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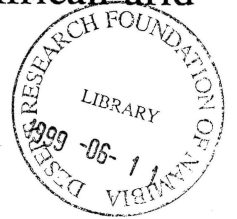
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## Floristic biodiversity and history of African arid regions

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The phytochorological patterns of the arid flora of Africa are discussed on various levels. The arid regions of the African continent are linked by a large number of taxa with disjunct distribution. Analysis of these disjunct patterns supports the hypothesis of fragmentation of a once continuous arid belt running from the Namib desert region to the Western Sahara via East Africa. The flora of the arid regions of Southern Africa shows regular patterns, e.g. identical fragmentation of distribution areas of several taxa on an infrafamilial or infrageneric level, allowing formulation of a hypothesis concerning the sequence of differentiation steps during formation of the floras. Very interesting patterns can be attributed to effects of the last glaciation. For example, disjunct distribution patterns in the Namib region can be interpreted as a result of survival of palaeotropical taxa in warm refuge areas during the last glaciation.

*Keywords:* Africa; arid regions; disjunctions; history; phytogeography.

### Introduction

African arid regions are of considerable age. This hypothesis is supported by the very high biodiversity of arid-adapted taxa. On the other hand, palaeobiology, geosciences and archaeology have shown that, during the past, the extent and the geographical location of African arid regions varied considerably at various time scales (Axelrod, 1975; van Zinderen Bakker, 1975, 1978; Axelrod and Raven, 1978). Details of the history of aridity are still under discussion and there are some controversies with respect to the interpretations proposed by different scientific disciplines. Therefore, a contribution from a phytogeographical point of view might supply additional evidence, allowing the formulation of several additional questions and hypotheses. Observations shall be presented in a sequence from probably old to probably recent processes.

### Methods

Distributional data were derived from the sources indicated in the text and from my own extensive field work in the Southern African arid regions. These data are interpreted phytochorologically and linked to general ecological gradients, specific qualities of the taxa involved, and published knowledge about their phylogeny.

### Results

#### CONTINENTAL PATTERNS

It has been long known that arid regions of the African continent are phytogeographically linked by a large number of taxa with disjunct distribution. These disjunct patterns have

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been described from a Northern hemisphere point of view by Axelrod (1975), Bramwell (1976, 1985), Deil and Müller-Hohenstein (1984), Thiede (1994) and Thulin (1994, including the most recent review of older literature), while de Winter (1971) has been emphasizing the floristic relationships of arid Africa from a Southern hemisphere viewpoint. A general view has been provided by White (1990). In these publications the general observation of continent-wide arid disjunctions is presented.

A disjunct area of distribution is of rather special appearance and not easy to interpret, as could be exemplified by *Rogeria adenophylla* (Fig. 1). However, the situation becomes more understandable when numerous taxa with similar continental disjunct patterns are grouped together and shown additively in one map. Figures 2 to 4 show those regions in

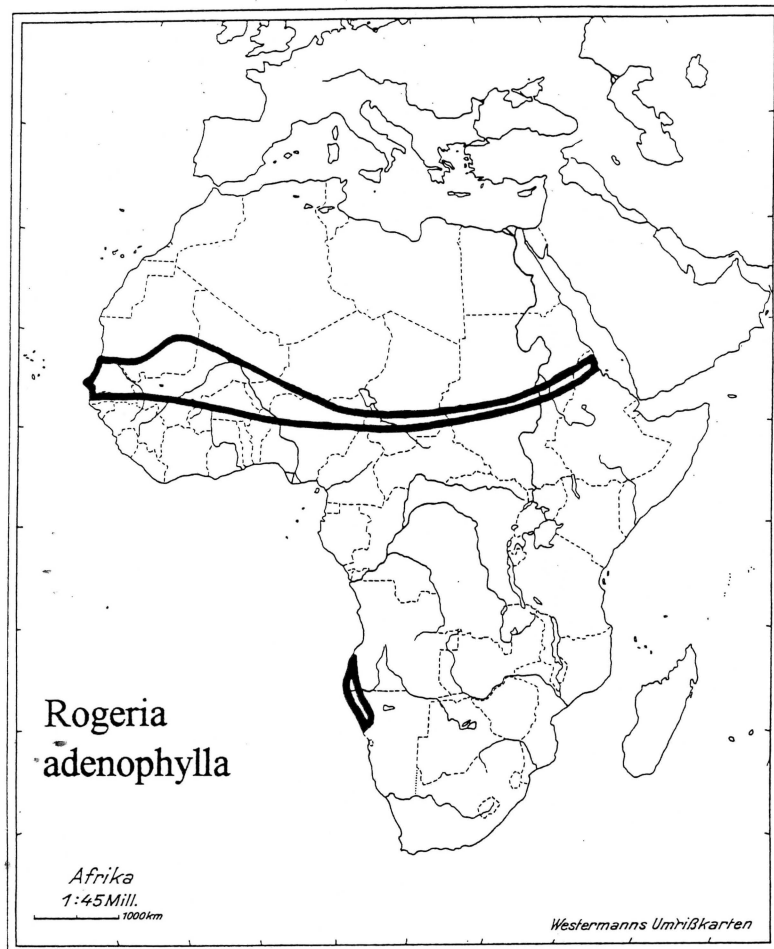


Figure 1. Area of distribution of *Rogeria adenophylla* (Pedaliaceae) (from Ihlenfeldt, 1994a).

