vasculaires). Des enregistrements additionnels ont considérablement augmenté la zone de distribution de quelques espèces (Fig. 22-24) et 32 espèces sont nouvelles au Libéria:

Elaphoglossum isabelense
E. salicifolium
Lycopodium mildbraedii
Pyrrosia mechowii
Xiphopteris oosora

Ancistrochilus recurvus
Angraecopsis elliptica
Angraecum classensii
Bulbophyllum bifarium
B. josephii
B. lucifugum
B. lupulinum
B. magnibracteatum
B. pavimentatum
B. phaeopogon
B. rhizophorae
B. saltatorium
B. schimperanum
Cyrtorchis aschersonii
Diaphananthe densiflora
Eurychone rotschildiana
Podangis dactyloceras
Polystachya saccata
P. subulata
P. tenuissima
Rangaëris brachyceras
Rhipidoglossum paucifolium
Stolzia repens
Tridactyle crassifolia
T. tridactylites
T. tridentata

Begonia rubro-marginata

La flore épiphytique comprend des éléments de la forêt dense humide de basse et moyenne altitudes par exemple les *Cyrtorchis monteiroae* et *Angraecum birrimense* (Fig. 19), de la forêt décidue dans la mosaïque forêt-savane par exemple les *Ansellia* africana et *Rangaëris rhipsalisocia* (Fig. 20) et des communautés de montagne par exemple les *Polystachya dalzielii* et *P. leonensis* (Fig. 21).

Biologie de quelques épiphytes

Les orchidées peuvent fleurir chaque mois de l'année mais on remarque deux pointes de floraison (Fig. 49). Le genre *Bulbophyllum* a une pointe de floraison à la fin de la saison pluvieuse tandis que le genre *Polystachya* présente une pointe correspondante au début de la saison sèche ou de la saison pluvieuse. Parmi les insectes fréquentant les fleurs d'orchidées on a pu observer trois espèces avec pollinies adhérente : *Polistes marginalis* (Tab.) et *Polybiodes tabida* (Tab.) de *Bublophyllum schinzianum* et *Euchromia lethe* (F.) (Fig. 52) de *Diaphananthe pellucida.*

Formes de vie et hydrométrie

La résistance des épiphytes à la sécheresse se réfléchit dans différentes adaptations xéromorphiques (Fig. 59). Les épiphytes peuvent être divisées en plantes tolérantes à la sécheresse et plantes évitant la sécheresse. Ce dernier groupe est décidu et évite ainsi que l'eau ne se perde par la transpiration des feuilles durant la saison sèche trés rigoureuse. Les feuilles des plantes tolérant la sécheresse persistent pendant la saison sèche. Des valeurs trés élevées de transpiration ont été obtenues pour un certain nombre de plantes évitant la sécheresse par ex. *Polystachya leonensis* et *Polystachya dalzielii,* provenant des parties les plus hautes et les plus humides de la zone, et *Graphorchis lurida* et *Polystachya puberula* d'altitudes plus basses. Des valeurs élevées ont été ainsi obtenues pour *Asplenium geppii* et *Begonia rubro-marginata* (Tableau 12).

C'est parmi les orchidées que l'on a obtenu les valeurs les plus faibles de transpiration, spécialement parmi celles qui ont une croissance monopidiale par ex. *Bolusiella talbotii, Calyptrochilum christyanum, Chamaeangis vesicata* et *Neprhangis filiformis* (Tableau 13).

Répartition des épiphytes sur les arbres

Méthodes. Sur 463 phorophytes (arbres hôtes) la

répartition des épiphytes a été enregistrée. Pour simplifier l'enregistrement le phorophyte a été divisé en cinq sections (Fig. 76). On a appliqué trois méthodes différentes de dénombrement : les observations proches, les observations à distance et les observations occasionnelles. L'observation proche implique des investigations sur des arbres abattus, l'observation à distance est une étude du tronc et d'une branche complète (ou plus rarement un arbre entier) d'un arbre sur pied à l'aide de jumelles ou d'un téléscope sur trépied.

L'observation occasionnelle est réduite aux investigations obtenues à partir seulement d'une partie limitée du phorophyte. Les résultats de cette dernière méthode ne sont utilisés que pour compléter ceux des deux autres.

On a également examiné le substrat et l'éclairement au lieu de croissance de l'épiphyte individuelle. Le substrat a été divisé en trois classes : écorce, écorce avec dépôts faibles d'humus, et dépôts importants d'humus. La lumière a aussi été divisée en trois classes : plein soleil, demi-obscurité et obscurité.

Occurence des épiphytes

Dans la haute forêt 50,4 % des arbres hauts de dix mètres ou plus portaient des épiphytes, par contre dans une forêt "secondaire" on descendait à 14,8 %. Il était donc évident que particulièrement les orchidées étaient rares dans une forêt "secondaire". Certaines espèces d'arbres peuvent abriter un grand nombre d'espèces d'épiphytes par ex. *Heritiera utilis* (30 spp.) *Mitragyna ciliata* (28 spp.) (Tableau 42). Aussi le nombre des individus ("stands") d'épiphytes sur certains arbres était-il trés grand, par exemple un seul *Heritiera utilis* ne portait pas moins de 1857 épiphytes et un *Parinari excelsa* 1171.

