

PHYTOGEOGRAPHY AND VEGETATION OF TROPICAL INSELBERGS

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Résumé : Un bref aperçu de la végétation des inselbergs néo- et paléotropicaux est présenté. Les données proviennent d'études effectuées sur le terrain en Afrique de l'Ouest (Côte-d'Ivoire, Guinée, Cameroun), en Afrique de l'Est (Malawi), à Madagascar, au Brésil, au Venezuela et en Guyane française. Les habitats rocheux isolés sont occupés par une flore adaptée à ce milieu particulier qui diffère presque complètement de la végétation environnante. Ils constituent ainsi des modèles pour l'étude de l'écologie insulaire.

Les surfaces de roche apparemment nues sont ordinairement couvertes de cyanobactéries (ex. Guyane française) ou de lichens (ex. Côte-d'Ivoire). La végétation discontinuée d'Angiospermes est constituée d'une mosaïque de différentes formations. Les plus remarquables sont caractérisées par des tapis de Monocotylédones (Broméliacées dans la région néotropicale et Cypéracées dans la région paléotropicale), des végétations marécageuses sur dalle granitique humide (plusieurs espèces d'*Utricularia*, de *Genlisea*, de *Burmannia* ainsi que d'Eriocaulacées) et des groupements saisonniers de plantes dans les cuvettes rocheuses (ex. Scrophulariacées). On trouve des types biologiques convergents dans les régions paléo- et néotropicales (ex. rosettes caulescentes chez les Cypéracées et Velloziacées).

Mots-clés : Biodiversité, géobotanique, inselbergs, écologie insulaire, phytogéographie, rochers découverts. Broméliacées, Cactacées, Velloziacées.

Abstract: A short survey of the vegetation of neo- and paleo-tropical rock outcrops (inselbergs) is provided. The data are based on field studies in West Africa (Ivory Coast, Guinea, Cameroon), East Africa (Malawi), Madagascar, Brazil, Venezuela and French Guyana. The insular rock habitats are covered by a highly adapted flora differing almost totally from the surrounding vegetation and thus provide models for studying questions of island ecology.

Apparently nude rock surfaces are usually covered almost completely by cyanobacteria (e.g. French Guyana) or lichens (e.g. Ivory Coast). The fragmented angiosperm vegetation consists of a mosaic of different vegetation types. Characteristic are monocotyledonous mats (Bromeliaceae in the neotropics and Cyperaceae in the paleotropics), flush vegetation (many *Utricularia* spp., *Genlisea* spp., *Burmannia* spp., Eriocaulaceae) and seasonal plant communities in rock pools (e.g. Scrophulariaceae). Phenotypic similar life forms occur convergently in the paleo- and neotropics (e.g. caulescent rosette-trees in Cyperaceae, Velloziaceae).

Keywords: Biodiversity, geobotany, inselbergs, island ecology, phytogeography, rock outcrops. Bromeliaceae, Cactaceae, Velloziaceae.

