

ON THE COMPARISON OF THE FLORA AND VEGETATION OF THE ISLAND GROUPS OF SOCOTRA AND MACARONESIA

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With 3 figures and 1 table

ABSTRACT. The island groups of Socotra and Macaronesia are situated East and West aside the African continent in comparable Northern latitude and for Socotra under a similar climate regime to the Cape Verde Islands. Striking floristic similarities in biogeography may base upon plant distribution and movement patterns of the arid Southern Tethys belt since the late Cretaceous. Biogeographically, the island groups of Macaronesia and Socotra are evenly related to the arid floras of South and East Africa.

INTRODUCTION

Whereas the island groups of the severely studied Macaronesia is placed West of the African and the European continental plates, some less known islands are situated at the horn of Africa at a latitude equal to the islands of Cabo Verde. West of the continent, the volcanic island groups of the Azores, Madeira, the Canaries, and the Capeverdes stretch from 39° to 13° (N latitude) from a cold-temperate climate in the North Atlantic Ocean to a subtropical arid climate towards the equator. In the East the - scientifically fairly less known - Socotran islands comprise an archipelago with the islands Socotra, Semha, Darsa ("The Brothers"), and Abd-El-Kuri, comparable in size (3549 km²) to the Canaries, but not of volcanic origin. The island of Socotra is situated at 12°19' - 12°42'N latitude and 53°18' - 54°32'E longitude and reaches 110 km from East to West, rarely exceeding 30 km from North to South (Fig.1). The westernmost point is 240 km off the Cape Guardafui in Somalia, the tip of the horn of Africa. The other three islands are even nearer to the African coast. All together they lie on the same continental shelf or partition of a plate as Somalia, which are geologically separated from Arabia through the Red Sea and the Gulf of Aden, and are drifting away from Africa through the rupture of the Afar and Ethiopian rift (prolonging to the East African rift valley). Whereas the Macaronesian archipelagos rised above sea level

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in late Tertiary (Miocene) the island group of Socotra dates back to late Cretaceous with its limestone areas and is certainly very much older (paleozoic?) in the central granite parts of the islands (KOSSMAT, 1907).

The comparable latitudinal position, West and East to the African continent, the similar sizes of the archipelagos, and some striking examples among both floras support that both floras can be related through long-distance dispersal. Alternatively, they could be homologous in the sense of similar paleoclimatic conditions, or they could have been connected in geological times? The examination of the actual flora and vegetation may add a brick to the puzzle of the paleotropical plant geography since the settlement of vascular plants in this region.

THE MACARONESIAN CLIMATE AND FLORA

The Macaronesian archipelagos lie in the subtropical zone of the NE trade-winds under constant direction, delivering a constant precipitation through clouds, rain and fogs. In the winter half-year the northernmost Azores lie in the westwind zone with low pressure cells and heavy winds and rains. Most of the precipitation of the three northern archipelagos (Azores, Madeira, Canaries) is supplied in winter (Mediterranean climate type). The southernmost islands of Cabo Verde are reached by fringes of the intertropical convergence zone, expressing a irregular and short rainy season from August to October. While the temperatures are moderately between 15° to 23°C degrees on the Northern archipelagos, the Eastern islands of the Canaries and the whole Capeverdes to the South are drier and hotter in macroclimate, being connected to the Sahel climatic belt. The highest peaks of the Atlantic Islands' volcanoes reach or even exceed 3000 m and bear some alpine to Mediterranean-alpine and afroalpine geoelements following a North to South gradient. The vegetation belts of the Atlantic Islands are very heterogenous in origin and actual floristic composition (BEYHL *et al.* 1993). Detailed accounts on the comparably well-known floras and vegetations of the archipelagos in the Atlantic Ocean are given e.g. for the Azores by LÜPNITZ (1975, for further informations see there), for Madeira by VAHL (1905), CHRISTENSEN *et al.* (1970), and SJÖGREN (1974), for the Selvagens by LOWE (1869), for the Canaries by BØRGESEN (1924), SUNDING (1972), and KUNKEL (1980), and for the Capeverdes by LOBIN (1980). The flora of all Macaronesian island groups comprises approx. 3100 species at the whole, with more than half of them due to anthropogenic activities (see HANSEN & SUNDING 1993). LÖSCH *et al.* (1990) stress the North to South gradient in vegetation following the increasing insolation and temperature and the decreasing humidity towards the equator.

THE SOCOTRAN CLIMATE AND FLORA

On the same latitude like the Capeverdean archipelago the Socotran islands are

affected through the trade-winds as well, but the rain is supplied twice a year by the SW/W monsoon in summer (April - May) and the NE monsoon in winter (Sep. - Dec.), bringing heavy thunderstorms and hurricanes. The summits of the central granite Hagher range (Jebel Hagher 1506 m appr.) gain sufficient dew precipitation throughout the year. The lowest temperatures there were recorded with 13.5°C, while the mean temperatures in the lowlands range between 24°C and 35°C throughout the year, exceeding this value in fully sunexposed inland valleys. The mean elevation of the island above sea-level is 400 to 500 m, built by great limestone plateaus which surrounds the central mountain ranges.

The vascular flora of Socotra counts actually to approximately 800 species from which nearly 20% are regarded as endemics (BALFOUR 1888, VIERHAPPER 1907, ENGLER 1910, MIES 1994; in the following the species' authorities refer to MIES 1994. Since the late 19th century, the almost unaccessible Socotran islands became most interesting to dispatch botanical expeditions for reasons of a plenty of living fossils, absent from the African mainland (BALFOUR 1888, SCHWEINFURTH 1891, FORBES 1903, VIERHAPPER 1907, POPOV 1957, Radcliffe-Smith in Hook.Ic.Plant.1967). The occurrences of genera like *Dracaena*, *Micromeria*, or *Polycarpaea* and possibly vicariant species in the same ecological niches made the easternmost African island group famous also among "Macaronesian botanists". *Dracaena cinnabari*, e.g., is similar in altitude and shape to *D. draco*, the Canarian drago morphotype of the Atlantic islands.