Groupements épiphytiques

On dit qu'il y a groupement épiphytique quand trois espèces au minimum d'épiphytes forment une unité et quand la distance entre deux de ces épiphytes et la troisième ne dépasse pas 0,5 m. On distingue sept groupements épiphytiques différents au-dessous de 1000 m et trois autres de plus à des altitudes supérieures (Tableau 30).

Les fougères forment la base de sept des dix groupements. Il semble que ce soit leur capacité de formation de substrat qui attire les autres épiphytes.

Colonisation et effets sur les phorophytes

Les différentes méthodes indiquent que ce sont particulièrement les phorophytes les plus grands qui sont de préférence colonisés par les épiphytes. Les ptéridophytes semblent être les épiphytes pionniers tandis que les orchidées sont les dernières à s'établir (Fig. 87). Certains arbres ayant une riche flore épiphytique par exemple *Mitragyna ciliata* et *Parinari excelsa,* souffrent apparemment "d'épiphytosis" (Ruinen 1953). Les effets des orchidées sans feuille sur les phorophytes peuvent aussi indiquer un parasitisme partiel.

Influences de l'environnement sur les épiphytes

Climat. Le rapport ptéridophytes épiphytiques/orchidées se modifie avec l'altitude. A la base de la zone (500-700 m) la proportion ptéridophytes/orchidées est approximativement de 1:3 mais, à 1000-1300 m, elle est de 1:1. Des variations similaires ont également été observées sur les hautes montagnes d'Afrique orientale.

Dans les milieux secs, ainsi qu'on l'a observé en Tanzanie, le nombre des épiphytes décroît rapidement (spécialement les ptéridophytes) mais l'abondance de certaines orchidées épiphytiques peut surprendre. Dans les montagnes méridionales de Tanzanie on a observé que tous les arbres ($\geqslant$ 4 m) d'une terre boisée Brachystegia portaient l'orchidée *Tridactyle tricuspis.*

Substrat. La valeur pH d'échantillons d'écorce provenant du même phorophyte présentait d'assez grandes variations. C'est dans les parties extérieures des grandes branches et la partie supérieure du tronc principal que l'on trouvait les valeurs les plus basses. On n'a cependant pas pu trouver de corrélation pertinente entre la valeur pH de l'écorce et la flore épiphytique. Les valeurs pH des dépôts d'humus étaient beaucoup plus élevées que celles de l'écorce.

La majorité de l'espèce ptéridophyte "préférait" les dépôts mineurs d'humus tandis que les orchidées poussaient surtout sur l'écorce et les autres épiphytes vasculaires dans les grands dépôts d'humus.

Corrélation entre l'abondance d'épiphytes et l'espèce de phorophyte

Les grands spécimens d' *Heritiera utilis, Lophira alata, Mitragyna ciliata* et *Parinari excelsa* sont riches en épiphytes tandis que par exemple *Anthocleista nobilis Fagara tessmannii, Terminalia*

ivorensis et *T. superba* sont fréquemment plus ou moins dépourvus d'épiphytes. On n'a pas observé de corrélation spécifique entre l'épiphyte et le phorophyte.

Lumière. L'intensité de la lumière au sol dans une haute forêt à la base de la zone était de 0,36 % de la lumière extérieure mais dans une forêt *Parinari* à 1300 m d'altitude elle était de 6,65 % (Tableau 42).

Dans les parties de base et les parties centrales des grandes branches d'un arbre *Parinari excelsa* à 1300 m la lumiére était réduite de 70-85 % par rapport à celle de la demi-obscurité (Tableau 43). La variation quotidienne dans l'intensité de la lumière au lieu de croissance de certains épiphytes a révélé des différences trés significatives entre les différentes espèces (Fig. 106-108). En général, on trouve les ptéridophytes dans la demi-obscurité tandis que les orchidées sont plus également réparties entre l'habitat en demi-obscurité et l'habitat en plein soleil.

La distribution des épiphytes dans le phorophyte
Chacune des cinq sections du phorophyte est dominée par un groupe d'épiphytes (Fig. 115).

La plupart des espèces d'épiphytes ont une distribution plutôt limitée sur le phorophyte, c'est-à-dire dans une ou deux sections. La majorité des espèces poussent dans la couronne. On distingue six modèles différents de distribution sur les grandes branches (Fig. 119).

La distribution des épiphytes ne dépend pas seulement de l'évaporation (Pessin 1925) mais elle est également influencée par la préférence marquée d'une certaine sorte de substrat et d'éclairement. Les ptéridophytes présentent une distribution qui va à l'encontre d'un accroissement possible de l'évaporation. La distribution des orchidées semble toutefois être le résultat d'un équilibre entre le désir d'une grande intensité de lumière et la capacité de résister à une plus grande évaporation d'air qui s'ensuivrait.

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