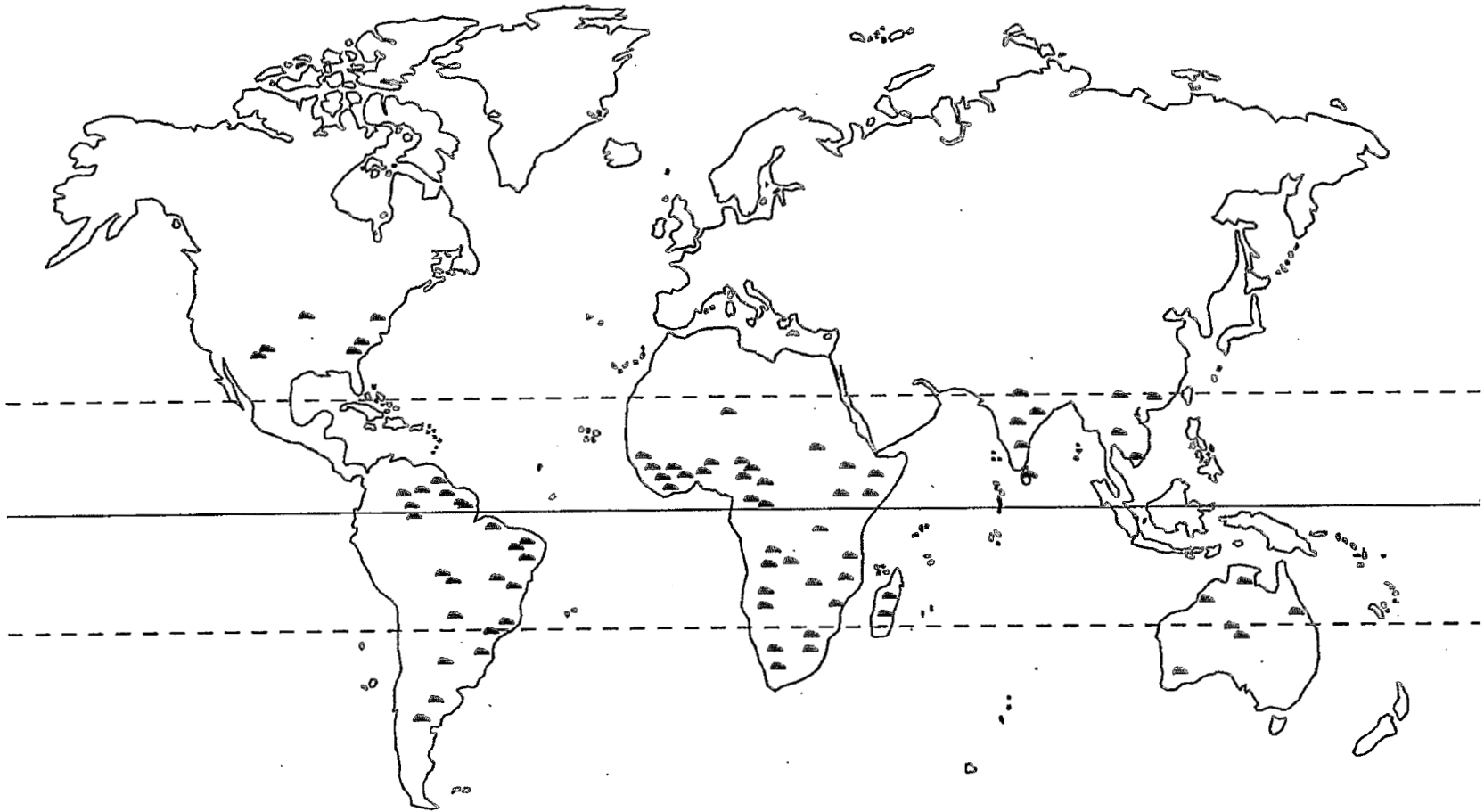


Figure 1

Global distribution of inselbergs. The symbols indicate clusters of inselbergs concentrations.

Introduction

Inselbergs are isolated tropical (rarely extratropical) rock outcrops, mostly of precambrian granitic or gneissic origin (figs 1, 2). They are geomorphologically very old structures up to 70 million years old.

The geographer W. BORNHARDT (1900) introduced the term "insel-berg" to describe the dome-shaped monoliths in East Africa. The geomorphology and geology of inselbergs has been studied worldwide; a monographic survey is provided by BREMER & JENNINGS (1978).

However, little is known about the biotic cover of inselbergs. This is most surprising, because they bear an extremely adapted vegetation differing almost completely from the surrounding forests or savannas. This was pointed out already by Alexander von HUMBOLDT in 1819 based on his observations of rock outcrops along the Orinoco in 1799.

The botanical exploration of "inselbergs" was initiated in Ceylon by WILLIS (1906). Floristically best known is the vegetation of West African inselbergs (e.g. MILDBRAED, 1922; MIEGE, 1955; RICHARDS, 1957; HAMBLER, 1964; ADJANOHOON, 1964; BONARDI, 1966; SCHNELL, 1952; GUILLAUMET, 1967; LETOUZEY, 1968; VILLIERS, 1981; REITSMAR *et al.*, 1992; POREMBSKI & BARTHLOTT, 1992).

Inselbergs are usually isolated "insular" structures under edaphic, floristic, and microclimatic (POREMBSKI *et al.*, 1994) aspects. As "terrestrial islands" (in the sense of McARTHUR & WILSON, 1967), they are suitable models for studying questions of island ecology. For studying processes of eco-geographical differentiation, speciation and mechanisms of regulation of biodiversity (deterministic and stochastic influences) they may provide better models than true marine islands (BARTHLOTT, GROEGER & POREMBSKI, 1993).