Abd El Kuri merely has a grassland type of vegetation, from which the peculiar *Euphorbia abdelkuriensis* has become famous because its lack of spines and yellow milky juice, resulting in an isolated position within the Euphorbiaceae. The Brothers have a fairly less known flora and vegetation, but they may be comparable to Abd El Kuri. The 1506 m high island of Socotra bears a sequence of vegetation belts from the coast up to the peaks of the Hagher range. Nevertheless a laurel forest adequate is lacking on Socotra. A detailed account on the vegetation was given by POPOV (1957), MIES & ZIMMER (1993, 1994), MIES *et al.* (1995), and LAVRANOS (1995). The man-high shrubby vegetation of the highlands consists of Euphorbiaceae, Rubiaceae, Buxaceae, Hypericaceae and more paleotropical plant families. The dry coastal lowlands of Socotra are mainly covered by featherduster-bush species, mainly of Euphorbiaceae and Acanthaceae. Abundant are *Croton socotranus*, *Jatropha unicostata*, *Trichocalyx* spp. and others, which form a uniform thicket of umbrella-like shrubs. Within the plain's vegetation and up to the lower limestone slopes one finds succulent shrubs of *Cissus hamaderoensis*, *C. subaphylla* (Vitaceae), *Caralluma socotrana* (one or more Aselepiadacean species, the synonymy of which is still not quite clear), *Euphorbia septemcostata*, and *Eu. spiralis*. The 4-5 m high, aphyllous and succulent *Euphorbia arbuscula* trees (section Tirucalli within the genus) resemble in shape *Eu. aphylla* from the Canaries very much. The vegetation of the lowlands and plains is heavily damaged through pasture of goats and sheep flocks, in general. The abundance of *Aloe* (Liliaceae) and *Kalanchoe* species (Crassulaceae) is typical for these areas.

On the slopes the vegetation varies greatly in aspect with the character of the rocks. In the lowlands on limestone gravel plains, rocky slopes and rocks we find the famous caudiciform succulents as bottle-trees ("pachycaul succulents") *Adenium socotranum* (Apocynaceae), *Dorstenia gigas* (Moraceae) and *Dendrosicyos socotrana* (melon tree, Cucurbitaceae). Whereas *A. socotranum* and *D. gigas* are still abundant, the melon tree is becoming extinct, because it is palatable to grazing goats and sheeps (MIES & ZIMMER 1993). Above 400 m a.s.l. *Dracaena cinnabari* becomes frequent. Inland the valleys are even richer in arborescent forms like *Ziziphus* spp. (Mimosaceae) or in endemics of *Boswellia* spp. (frankincense), *Commiphora* spp. (myrrhs, both Burseraceae), *Clerodendron* spp. (Verbenaceae), *Euclea* spp. (Ebenaceae), *Lannea transulta* (Anacardiaceae), *Pseudomussaenda capsulifera* (Rubiaceae), *Sterculia rivae* (Sterculiaceae), concerning some trees only (MIES & ZIMMER 1993, MIES *et al.* 1995). In the heights the arborescent impressions vanishes, and the man-high indigenous forest of the Hagher range above 800 m a.s.l. consists of little trees like *Buxus hildebrandtii* (Buxaceae), *Cephalocroton socotranus* (Euphorbiaceae), *Hypericum* spp. (Hypericaceae), *Euphorbia socotrana*, *Ficus socotrana* (Moraceae), *Graderia fruticosa* (Scrophulariaceae), *Ruellia* spp. (Acanthaceae), *Sideroxylon* spp. (Sapotaceae), and understorey shrubs like *Gnidia socotrana* (Thymelaeaceae), *Euryops socotranus*, *Psiadia schweinfurthii* (Compositae), *Hypericum* spp., and much more. Here, we find also both stem succulent *Kleinia* species, also typical for the paleotropical arid zones. The very peculiar *Cocculus balfourii* (Menispermaceae) forms with its cladodes impenetrable thorny clusters to the livestock, greedy to the more delicate herbs growing within.

Over 200 vaseular species has been described as endemic from Socotra. The already mentioned *Cocculus balfourii*, *Lachnocapsa spathulata* in the Crucifers, *Haya obovata* and *Lochia* spp. in the Caryophyllaceae, the mentioned *Graderia fruticosa* and *Xylocalyx* spp. in the Scrophulariaceae, *Ancalanthus paucifolius*, *Ballochia* spp., *Neuracanthus* spp. and *Trichocalyx* spp. in the Acanthaceae, *Coelocarpus socotranus* in the Verbenaceae, *Punica protopunica* in the Punicaceae, *Thamnosma socotrana* in the Rutaceae, *Socotranthus socotranus* and *Socotora aphylla* (perhaps to *Periploca*?) in the Asclepiadaceae, *Wellstedia socotrana* in the Boraginaceae (possibly to this family), and *Ischnurus pulchellus* in the Poaceae are plant forms of a systematically unique position in the particular plant families; some of them very antiquated. In our own investigations 1993 and 1994 we were not able to find the living fossils *Dirachma socotrana* (Dirachmaceae, to Rosales or Geraniales?), which the collectors BAILEY BALFOUR 1880 and GEORG SCHWEINFURTH 1881 encountered on the Hagher Mountains sporadically. Even in the early times of island exploration and botanical discovery the Apiacean tree *Nirarathamnos asarifolius* has been regarded as on the way to extinction, nowadays this living fossil seems to be lost. Obviously as neoendemics, based on ancestor species, a variety of endemic *Aloe*, *Boswellia* and *Commiphora*, *Cissus*, *Barleria* and *Ruellia* (Acanthaceae), *Boerhavia* and *Commicarpus* (Nyctaginaceae), *Carum* (Apiaceae),