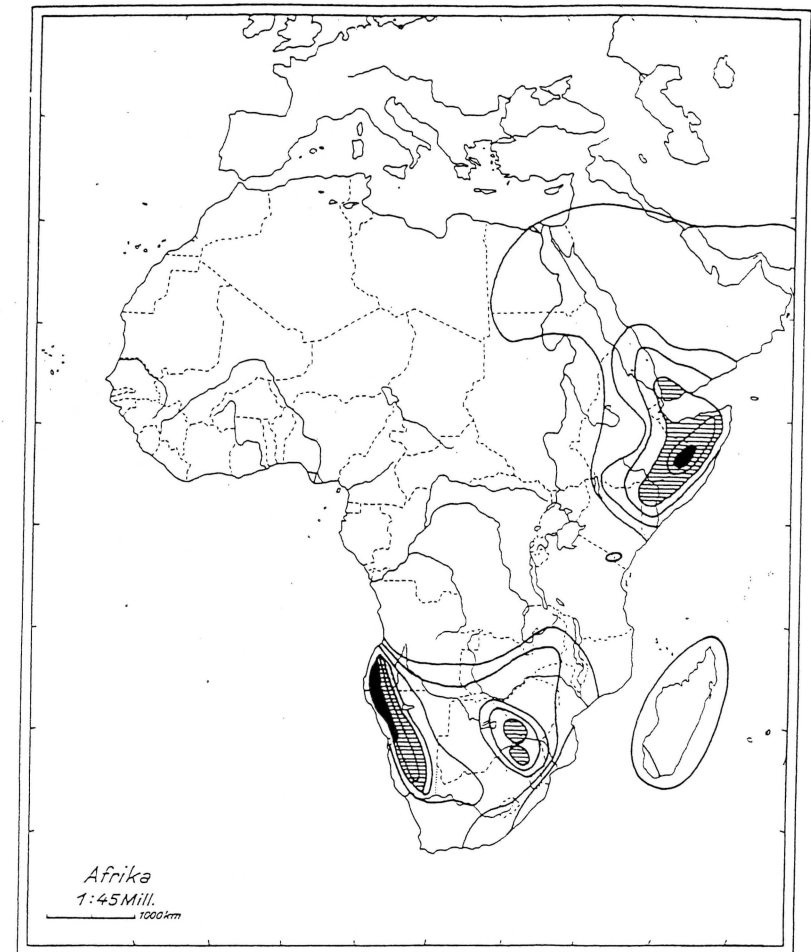
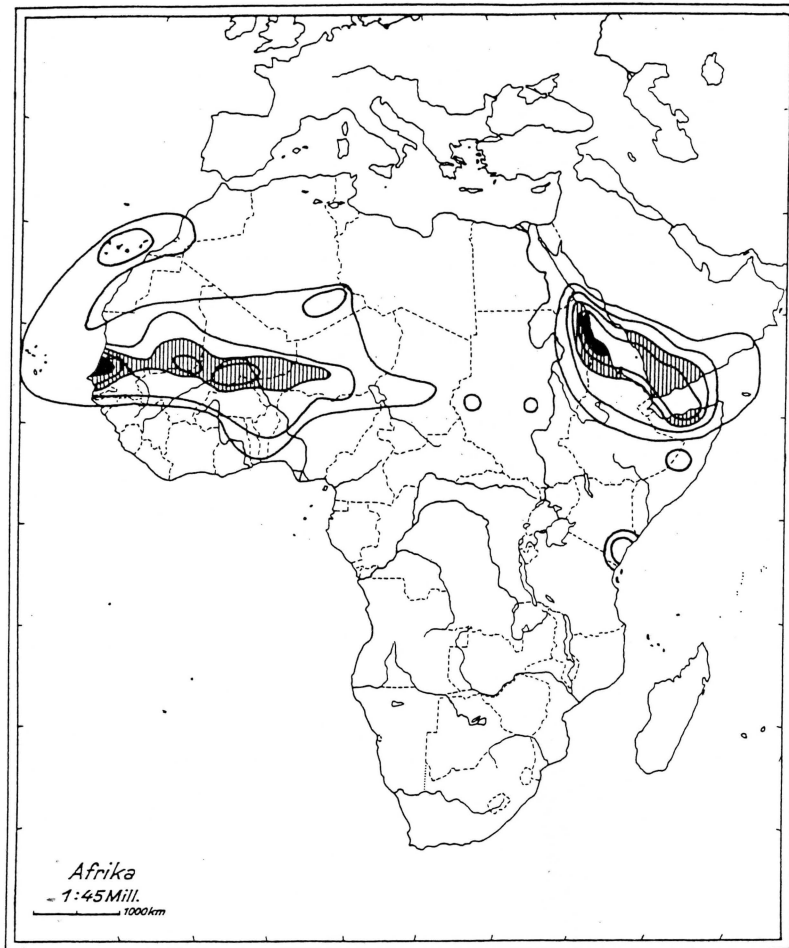
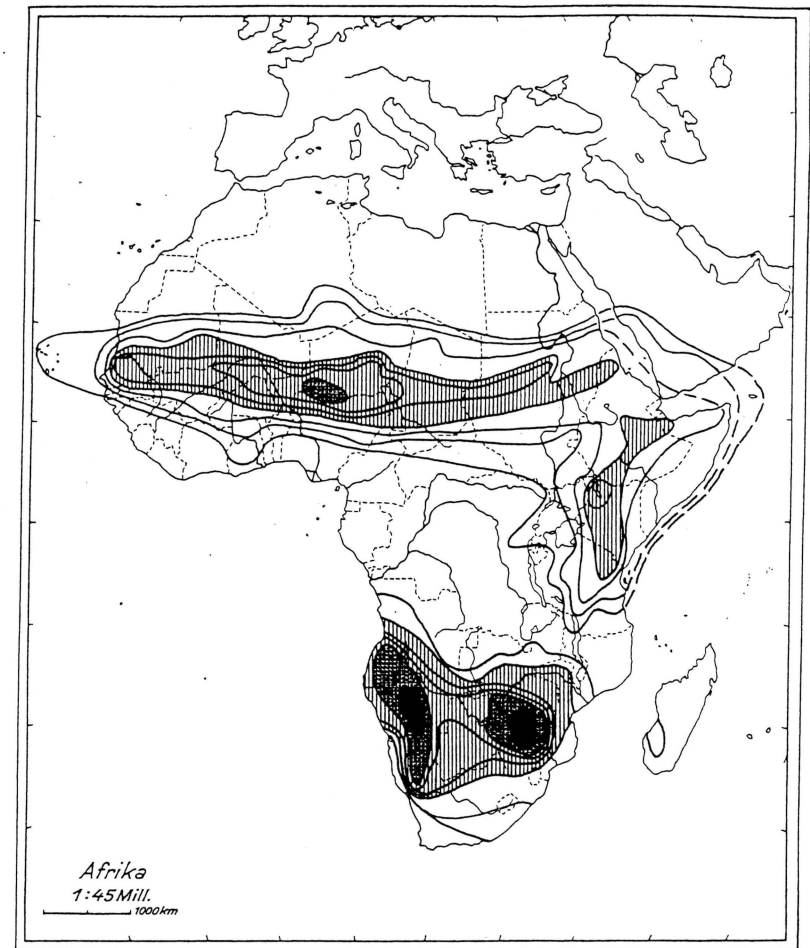