They vary in size from mountains (fig. 2) to miniature islands of a few square meters in minimum size, which still show their typical biotic cover (fig. 3). In contrast to oceanic islands they may occur as continental systems over short distances in steep climatic gradients (compare map fig. 1). Contrary to marine islands they represent often the last intact ecosystems in landscapes disturbed by man.

Geographical occurrence of inselbergs

Inselbergs occur throughout the perhumid and semihumid tropics; occasionally in arid, subtropical (Australia) or even temperate regions (e.g. USA). In the neotropics inselbergs are mostly distributed in atlantic Eastern Brazil and the western orinocan (Venezuela) and eastern border (Guianas) of



Figure 2

Mont Niangbo, southern summit of the largest inselberg in Ivory Coast, West Africa. Different habitats and vegetation types are visible: belt forest, exposed rock surface with numerous drainage channels, *Afrotrilepis*-mats and small woody patch on top.



Figure 3

Small rock outcrop: a miniature "shield"-inselberg with its typical representative *Melanocactus ferreophilus* Buining and Bredero (Bahia Brazil).

the Guyana Shield. The paleotropic occurrence is concentrated in Africa (Upper Guinea, Cameroon and Central Africa to Angola; semiarid East Africa); they are also present in Central and South Madagascar. Inselbergs also occur in India and Ceylon, between South China and Malaysia, and in Australia. Table-Mountains like the Tepuis are not considered as "inselbergs" in our context.

The concentration of inselbergs coincides to a high degree with the regional centers of biodiversity. This emphasizes the importance of studies in these very little known biota.

Habitats and vegetation types on inselbergs

Edaphic conditions and thus habitat types and subsequently vegetation communities on inselbergs are drastically different from the surrounding.

(1) Exposed rock surfaces are usually covered by crustose lichens or cyanobacteria; (2) drainage channels (fig. 2) bear a slightly differing cryptogamic flora. (3) Rock crevices and boulder-falls may be colonized by perennials or even woody plants. (4) Rock pools are seasonally water filled and colonized by aquatic or semiaquatic ephemerals and occasionally geophytes, similar are (5) Flat depressions which harbour seasonally inundated communities. (6) Monocotyledonous mats are a most characteristic uniform plant community inhabiting rock slopes; in the paleotropics they are usually dominated by Cyperaceae, in the neotropics by Bromeliaceae and Velloziaceae. (7) Ephemeral flush vegetation often develops adjacent to monocot mats or larger rock pools on thin layers of peaty soil: the most diverse habitat type concerning species numbers on inselbergs (e.g. *Genlisea*). (8) Wet flush vegetation, a less diverse community of few highly adapted species (e.g. *Utricularia*), may occur during the rainy season in water films on bare rocks. Two additional vegetation types are often associated with larger inselbergs. (9) Wood patches occurring in depressions (e.g. *Clusia* on the Guyana shield inselbergs) or even as summit forest; (10) belt forests often surround larger inselbergs like gallery forests even in xeric vegetation types (e.g. savannas) caused by the local water runoff.



Figure 4

Floristic elements of an inselberg in Central Madagascar: *Pachypodium densiflorum* Baker, *Xerophyta dasyliroides* Baker, and *Coleochloa setifera* (Ridley) Gilly.