Crotalaria (Papilionaceae), *Dirichletia* (Rubiaceae), *Croton* and *Euphorbia*, *Exacum* (Gentianaceae), *Oldenlandia* (Rubiaceae), *Lindenbergia* (Scrophulariaceae), *Heliotropium* and *Trichodesma* (Boraginaceae), and *Helichrysum*, *Pluchea* and *Pulicaria* (Compositae) species spread in an adaptive radiation to all available ecological niches on the islands. Since the beginning of this century a lot of Socotran endemics have been found in the Eritreo-Arabian floristic province also, so that the degree of endemism counts to appr. 20% today. BAILLON (1887) mentioned *Dendrosicyos socotrana* also on the coasts of French Somaliland (Djibouti) as a living evidence for a formerly widespread species. Nowadays it can be regarded as extinct there. The neophytes of Socotra share less than 3% of the total flora which equally contributes to the fact of an isolated position of the islands, actually.

VICARIANT TAXA OF MACARONESIA AND SOCOTRA

The keen work of BALFOUR (1888) about the botany of Socotra and Abd El Kuri inspired the works on the biogeography of Macaronesia since the time of publication as well. Macaronesia and the Eritreo-Arabian floristic region of the paleotropical kingdom at a whole are linked by various taxa of vascular plants and even cryptogams. Some examples for striking homologous genera and species of Macaronesia and Socotra are presented in the following; they are systematically related and vicariants at the Eastern and Western points of the African continent besides the Saharan desert.

(1) First example: The genus *Euphorbia* comprises stem-succulent species like

- the 0.5 m high *Euphorbia spiralis* and *Eu. septemsulcata* (Socotra) are vicariants to *Eu. handiensis* (Lanzarote) with a cactoid morphology.

- *Eu. abdelkuri* (Abd El Kuri) with the same habitat, size and shape like *Euphorbia canariensis* (Canary). Both belong to the section *Diacanthium* of the genus. *Eu. abdelkuri* has a somehow isolated position in the section, because it expresses no thorns and has a yellow milky juice because of flavonoids. The former may be regarded as a pseudo-vicariant species to the latter in a similar habitat on the slopes of Jebel Saleh on Abd El Kuri from 200 to 500 m a.s.l.: *Eu. canariensis* occurs in middle coastal altitudes between 100 and 500 m altitude (extrazonally even higher on sunny rock faces) on all Canary islands:

- *Eu. socotrana* (Socotra) is a related species out of the *Tithymalus* group which comprises a dozen species on the Atlantic islands [*Eu. atropurpurea* (Canaries), *Eu. balsamifera* (Canaries, North Africa, Portugal, Arabia), *Eu. bourgaeana* (Canaries), *Eu. bravoana* (Canaries), *Eu. broussonetii* (Canaries), *Eu. lambii* (Canaries) *Eu. mellifera* (Azores, Madeira, Canaries), *Eu. obtusifolia*, (Canaries, Selvagens), *Eu. piscatoria* (Madeira), *Eu. tuckeyana* (Cabo Verde)]. The hemispherical canopy shape of the individuals relies on terminal leaf rosettes, closely arranged to a 'leatherduster-bush' shape habit. Inside of each bush the temperature remains lower and the wind velocity is retarded to avoid high evapotranspiration.

- *Euphorbia arbuscula*, *Eu. obcordata*, *Eu. oblanceolata* and *Eu. schimperi* (Socotra) out of the Tirucalli group resemble *Eu. aphylla* (Gran Canaria, Gomera, Tenerife) very much. The terminal, green branches act photosynthetically, the leaves are only present on growing young shoots.

(2) The genus *Dracaena* is present with *Dracaena cinnabari* as mentioned before, resembling the Atlantic species *D. draco* (Madeira, Canaries, Cabo Verde) in morphology. They grow to 8-10 m high trees with a single and secondary thickened trunk, which is dichotomously branching and ending in terminal leaf rosettes, expressing an umbrella-shaped crown. The leaves are sclerophyllous and probably both species able to gain CO₂ over night by Crassulacean Acid Metabolism. *D. cinnabari* differs from the latter in a more regular dichotomous branching, red fruits, and more xerophyllous leaves. [Besides, in the author's opinion the ontogenetically early branching hemispherical type of the Capeverdean draco may justify a special taxonomic treatment or a subspecies of its own (see also BYSTRÖM 1960). Unfortunately the plantation of ornamental "dragos" on the Canaries and more often on the Portuguese island Madeira was carried out with seeds from Capeverdean origin also. A careful examination must rely on surely originating and wild collected herbarium material.]

(3 ff.) Further species examples - shared by both regions - are *Achyranthes aspera*, *Aerva lanata*, *Adiantum aethiopicum*, *A. capillus-veneris*, *Ageratum conyzoides*, *Aizoon canariense*, *Asphodelus tenuifolius*, *Cenchrus ciliaris*, *Citrullus colocynthis*, *Commelina* spp., *Limonium* spp., *Lotus* spp., *Momordica charantia*, *Micromeria varia*, *Periploca laevigata*, *Reichardia tingitana*, *Sarcostemma viminale*, *Tribulus terrestris*, *Withania somnifera*, *Zygophyllum simplex*, etc., mostly pantropical, saharo-sindian or Mediterranean weeds. Some more vicariant endemics or species pairs/groups among the vascular floras common to both regions are shown in table 1.

(4) Also cryptogams express some obviously old relations through related monotypic genera; the lichen *Roccellographa cretacea* (Socotra, Somalia) is closely related to the Capeverdean *Gorgadesia mira* (STEINER 1907), e.g.; TEHLER (1980) reports some disjunctive taxa out of the genera *Dirina* and *Roccellina* in this biogeographical sense.