Figure 2. Disjunct type of distribution with one partial area in arid Northeastern Africa (N) and one partial area in arid Southwestern Africa (S) (11 taxa, black = >4 species present, horizontal lines = >4 species present, etc., outside line = 1 sp., further explanation in the text). Taxa included: *Cibirhiza dhofarensis* (N) and *C. albersiana* (S) (Asclepiadaceae) (Kunze, Meve and Liede, 1994), *Commicarpus mistus* (N) and *C. squarrosus* (S) (Nyctaginaceae) (Thulin, 1990), *Duvalia* sect. *Arabica* (N) and *D.* sect. *Duvalia* (S) (Asclepiadaceae) (Meve and Albers, 1990), *Endostemon tenuiflorus* (Lamiaceae) (Paton *et al.*, 1994), *Kissenia arabica* (N) and *K. capensis* (S) (Loasaceae) (Thulin, 1994), *Moringa* (Moringaceae) (Verdcourt, 1984), *Pterodiscus* (Pedaliaceae) (Ihlenfeldt, 1994a), *Sesamothamnus* (Pedaliaceae) (Ihlenfeldt, 1994a), *Thamnosma* (Rutaceae) (Thulin, 1994), *Tribulocarpus dimorphanthus* (Aizoaceae) (Verdcourt, 1957), *Wellstedtia* (Boraginaceae) (Thulin, 1994).



**Figure 3.** Disjunct type of distribution in the Southern Sahara, with one partial area in the Western part of the Southern Sahara, the other partial area in the Eastern part of the Southern Sahara (7 taxa, black = >4, upright lines = >2, etc., outside line = 1, further explanation in the text). Taxa included: *Campylanthus* (Scrophulariaceae) (Miller, 1980), *Caralluma acutangula* (Asclepiadaceae) (Thiede, 1994), *Caralluma adscendens* (Asclepiadaceae) (Thiede, 1994), *Caralluma edulis* (Asclepiadaceae) (Bruyns, 1989), *Euphorbia balsamifera* (Euphorbiaceae) (Bally, 1965), *Pachycymbium decaisneanum* (Asclepiadaceae) (Thiede, 1994), *Trichoneura mollis* (Poaceae) (Lebrun 1981).