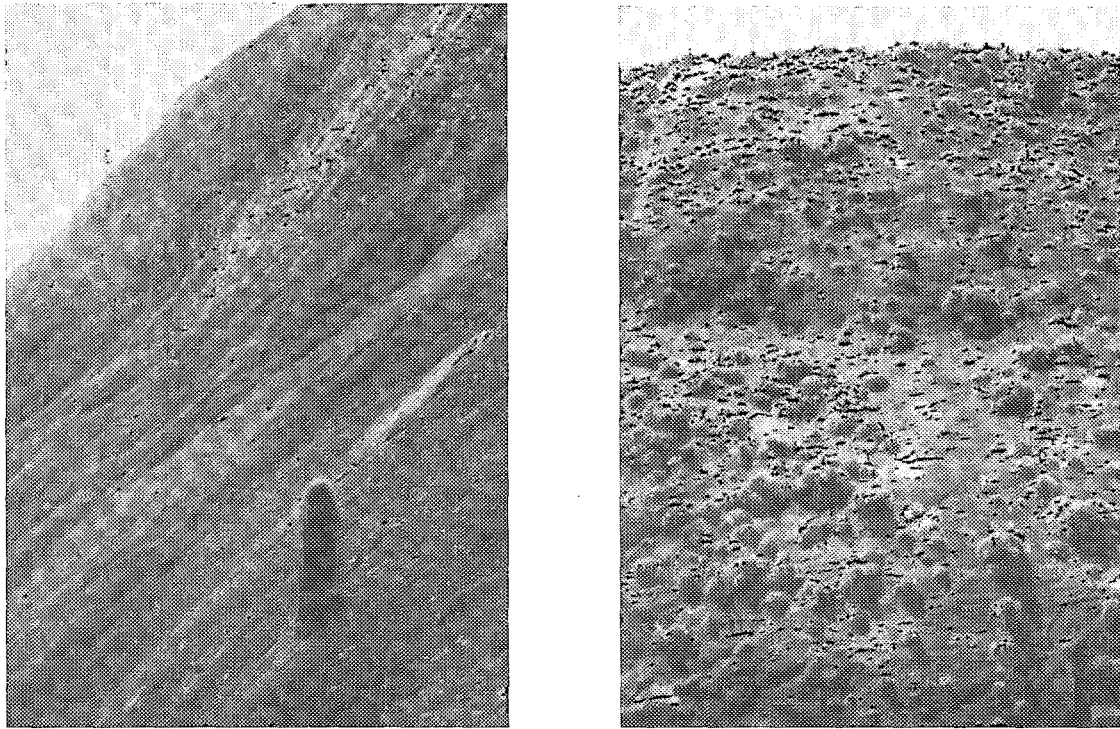


Figure 5

Colecephalocereus fluminensis (Miquel) Backeberg inhabiting a tropical Atlantic rain forest inselberg (Espírito Santo, Brazil).

The vegetation of neotropical inselbergs

Inselbergs are restricted to the Guyana and Brazilian shield (up to East Bolivia); they are absent in Central America and the Caribbean (the Cuban karst mountains of the "mogotes-type" are not considered here). The classical whale back and sugar loaf forms (Rio de Janeiro!) dominate. They are locally known as "morros" or "lajas". Vegetation studies are published from French Guyana (de GRANDVILLE, 1978, 1982; SARTHOU, 1992; LARPIN, 1993) and Surinam (THEUNISSEN & WILDSCHUT, 1979); only few notes are published on Venezuela (HUBER 1980), and Brazil (e.g. EGGI, 1992).



Figures 6 and 7

Two neighbouring inselbergs in Northern Espiritu Santo, Brazil, showing a totally different vegetation: uniform cover of mats of *Echolirium horridum* L. B. Smith (left) in contrast to white tufts of *Tillandsia kurt-horstii* Rauh & Grob with a single short column of *Coleocephalocereus brevicylindricus* (Buining) Ritter (right).

The almost blackish colour of the Guyana shield inselbergs, which HUMBOLDT (1819) expected to be efflorescing mangan and iron, is mainly caused by cyanobacteria (e.g. *Scytonema*, *Stigonema*).

The monocotyledon mats are usually formed by Bromeliaceae like *Pitcairnia* spp. on the Guyana shield and by *Dyckia*, *Encholirium*, *Tillandsia* and *Vriesea* on the Brazilian shield. In NE Brazil Velloziaceae (*Vellozia*, *Barbacenia*) in association with Bromeliaceae may dominate these mats, in South Brazil Apiaceae are associated like the Bromeliad-like *Eryngium pristis*. Restricted to Velloziaceae as host plants are particular epiphytic orchids (*Pseudolaelia*: fig. 9 and *Constantia*). Wood patches seem to be characteristic of the Guyana shield inselbergs. They are often composed by *Clusia* spp. and semideciduous tree species obviously derived from deciduous sister taxa inhabiting the surrounding forests.