Additionally, there are some more 20 examples of vascular plants with wider distribution and a relationship to the area of Macaronesia (BALFOUR 1888). In the geographical vicinity of Yemen, DEIL & MÜLLER-HOHENSTEIN (1984) constructed relationships between the flora and vegetation of mainland Arabia and Macaronesia on the base of a phytosociological evaluation of plant communities, but at least focussed on a single species, *Euphorbia balsamifera*, which is present also in Arabia in the subspecies *adenensis* (but not on Socotra itself, only on Abd-Elkuri).

DISCUSSION

Are the before mentioned parallel occurrences of species a true and sufficient evidence

for constructing a biogeographical relation between Macaronesia and Socotra? Making a census of the flora, the majority of genera and species common to both areas belong to wider distributed types. Some are growing over the whole Saharo-Sindian belt, some have relatives in the dry region of the Mediterranean, some are pantropical, and some were also introduced by man. Endemic species of the genera *Withania*, *Heliotropium*, *Helichrysum*, *Polycarpaea*, *Indigofera*, *Statice*, *Micromeria* and certain groups like some taxa among the Euphorbiaceae, e.g., may be regarded as schizo- or neoendemics on either the Atlantic archipelagos or the Socotran island group, deriving from ancestor species with a wider paleogeography.

More evidence is given by the examination of paleoendemics and their biogeographical relations. The use of the term 'paleoendemic' here is slightly different from regarding monotypic genera, exclusively. It comprehends species which are still persistent from an ancient flora and the time of speciation, have not split up into neoendemic species through adaptive radiation, and can be related to disjunctive taxa at the family -, genus -, or species level. Since the beginning of the 20th century disjunctive species like *Aeonium leucoblepharum* (Arabia), *Canarina eminii* (Ethiopia), e.g. from the Eritreo-Arabian floristic province contributed to the analyse of the Macaronesian flora as well. LÖSCH & FISCHER (1994) suggest, that the Macaronesian and the Central African ericaceous shrub communities in montane habitats rely upon a taxonomically and ecologically undivided area, which split up possibly in the late Tertiary. In the case of the xeric vegetation they refer to the opinion of AXELROD & RAVEN (1978), that the xerotherm elements of the North African area originates on the South African flora.

The genus *Dracaena* comprises approximately 60 described species, mainly in the moist tropical belt of the paleotropics. BEYHL (1995) deals with the morphology of both dragon trees in detail, *Dracaena draco* and *D. cinnabari*. But the distribution of the 11 xerophytic and systematically related species yields a remarkable result (Fig. 2a, the biogeographical areas in the following were deduced from ENGLER & DRUDE see ENGLER 1910, in their subsequent issue of the flora vegetation of Africa or out of special literature). The Atlantic *Dracaena draco* has a somehow isolated distribution; the remaining 10 species grow from Arabia to South Africa along the eastern part of the African continent. Of course, xerophytic species are not present in the Congo Basin and the Guinean rain forests, but also Northern Africa, mainly the Atlas Mountains, Ahaggar and Tassili, lacks members of this Agavacean group. The Tirucalli group out of Euphorbia (Fig. 2b) expresses a quite similar biogeographical pattern. The Canarian *Euphorbia aphylla* has one relative, *Eu. latiflora*, in West Africa, but more than 20 species in South Africa, Madagascar, East Africa to Arabia and stretching as far as the Indian subcontinent. The Tithymalus group out of Euphorbia (Fig. 2c) shows a similar disjunction across the African continent. *Eu. balsamifera* is a common species at both ends of Northern Africa in two subspecies, ssp. *balsamifera* and ssp. *adenensis*. The Western Mediterranean *Eu. dendroides* does not fill the gap between West and East.

The Fig. 2 exemplifies a general biogeographical distribution type of the xeric taxa

in the area of Africa and Arabia. Related taxa to either Socotra or Macaronesia occur either in South Africa or along the East African rift valley and mountain range system. The flora of the Saharan desert region is floristically not related to the eastern and western islands of the continent; connecting links are missing there. Obviously the geologically old Congolese rainforest areas (Hylaea) could not be colonized by a xeric vegetation. Nevertheless, a missing link between the islands of Macaronesia and Socotra has often to be looked for in the South African region of the continent. The Fig. 3 tries to figure a concluding scheme exemplified by a section of *Senecio*, the stem-succulents of the subgenus *Kleinia*, which is present with *Kleinia nerifolia* on the Atlantic Islands and with *Kl. scottii* and *Kl. longiflorus* on Socotra. The centers of high species diversity can be found in South Africa and Madagascar today.

The dispersion of seeds of endemics is improbable, if they might originate from regions of origin as far as South Africa or as the islands of the Atlantic Ocean from the Socotran archipelago, as AXELROD & RAVEN (1978) postulated. Euphorbiaceae and *Dracaena* e.g. have fruits, too heavy for wind dispersal (the distribution through the intestines of birds is improbable in the case of the spurges). The mentioned authors suppose a migration path along the East African mountain ranges. This does not fit to the distance to the Atlantic Islands in the mentioned cases. The authors regard the paleoclimatic conditions of the mainland Africa as more humid than today, resulting in greater areas of rainforests and savannahs in the late Cretaceous and early Tertiary periods, so that the centers of xerophytic vegetation in South Africa, Arabia and Macaronesia have been isolated to each other.

The Atlantic islands did not arise above sea level before Miocene 7 to 10 mio years b.p., so that they must have been colonized from the adjacent regions. Regarding the geological old age of the island of Socotra the plant groups (mentioned above) represent remnants of an aridity adapted flora at the end of the Cretaceous until the mid of the Tertiary period. Regarding the floristic relationships it is possible to think of a continuous belt from West Africa to Socotra. In this time the equator has been situated approximately 16° far North than today. High pressure cells have been present South of this Cretaceous equator, leading to an arid subtropical belt.