Africa which are frequently inhabited by continental-disjunct arid taxa. Figure 2 includes a number of taxa with a disjunct distribution possessing one partial area in arid Southwestern Africa and one partial area in arid Northeastern Africa/Southwestern Arabia. Figure 3 shows taxa with a disjunct distribution in the Southern Sahara, one partial area in the Western part of the Southern Sahara, the other partial area in the Eastern part of



**Figure 4.** Disjunct type of distribution with one partial area in the arid regions of Southern Africa, the other partial area in the arid regions of Northern Africa (12 taxa, black = >7, dots = >6, upright lines = >3, outside line = 1, further explanation in the text). Taxa included: *Adenium* (Apocynaceae) (Plaizier, 1980), *Anticharis senegalensis* (Scrophulariaceae) (Lebrun, 1979), *Blumea gariepina* (Asteraceae) (Lebrun, 1981), *Cienfuegosia digitata* (Malvaceae) (Fryxell, 1967, after Lebrun, 1981), *Dicoma capensis* (Asteraceae) (Lebrun, 1981), *Endostemon* sect. *Oblongi* (Lamiaceae) (Paton *et al.*, 1994), *Gossypium anomalum* (Malvaceae) (Fryxell, 1967, after Lebrun, 1981), *Indigofera disjuncta* (Fabaceae) (Lebrun, 1981), *Monsonia angustifolia* (Geraniaceae) (Venter, 1979), *Monsonia senegalensis* (Geraniaceae) (Venter, 1979), *Rogeria adenophylla* (Pedaliaceae) (Ihlenfeldt, 1994a), *Sesamum* sect. *Sesamoides* (Pedaliaceae) (Ihlenfeldt, 1994a).

the Southern Sahara (some of these taxa also occur in India and Pakistan). Figure 4 includes a number of disjunct taxa with a more general North-South disjunct distribution, with one partial area in the arid regions of Southern Africa, the other partial area in the arid regions of Northern Africa. Species with such disjunctions were, as opposed to the disjunct genera, regarded by Thulin (1994) as either Pleistocene relicts or results of fairly recent long-distance dispersal. As shown on Figs 2 and 4, some taxa link the continental African with the Madagascan arid regions, e.g. *Moringa* (extending up to India; Verdcourt, 1984), the well-known *Adansonia* (also in Australia; Baum, 1995) or *Pachypodium* (restricted to Africa and Madagascar; Rowley, 1983). These three examples include only cases which have partial areas being separated by a large interval. The resulting additive patterns highlight those parts of Africa which form the (partial) centres of the continental disjunctions. While these centres in Figs 2 and 3 are also separated by large intervals between them, the patterns of Fig. 4 show the presence of partial areas in a nearly continuous distribution all around the bow of African savanna habitats. This observation leads to the general proposal that, in the past, there has been a continuous belt of arid habitats, forming a bow around the once smaller humid habitats, i.e. forest and more humid savanna biomes. For the interval between Southern and Eastern Africa, e.g. Engler (1921, p. 853) and Verdcourt (1969) similarly pointed out that even today a corridor of relatively arid climates is still linking the arid regions of Southern and Eastern Africa. In addition to this hypothesis, the patterns of Figs 2 to 4 support the hypothesis of a huge but fragmented arid belt reaching from the Namib Desert to the Western Sahara (including arid parts of the Cape Verde and Canary Islands) via Eastern Africa. In this context it is of interest that today a more or less uninterrupted vegetation belt still exists with respect to savanna type habitats, linked to the phytogeographical Sudano-Zambezian Region of the Palaeotropics. While areas of many taxa of this unit still form an uninterrupted bow around the present lowland rainforest region, many arid elements are fragmented into parts of this bow. The degree of fragmentation increases with the level of aridity the taxa are adapted to.

The fragmentation of the once-uninterrupted arid belt took place by development of certain intervals. These can be listed as:

- Tchad-Sudan gap (Fig. 3)
- Kalahari gap (Figs 2 and 4)
- Malawi gap (Fig. 4)
- Kenya-Malawi gap (Fig. 2)

These interruptions are situated in regions with continental climate (Tchad-Sudan gap in Fig. 3, Kalahari gap in Figs 2 and 4), in regions with higher humidity (Malawi gap in Fig. 4, Kenya-Malawi gap in Fig. 2), or in regions with peculiar soil conditions (the Kalahari gap in Figs 2 and 4 could be due to the deep sandy soils in the Kalahari region). This belt has not necessarily always been in its recent position, but might have been positioned somewhat closer to the actual lowland rainforest region during the past. For example, the important Southern African disjunction formed by the Kalahari gap could be due to a southward migration of an arid phytogeographical unit which was split up by the Kalahari sand habitat into a Western and an Eastern branch.