The Brazilian inselbergs are particularly rich in endemic species often restricted to very small areas. The beta-diversity between almost neighbouring inselbergs may vary dramatically as illustrated in figs. 6 and 7: two inselbergs in sight distance in northern Espiritu Santo, one almost exclusively colonized by *Encholirium horridum* (fig. 7), the other one by the white tufts of *Tillandsia kurt-horstii* in combination with few specimens of *Coleocephalocereus brevicylindricus* (fig. 6). Cactaceae is ultimately the family which characterizes the inselbergs of the Brazilian shield. They are derived from three different systematic groups (BARTHOLOTT & HUNT, 1993). The inselbergs in Rio Grande do Sul bear small globular Notocactaceae (*Parodia* incl. *Notocactus*, *Brasilicactus*) with relatives in the semiarid regions of the La Plata States. Inselbergs in the tropical atlantic rainforest and adjacent caatinga and campo cerrado regions show a particular characteristic cactus flora of genera belonging to the Cereaceae: derived from large arborescent forms (e.g. many *Cereus* and *Pilosocereus* spp.) they are reduced to solitary columns in the genus *Coleocephalocereus* (fig. 5) which may become procumbent or even very short and stout (fig. 6) and thus show almost a complete transi-

tion to the globular *Melocactus* spp. (fig. 3). A last group of Cacti is derived from a completely differing systematic and ecological group: a few members of the epiphytic tribe Rhipsalideae are specialized on rock outcrops (e.g. *Rhipsalis epiphyllanthoides*, *R. russellii*).

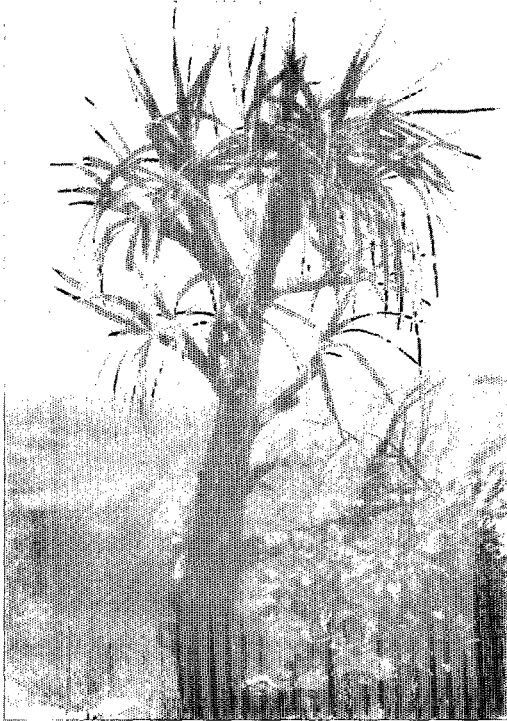


Figure 8

Xerophyta splendens (Rendle) N. Menezes, Velloziaceae (Malawi).



Figure 9

Vellozia candida Mican, Velloziaceae with its specific epiphyte *Pseudolaelia vellozicola* (Hoehne) C. Porto & Brade (Bahia, Brazil).

The epiphytic *Rhipsalis baccifera* is the only cactus occurring naturally in the paleotropics: interestingly enough in Madagascar this species found a secondary evolutionary center with neotenic polyploid forms (BARTHLOTT, 1983) colonizing inselbergs (fig. 13). The species richness of neotropical inselbergs is high and many more families could be listed. Amongst these the Orchidaceae are to be mentioned (with e.g. many xeromorphic or even succulent *Pleurothallis* spp., *Laelia* spp.), *Utricularia* spp. and Eriocaulaceae of the ephemeral flush vegetation. The "geophyte" (MARTINELLI, 1984) *Worsleya rayneri* produces giant bulbs on bare rock surfaces in Eastern Brazil.

The vegetation of inselbergs in Africa and Madagascar

Inselbergs occur throughout perhumid to semiarid Africa (geomorphologically in Southern and Eastern Africa often "kopje"-types) and in Central and Southern Madagascar.