The concept of AXELROD & RAVEN (1978) based only on scarce and local palynological data from Southern Sudan for the whole area of Northeast Africa and Arabia. In general the biogeography and plate tectonics especially of the Eritreo-Arabian region is still not quite clear. The paleoendemics of Macaronesia and Socotra may give evidence to think of remnants of a dry subtropical Southern Tethys flora. The forerunner of the Mediterranean Sea was closed in Tertiary as the African plate moved northward and the belts of the moist tropics and xeric subtropics displaced to their actual geographical position. Subsequently, the humid tropical belt shifted from the European continent in late Cretaceous to early Tertiary times southwards to its present position. According to AXELROD & RAVEN (1978) the arid regions in the West, East, and South of the African continent appeared to be isolated by humid vegetation belts in Middle Tertiary. In late Tertiary the Holarctis colonized

the central parts of Northern Africa and Arabia forming the Saharan belt. In this movements, islands and mountain ranges offered persistent ecological niches and survival for species at the margins instead of an improbable long distance dispersal (see GAMS 1964, HEDBERG 1970). The aridity adapted geoelements may have remained as vestiges on the East African mountains to South Africa. So-called 'trail-relics' survived in adequate microhabitats in the continuous mountain ranges of East Africa and on islands off the coast, the Socotran archipelago and parts, even older, of the Malagasy flora. The continental xeric vegetation belt may have moved to South, evolving the species in itself, losing parts of the original flora and vegetation, or integrating elements on its way towards South Africa. Regarding the geological time or timing of the splitting of this uniform belt, it must have been before the late Cretaceous period. The deep Congo Basin and the humid Guinean rainforest area offered no possibilities for remnants of a xeric vegetation belt, being as old as the mentioned subtropical Southern Tethys flora. The Atlantic islands have been colonized from adjacent areas since the time of their origin in Miocene, proven by their heterogenic biogeographical relations of its vegetation elements and the still persistent adaptive radiation of some neogenic groups (*Euphorbia*, Crassulaceae, e.g.). In the sense of continuous distribution areas, the ancestor species of the 'Atlantic trail' are now extinct because of the geomorphological lack of mountain ranges, inselbergs, e.g. on the adjacent mainland. In former biogeography, we were victims of the vicissitudes of the times of botanical discovery, in that island floras were investigated before the continents were explored, constructing relationships between the Western and Eastern tips of the African continent. Thus, the knowledge of island floras contributes to a better understanding of biogeography of the paleotropics in the light of relics and evolution.

LITERATURE

AXELROD, D. I. & P. H. RAVEN:

1978. Late Cretaceous and Tertiary vegetation history of Africa. In 'Biogeography and ecology of Southern Africa' (M.J.A. Werger, ed.), 77-130, The Hague.

BALFOUR, I. B.:

1888. Botany of Socotra. Transact. Roy. Soc. Edinburgh, **31**: 1-446.

BEYHL, F. B.:

1995. Der Drachenbaum und seine Verwandtschaft. II. Der Echte Drachenbaum, *Dracaena cinnabari*, von der Insel Sokotra. Der Palmengarten, **59**: 140-145.

BEYHL, F. B., R. LÖSCH, B. MIES & B. SCHWEIHOFEN:

1990. Bilden die Kapverden ein einheitliches Florengebiet? Cour. Forschungsinst. Senckenberg, **129**: 47-53.

BØRGESEN, F.:

1924. Contributions to the knowledge of the vegetation of the Canary Islands (Teneriffe and Gran Canaria). D. Kgl. Danske Vidensk. Selsk. Skr., Naturvid. Mat. Afd., 8, 6.3: 285-399.

BYSTRÖM, K.:

1960. *Dracaena draco* L. in the Cape Verde Islands. Acta Horti Gotob., **23**: 179-214.

CHRISTENSEN, T.B., DALGAARD, V. & HAMANN, O.:

1970. Oversigt over Madeiras Flora. Køb. Univ. Fond, København.

DANSEREAU, P.:

1966. Etudes macaronésiennes. III. La zonation altitudinale. Natur. Canad., **93**: 779-795.

DEIL, U. & K. MÜLLER-HOHENSTEIN:

1984. Fragmenta Phytosociologica Arabiae-Felicis I. Eine Euphorbia-balsamifera-Gesellschaft aus dem jemenitischen Hochland und ihre Beziehungen zu makaronesischen Pflanzengesellschaften. Flora, **185**: 407-426.

ENGLER, A.:

1910. 2.Kap., 19. Socotra. In "Die Pflanzenwelt Afrikas, insbesondere seiner

tropischen Gebiete. Grundzüge der Pflanzenverbreitung in Afrika und die Charakterpflanzen Afrikas. I. Allgemeiner Überblick über die Pflanzenwelt Afrikas und ihre Existenzbedingungen.", (A. ENGLER & O. DRUDE, eds.), 204-213; Leipzig.

FORBES, H. O.:

1903ed. A natural history of the islands of Socotra and Abd El Kuri. Being the report upon the results of the conjoint expedition to these islands in 1898-9, by Mr. W. R. OGILVIE-GRANT, of the British Museum, and Dr. H. O. FORBES, of the Liverpool Museums, together with information from other available sources forming a monograph of the islands. Botany of Sokotra and Abdel-Kuri. Liverpool Mus. Rep. Sokotra Exped., 443-582; Henry Young, London.

GAMS, H.:

1964. Die Bedeutung der afro-montanen und afroalpinen Floren für die Geschichte der mediterran-montanen und alpinen Floren. *Phyton*, **11**: 1-17.

HANSEN, A. & P. SUNDING:

1993. Flora of Macaronesia. Checklist of vascular plants. *Sommerfeltia*, **17**: 1-295.

HEDBERG, O.:

1970. Evolution of the afroalpine flora. *Biotropica*, **2**: 16-23.

HOOKE'S ICONES PLANTARUM:

1967. New or noteworthy species from Socotra and Abd Al Kuri. *Hook. Ic. Pl.*, 5. ser., (37), 7, 4: t.3673-3700.

KÄMMER, F.:

1982. Beiträge zu einer kritischen Interpretation der rezenten und fossilen Gefäßpflanzenflora und Wirbeltierfauna der Azoren, des Madeira-Archipels, der Ilhas Selvagens, der Kanarischen Inseln und der Kapverdischen Inseln, mit einem Ausblick auf Probleme des Artenschwundes in Makaronesien. Selbstverl., Freiburg i.Br.