The whole pattern as presented in Figs 2 to 4 clearly indicates that the African continent has experienced many more arid times during history. Thulin (1994) proposed that

the more widespread disjunctions between Northern and Southern Africa may be due to recent events, while the more specific disjunctions of smaller areas between Southern Africa and the Horn of Africa are very old. This is in line with the general assumption that taxa such as *Moringa*, *Kissenia*, *Tribulocarpus* etc. are very old elements (few species per genus, widely spaced disjunct areas, occurrence in other continents). However, there is as yet no evidence confirming repetitive formation of these arid North-South disjunctions. Future research will require a more thorough look at all existing disjunct patterns of the various ecological groups, levels of taxonomic distance of the taxa involved, and present knowledge about their phylogeny, to establish a solid basis for the interpretation of the past on the basis of phytogeography. For Southern Africa, more detailed analysis is already available.

#### SOUTHERN AFRICAN PATTERNS

##### *Phytogeographical subdivision*

The analysis of the arid regions of Southern Africa is of particular interest because the arid flora is taxonomically extremely rich (Court, 1981; van Jaarsveld, 1987; Cowling *et al.* 1989; Smith *et al.*, 1993) and shows high geographical regularity. Some of these regularities have been analysed only during the last 10 years. While the arid regions of Namib and Karoo have been understood as a separate phytogeographical region (Karoo-Namib Region) of the Palaeotropical Floral Kingdom by all authors including Werger (1978), this relationship has been questioned more and more in recent publications. Bayer (1984) was first to point out that some relationships exist between the Karoo and Cape Flora. Moll *et al.* (1984a, b) also recognize that there is a discrepancy between the phytogeographical position of the Karoo as part of the Palaeotropics and the winter rainfall ecology of some of the taxa of the Karoo, linking the Karoo to the winter rainfall Cape region. Gibbs Russell (1987) compared parts of the most important biomes of Southern Africa with numerical methods and found that the Succulent Karoo is more related to the Cape Flora and that the Nama Karoo is more similar to the Sudano-Zambezian Region of the Palaeotropics. Jürgens (1991) analysed the similarities and dissimilarities of ca 3000 areas of distribution of taxa of Namib and Karoo and came to the result that the concept of a palaeotropical Karoo-Namib Region (Werger, 1978) is untenable. In contrast: the most important floristic discontinuity of Southern Africa, dividing the temperate Cape Flora from the Palaeotropical Flora, runs right through the middle of Karoo and Namib. Therefore it is proposed to recognize the Floristic Kingdom of the Greater Cape Flora, including at least two partial areas, the Cape Floristic Region and the Succulent Karoo Region. In the summer rainfall part of Namib and Karoo, the Nama-Karoo Region and the Sudano-Zambezian Region both form subunits of the Palaeotropical Plant Kingdom (Fig. 5).

##### *Phytogeographical fragmentation of higher taxa*

A first look at the centres of diversity of important higher taxa of the Southern African region seems not to be in line with the above mentioned phytogeographical subdivision, shown in Fig. 5. For example, the family Mesembryanthemaceae (Fig. 6) is not limited to either the Nama-Karoo (Palaeotropics) or the Succulent Karoo (Greater Cape Flora). However, on infrafamilial level, groups of genera clearly form part of either Nama Karoo or Succulent Karoo (e.g. *Mitrophyllum* group in the winter rainfall Succulent Karoo Region, Fig. 7; *Titanopsis* group in the summer rainfall Nama Karoo region, Fig. 8). This

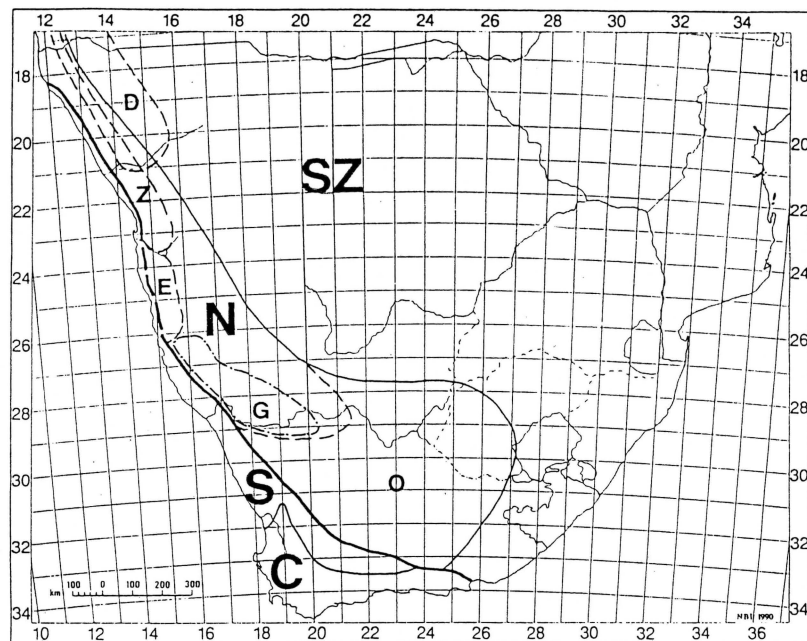


Figure 5. Phytogeographical subdivision of the arid regions of Southern Africa (from Jürgens, 1991, modified). C and S = Greater Cape Flora, N and SZ = Palaeotropical Flora; C = Cape Floristic Region, S = Succulent Karoo region, N = Nama Karoo Region, SZ = Sudano-Zambeian Region. O = Upper Karoo, G = East Gariep Centre, E = Namib Dunefield, Z = Central and Northern Namib Desert, D = Kaokoland-Damaraland Centre.