In Africa the inselbergs of Ivory Coast are best studied. Only some 400-600 species of vascular plants are known from these inselbergs, usually the vegetation of one particular inselberg is composed of about 70-100 species. Most characteristic are the Guineo-Congolian *Afrotrilepis pilosa* and the Sudano-Zambesian *Cyanotis lanata*. The West African inselbergs are rather uniform (higher diversity gradients between neighbouring inselbergs in the Cameroons: FISCHER & BARTHLOTT, 1994); a center of endemism is Guinea (e.g. *Microdracoides squamosus* also in Nigeria and Cameroon, fig. 10; the bromeliad *Pitcairnia feliciana*, fig. 12). The occurrence of particular species may be connected to a minimum size of rock surface (e.g. *Afrotrilepis* requires more than 50 000 m²). The biodiversity of particular subhabitats is differently influenced by deterministic (e.g. *Afrotrilepis*-mats) or stochastic (e.g. vegetation of rock-pools) factors.

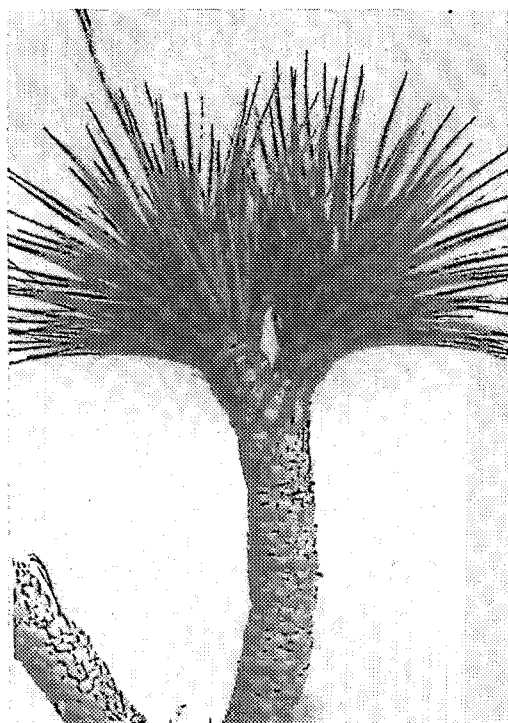


Figure 10
Microdracoides squamosus Hua, Cyperaceae (Guinea).

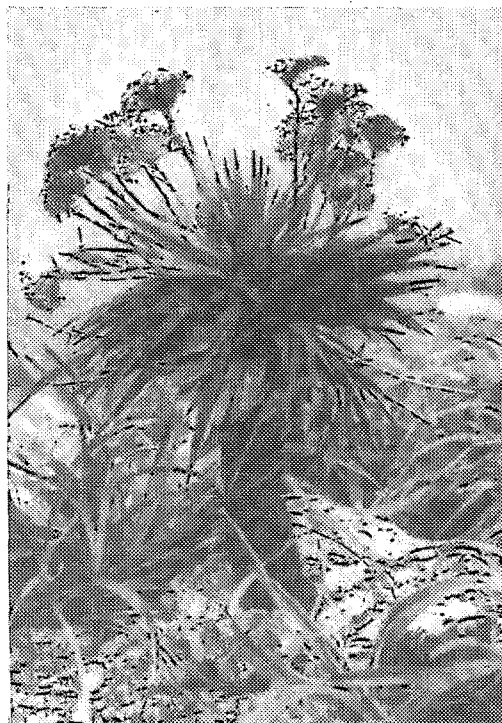


Figure 11
Paepalanthus robustus Silveira, Eriocaulaceae (Minas Gerais, Brazil).

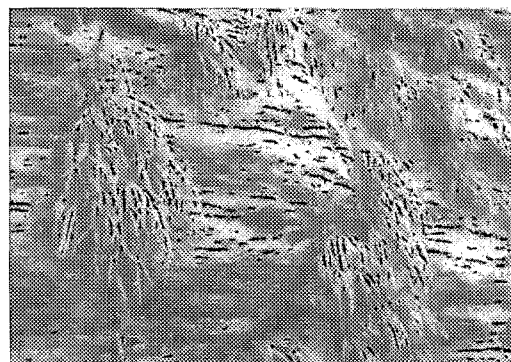


Figure 12
Pitcairnia feliciana (A. Chev.) Harms & Mildb., Bromeliaceae (Guinea).