KOSSMAT, F.:

1907. Geologie der Inseln Sokotra, Semha und Abd El Kuri. *Denkschr. Kais. Akad. Wiss. Wien, Mat.-Nat. Kl.*, **71**: 1-62.

KUNKEL, G.:

1980. Die Kanarischen Inseln und ihre Pflanzenwelt. Stuttgart, pp. 202.

LAUER, W. & P. FRANKENBERG:

1977. Zum Problem der Tropengrenze in der Sahara. *Erdkunde*, **31**: 1-15.

LAVRANOS, J. J.:

1995. Impressions from Socotra & Abd Al-Kuri. *Euph. J.*, **9**: 190-209.

LEMS, K.:

1960. Botanical notes on the Canary Islands. II. The evolution of plant forms in the islands: *Aeonium*. *Ecology*, **41**: 1-17.

LOBIN, W.:

1980. Untersuchungen über Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. *Cour. Forschungsinst. Senckenberg*, **53**: 1-112.

LÖSCH, R., F. BEYHL, B. MIES & B. SCHWEIHOFEN:

1990. Relative Standortkonstanz der Federbuschvegetation auf den mittelatlantischen Inseln und die klimatisch-orographischen Voraussetzungen einer Waldklimax auf den Kapverden. *Cour. Forschungsinst. Senckenberg*, **129**: 75-82.

LÖSCH, R. & E. FISCHER:

1994. Vikariierende Heidebuschwälder und ihre Kontaktgesellschaften in Makaronesien und Zentralafrika. *Phytocoenologia*, **24**: 695-720.

LOWE, R.T.:

1869. *Florulae Salvagicae Tentamen*. London.

LÜPNITZ, D.:

1975. Geobotanische Studien zur natürlichen Vegetation der Azoren unter Berücksichtigung der Chorologie innerhalb Makaronesiens. *Beitr. Biol. Pfl.*, **51**: 149-319.

MABBERLEY, D.J.:

1979. Pachycaul plants and islands. In "Plants and islands", (D. BRAMWELL, ed.), 259-277. London.

MIES, B.:

1994. Checkliste der Gefäßpflanzen, Moose und Flechten und botanische Bibliographie der Insel Sokotra und des Sokotrinischen Archipels (Republik Jemen, Indischer Ozean). *Senckenb. Biol.*, **74**: 213-258.

MIES, B., F.E. BEYHL & C. PRINTZEN:

1995. Die Waldformationen der Insel Sokotra (Indischer Ozean). *Nat. Mus.*, **125**: 122-133.

MIES, B. & H. ZIMMER:

- 1993a. Die Flora und Vegetation der Insel Sokotra im Indischen Ozean. *Nat. Mus.*, **123**: 253-264.
- 1993b. Die Populationen von *Adenium socotranum* (BALFOUR)VIERHAPPER und *Dendrosicyos socotrana* BALFOUR bei Ras Hebak (Insel Sokotra, Jemen) und ihre Gefährdung. *Kakt. u. and. Sukk.*, **45**: 1-5.
1994. Die Insel des Drachenbaums. Die Pflanzenwelt von Sokotra. *Jemen-Report*, Mitt. Deut.-Jem. Ges., **25**: 4-11.

POPOV, G.B.:

1957. The vegetation of Socotra. *J. Linn. Soc. London*, **55**: 706-720.

SJÖGREN, E.:

1974. Local climatic conditions and zonation of the vegetation on Madeira. *Agron. Lusit.*, **36**: 95-139.

STEINER, J.:

1907. Bearbeitung der von O.Simony 1898 und 1899 in Südarabien, auf Sokotra und den benachbarten Inseln gesammelten Flechten. *Denkschr. Kais. Akad. Wiss. Wien. Mat.-Nat. Kl.*, **71**: 93-102.

SUNDING, P.:

1972. The vegetation of Gran Canaria. *Skr. Norske Vidensk. Ak. Oslo, Mat.Naturvid. Kl., N.S.*, **29**: 1-186.

TEHLER, A.:

1980. The genera *Dirina* and *Roccellina* (Roccellaceae). *Op. Bot.*, **70**: 1-86.

VAHL, M.:

1905. Über die Vegetation Madeiras. *Bot. Jahrb.*, **36**: 253-349.

VIERHAPPER, F.:

1907. Beiträge zur Kenntnis der Flora Südarabiens und der Inseln Sokotra, Semha und Abd El Kuri. *Denkschr. Kais. Akad. Wiss. Wien, Mat.-Nat. Kl.*, **71**: 321-490.