is not an isolated observation but a pattern found repeatedly in a number of taxa, all being of high importance in the Succulent Karoo. Other examples are *Crassula* (Fig. 9, Jürgens, 1995), fragmented on section level into e.g. section *Squamulosae* (Fig. 10) in the winter rainfall region and e.g. section *Deltoideae* in the summer rainfall region (Fig. 11), or the genus *Zygophyllum* distributed in both Nama-Karoo and Succulent-Karoo (Fig. 12), but clearly separable into two species groups in either region with mutually largely exclusive distribution patterns.

Considering the high importance of vicariant speciation processes, this regular pattern would have to be interpreted as a sequence: the distribution patterns of the higher taxonomic level (family in the example Mesembryanthemaceae) are considered to be older than the ecological reason (or event) responsible for the fragmentation into Nama-Karoo Region and Succulent Karoo Region. This observation is in line with proposed hypotheses on the phylogeny of arid taxa. For example, Gerbault (1992a, b), in an analysis of *Anacampseros* (Portulacaceae) linked the phylogenetical pattern to the recent areas of distribution of the taxa by cladistic biogeography (sensu Humphries *et al.*, 1988). Her results support a sequence of phytogeographical fragmentation as follows: The first step of differentiation was dividing an ancestor group into (1.) a tropical and (2.) a temperate

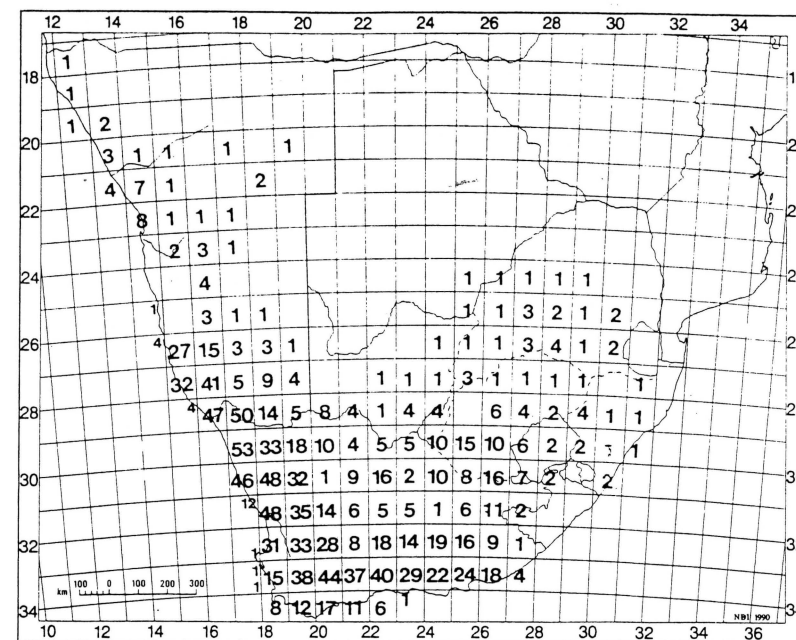


Figure 6. Centre of diversity (number of genera or subgenera per degree square) of Mesembryanthemaceae.

subgroup. The second step led to a separation of (1.1.; 2.1.) arid and (1.2.; 2.2.) humid subgroups in both groups. The last step is the differentiation into summer and winter rainfall seasonality (Fig. 13). This example should not be overinterpreted, because cladistic biogeography excludes the effects of long distance dispersal and many existing speciation processes. However, such results should be used as a working hypothesis which in the future can be tested and developed further. In any case, the sequence of ecological differentiation of *Anacampseros* and other arid adapted taxa during phylogenetical and ecological history of the subcontinent is in line with the results of other palaeosciences, also interpreting the formation of the winter rainfall climate as being a relatively young ecological event, not older than 4 to 5 million years. Obviously, this recent ecological innovation resulted in enormous speciation.