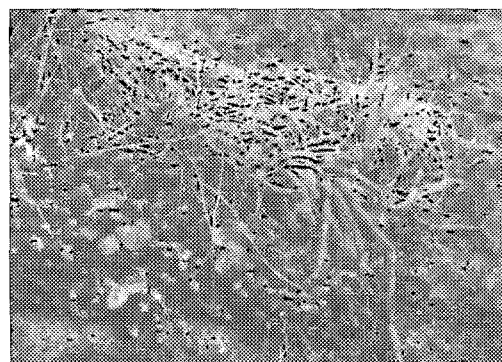


Figure 13
Rhipsalis baccifera ssp. *horrida* (Baker) Barthlott, Cactaceae, with *Xerophyta dasylroides* Bak. and *Stapelianthus decaryi* Choux. (South Madagascar).

The ephemeral flush vegetation harbours the highest number of species on paleotropical inselbergs and is dominated by Lentibulariaceae, Cyperaceae and Eriocaulaceae. In particular *Utricularia* is well represented, and *Genlisea* seems to be almost exclusively restricted to this type of vegetation in Africa (e.g. *G. africana*) and Madagascar (*G. margaretae*). Only a small number of species in vascular plants is common to neo- and paleotropical inselbergs, and most of them belong to the flush vegetation: e.g. *Utricularia pubescens*, *U. subulata*, *Neurotheca loeselioides*. Floristically the vegetation of African inselbergs seems to be related to the vegetation of ironstone outcrops ("Bowals", see

e.g. SCHNELL, 1952) and thus savannas in general. Even on inselbergs located within the rain forest belt (e.g. the Mt. Niénokoué in the Taï-forest) Sudano-Zambezian elements occur in high numbers.

In contrast to the neotropics epilithic orchids and other plants derived from epiphytic communities are relatively rare. However, convergently to the situation in Brazil we find orchids specifically bound to caulescent rosette-trees as host plants: e.g. *Polystachya microbambusa* on *Afrotrilepis pilosa* and *Polystachya johnstonii* on *Xerophyta splendens* (Malawi).

The West African *Afrotrilepis* is replaced by *Coleochloa setifera* in East Africa and Madagascar. A high number of other genera inhabits the *Coleochloa*-mats: e.g. succulent Aloe - and *Euphorbia* spp. In particular the inselbergs of Madagascar are characterized by a high number of dwarf succulents (*Aloe*, *Euphorbia*, *Kalanchoe*, *Pachypodium*, *Stapelianthus*, *Rhipsalis*: figs. 4-13); they share with Eastern and Southern Africa the poikilohydric genera *Myrothamnus* and *Xerophyta*.

Vegetation of Asian and Australian inselbergs

Apart from a few monolithic rocks, inselbergs are less dominating landscape elements on the Indian subcontinent, South East Asia and Australia. In India and Ceylon (WILLIS, 1906, 1911) dominate Cyperaceae, Orchidaceae (e.g. *Bulbophyllum* spp., *Eria* spp.), Lamiaceae, Scrophulariaceae; *Utricularia* spp. and succulent *Euphorbia* spp. Apart from a few studies (e.g. ORNDUFF, 1987) little is published about Australian inselbergs. Their vegetation differs significantly from the rock vegetation in other regions: dominating are Asteraceae, Stylidiaceae and Liliaceae s.l. (e.g. the poikilohydric *Borya sphaerocephala*) which represent about 40% of the species.

Inselbergs in temperate regions

Inselbergs in temperate regions are rare and considered as relicts of tertiary tropical climatic conditions (survey in KESEL, 1973). In particular in North America they occur between North Carolina and East Alabama and there are several floristic (McVAUGH 1943) and ecological studies (HOULE & PHILLIPS, 1988, 1989a, 1989b). The subhabitats are somewhat similar to tropical inselbergs. Generally, the vegetation is poorer than within the tropical counterparts and relatively uniform (KEEVER *et al.*, 1951). After McVAUGH (1943) the number of taxa on rock outcrops up the 100 000 m² size does not exceed 20 spp., whereas comparable inselbergs in West Africa harbour up to 100 species. On the other hand, MURDY (1968) has pointed out that granite outcrops are centers of diversity in Georgia and particular adapted species have evolved. The best example seems to be *Amphianthus pusillus* (Scrophulariaceae) in seasonal rock pools and thus being an ecological counterpart of its tropical relative *Chamaegigas intrepidus* from similar habitats on inselbergs of Namibia.

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