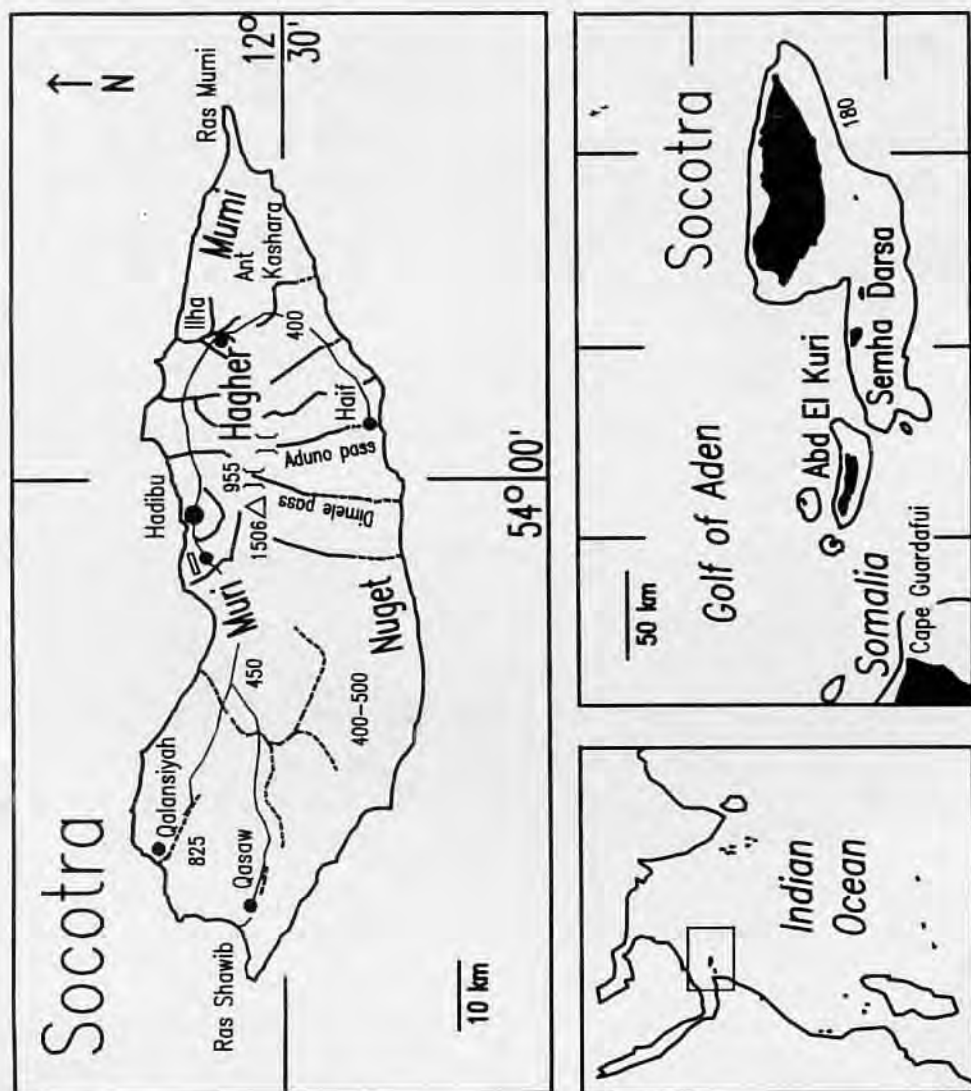
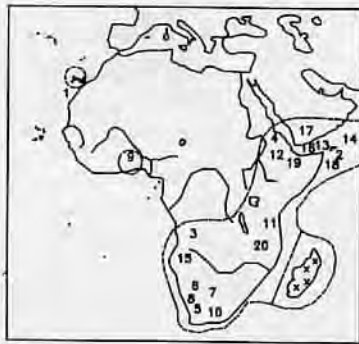


Figure 1 - Geographical position of the Socotran archipelago and map of Socotra



- ☒ *Dracaena angustifolia*
- *D. cinnabari*
- *D. draco*
- ▽ *D. ellenbeckiana*
- ▼ *D. hanningtonii*
- ◇ *D. hookerana*
- *D. ombet*
- × *D. reflexa*
- *D. serrulata*
- △ *D. schizantha*
- ▲ *D. steudneri*



- 1 *Euphorbia aphylla*
- 2 *Eu. arbuscula*
- 3 *Eu. berotica*
- 4 *Eu. consobrina*
- 5 *Eu. dregeana*
- 6 *Eu. fleckii*
- 7 *Eu. gregaria*
- 8 *Eu. gummifera*
- 9 *Eu. lateriflora*
- 10 *Eu. mauritanica*
- 11 *Eu. merkerii*
- 12 *Eu. nubica*
- 13 *Eu. obcordata*
- 14 *Eu. oblanceolata*
- 15 *Eu. rhipsaloides*
- 16 *Eu. schimperii*
- 17 *Eu. schimperiana*
- 18 *Eu. schweinfurthii*
- 19 *Eu. scoparia*
- 20 *Eu. tirucalli*
- x Malagasy species et al.



- 1 *Euphorbia anachoretea*
- 2 *Eu. atropurpurea/broussonetii*
- 3a *Eu. balsamifera*
- 3b *Eu. bals. ssp. adenensis*
- 4 *Eu. barbicollis*
- 5 *Eu. berthelotii*
- 6 *Eu. bravoana*
- 7 *Eu. dendroides*
- 8 *Eu. lambii*
- 9 *Eu. mellifera/stygiana*
- 10 *Eu. noxia*
- 11 *Eu. orthoclada*
- 12 *Eu. piscatoria*
- 13 *Eu. pseudogranti*
- 14 *Eu. punicea*
- 15 *Eu. quadrata*
- 16 *Eu. socotrana*
- 17 *Eu. tuckeyana*

Figure 2 - (a) the xeromorphic species of the genus *Dracaena*, indicated as symbols, and the general distribution of the genus. (b) the *Tirucalli* section of the genus *Euphorbia* and its general distribution. (c) the *Tithymalus* section of the genus *Euphorbia* and its general distribution.