#### *Refuge areas and other patterns which can be interpreted as effects of the last glaciation*

Besides the very regular patterns of Succulent Karoo and Nama Karoo, discussed above, Southern Africa shows some irregular patterns as well. For example, there are a very large number of taxa, concentrated to the Cape Floristic Region of the Greater Cape Flora, which, in addition, occur in a more or less wide portion of Succulent Karoo, Nama Karoo, or even Sudano-Zambeian Region. The northern extension of these widespread taxa of Cape or Succulent Karoo affinity is not random, but concentrated to two lines along the escarpment of the West and South Coast (Fig. 14). In these two regions mountainous

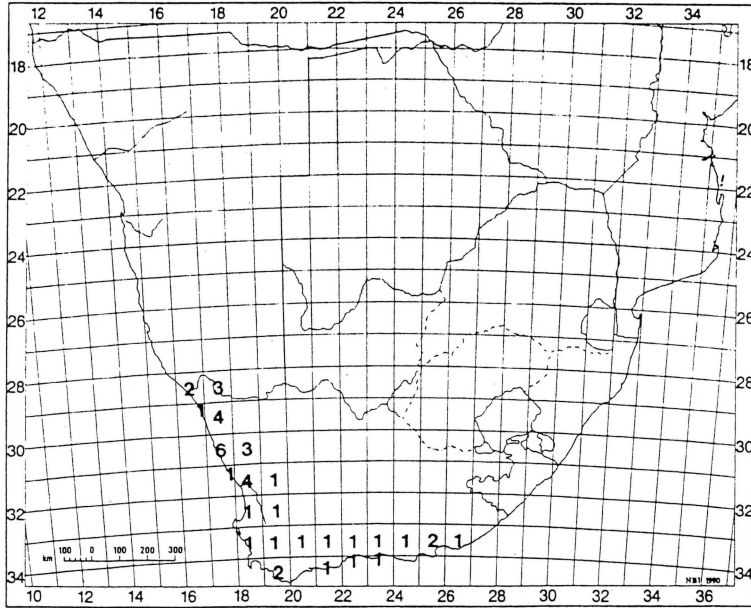


Figure 7. Centre of diversity (number of genera or subgenera per degree square) of the *Mitrophyllum* group (Mesembryanthemaceae) as defined by Hartmann (1991).

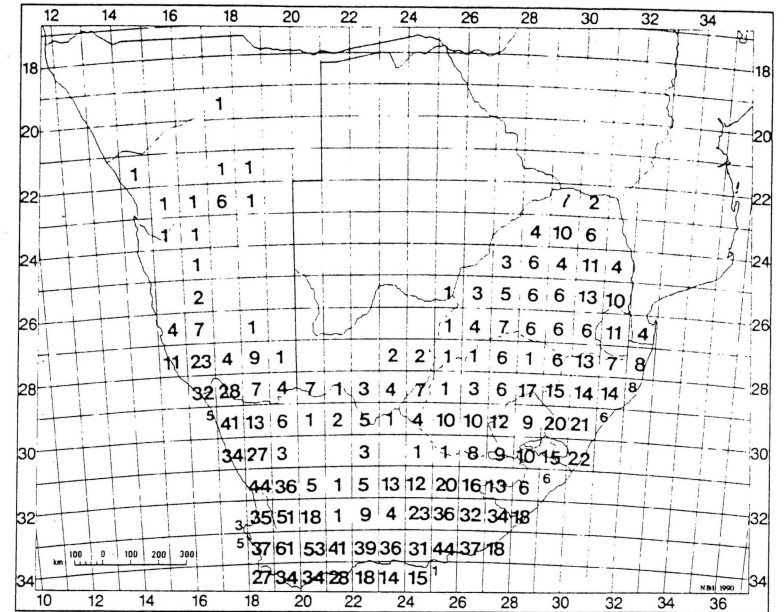


Figure 9. Centre of diversity (number of species per degree square) of the genus *Crassula* (Crassulaceae).

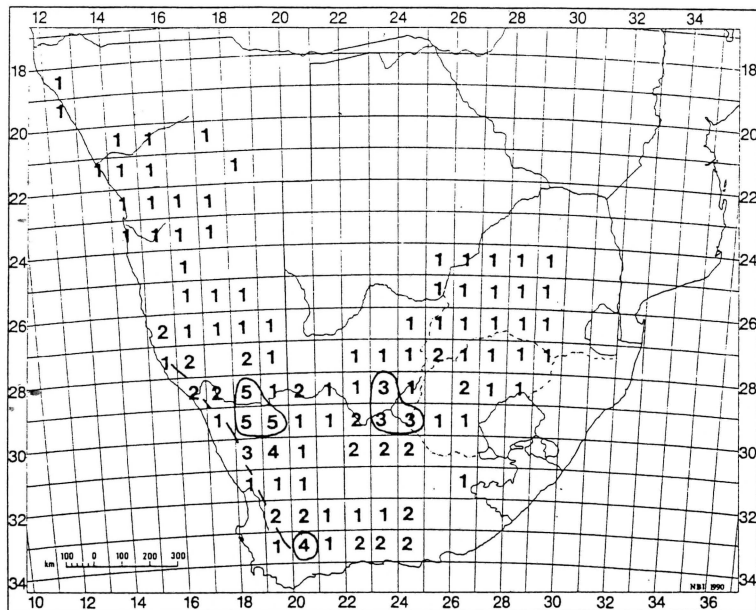


Figure 8. Centre of diversity (number of genera or subgenera per degree square) of the *Titanopsis* group (Mesembryanthemaceae) as defined by Hartmann (1991).