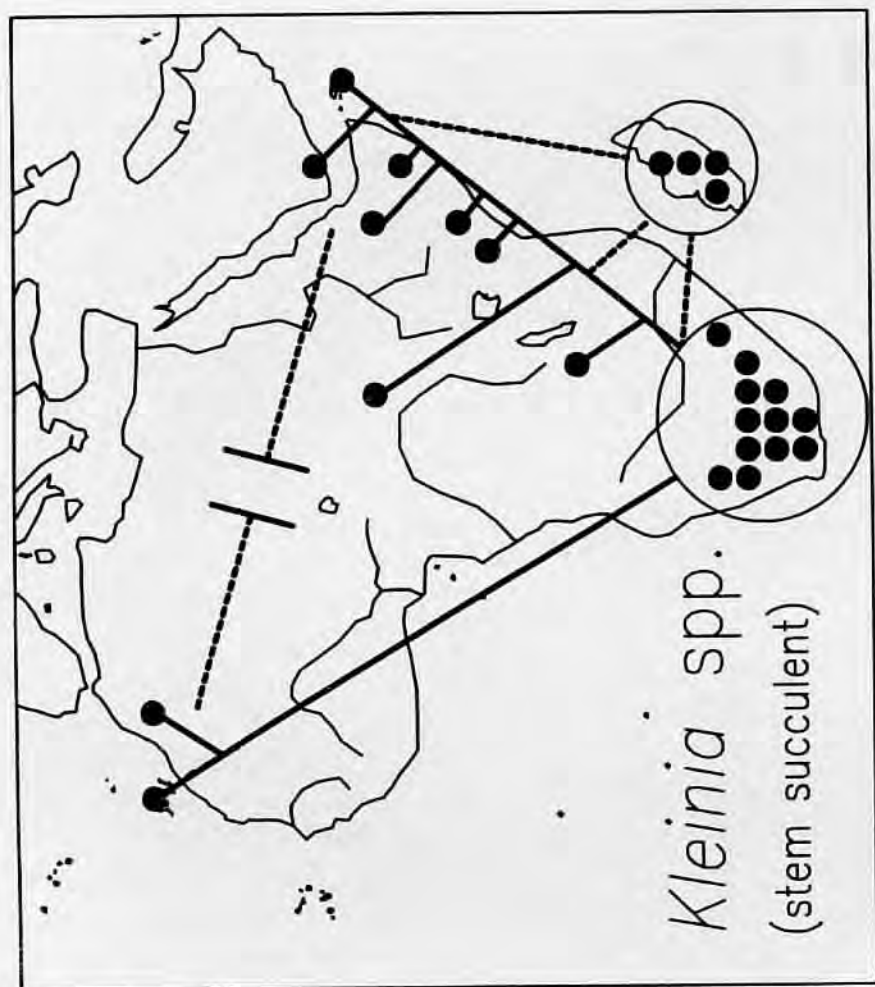


Figure 3 - Hypothetical scheme of geographical relations between the species of the genus *Kleinia* in the African paleotropics as 'trail-relics' (biogeography after ENGLER & DRUDE: 1910).

TABLE 1 - Vicariant endemic plant species of Macaronesia and the Socotran archipelago (some endemics of nearest mainland areas in vicinity included) [AEK Abd-El-Kuri; Afr African. Ar Arabian; Az Azorean; Can Canarian; CV Capeverdean; Eth Ethiopian; Mac Macaronesian; Mad Madeiran; Med Mediterranean; Soc Socotran; Som Somalian-Eritrean].

<u>Acacia</u> spp. (Mac. Afr)	<u>A.</u> spp. (Soc)
<u>Buxus sempervirens</u> (Az. Med)	<u>B. hildebrandtii</u> (Soc, Eth, Som)
<u>Campylanthus salsoloides</u> (Can)	<u>C. spinosus</u> (Soc)
<u>Clerodendron speciosissimum</u> (CV)	<u>C. galeatum</u> , <u>C. leucophloeum</u> (Soc)
<u>Dipcadi serotinum</u> (Can. Med)	<u>D.</u> spp. (Soc)
<u>Fagonia</u> spp. (Mac. Med)	<u>F.</u> spp. (Soc)
<u>Gnidia polystachya</u> (Mad. Can)	<u>Gn. socotrana</u> (Soc)
<u>Habenaria petromedusae</u> , <u>H. tridaetylites</u> (Mad,Can)	<u>H. socotrana</u> (Soc)
<u>Helichrysum</u> spp. (Mac. Med)	<u>H.</u> spp. (Soc)
<u>Hypericum</u> spp. (Az, Mad, Can)	<u>H.</u> spp. (Soc)
<u>Imperatoria lowei</u> (Mad)	<u>Peucedanum cordatum</u> (Soc)
<u>Justicia hyssopifolia</u> (Can)	<u>J. rigida</u> (Soc)
<u>Kickxia</u> spp. (Mac. Med)	<u>K. hastata</u> , <u>K. kuriensis</u> (Soc, AEK)
<u>Kleinia neriifolia</u> (Can)	<u>K. longiflorus</u> , <u>K. scottii</u> (Soc, Som)
<u>Lactuca palmensis</u> (Can)	<u>L.</u> spp. (Soc,A-E-K)
<u>Melhania ovata</u> (CV, Afr)	<u>M. muricata</u> (Soc)
<u>Osyris quadripartita</u> (Can)	<u>O. arborea</u> , <u>O. pendula</u> (Soc,Ar, Som)
<u>Polycarpaea</u> spp. (Can, CV)	<u>P.</u> spp. (Soc, AEK)
<u>Pulicaria</u> spp. (Can, CV)	<u>P.</u> spp. (Soc, AEK)
<u>Reseda lancerotae</u> (Can)	<u>R. viridis</u> (Soc)
<u>Sideroxylon marmulano</u> (Can, CV)	<u>S. discolor</u> , <u>S. fimbriatum</u> (Soc)
<u>Teucrium</u> spp. (Mad,Can)	<u>T. balfourii</u> , <u>T. socotranum</u> (Soc)
<u>Trichodesma africanum</u> (CV, Afr)	<u>Tr.</u> spp. (Soc, AEK)
<u>Urginea maritima</u> v. <u>hesperia</u> (Can)	<u>U. porphyrostachys</u> (Soc)
<u>Vernonia</u> spp. (Mac)	<u>V.</u> spp. (Soc, AEK)
<u>Withania</u> spp. (Can, CV,Afr)	<u>W. adunensis</u> , <u>W. riebeckii</u> (Soc)