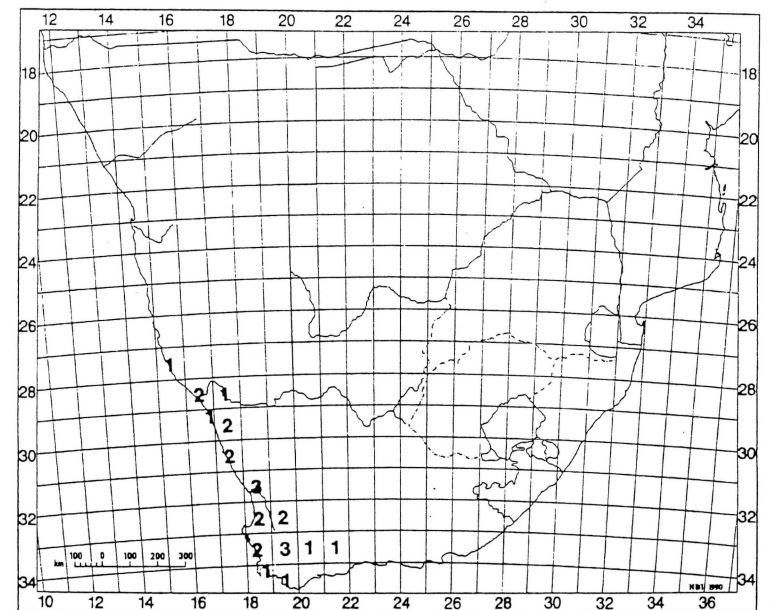


Figure 10. Centre of diversity (number of species per degree square) of *Crassula* sect. *Squamulosae* (Crassulaceae).

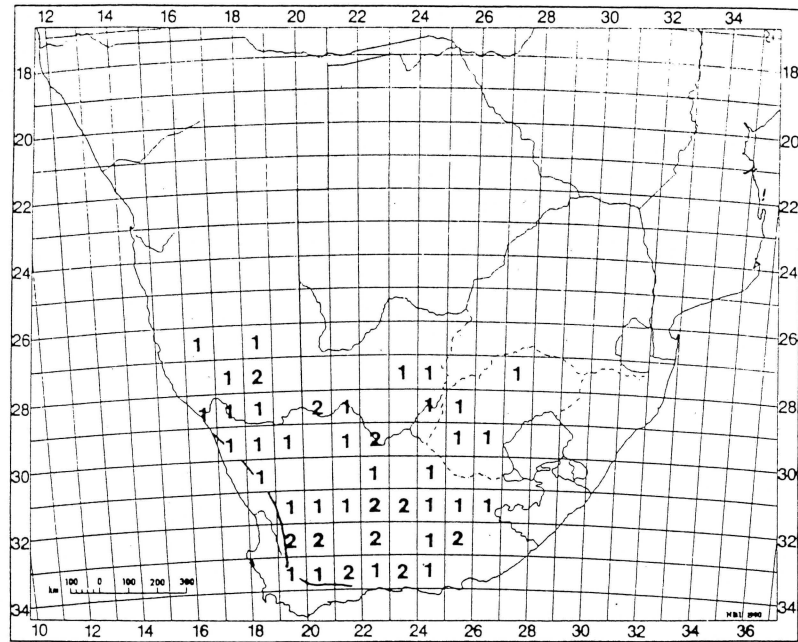


Figure 11. Centre of diversity (number of species per degree square) of *Crassula* sect. *Deltoideae* (Crassulaceae).

topography provides numerous habitat types suitable for survival of temperate taxa. It is not possible to provide absolute evidence that these patterns are, partly, relicts of the past as proposed by Werger (1983) rather than new populations created by long distance dispersal (the latter interpretation more probable in some taxa as e.g. species of *Crassula* possessing very small anemochorous seeds). However, the large distance between isolated populations (especially along the West coast, e.g. *Tylecodon* occurring near Windhoek) and the Cape suggests a relictual nature. Furthermore, isolated inselbergs in the Great Dune field of the Namib desert do not house a flora similar to the mainland at the same latitude, but an ancient flora with survival of numerous taxa of isolated geographical position compared to their main area of distribution (Burke *et al.*, in press).

Even more interesting is a disjunct pattern found in the Nama Karoo Region. This unit has a very important centre of distribution in the region along the Lower Orange River Valley, but east of the winter rainfall region, the East Gariiep Centre (Fig. 5; Jürgens, 1991). Numerous taxa of this unit have a disjunct distribution with a second partial area either in Central and Northern Namib (Fig. 15), or, in the Southern Cape (Fig. 16). While the gap between East Gariiep Centre and Central Namib could be interpreted by close proximity of the two dune fields (Fig. 17) of Namib and Kalahari, there is no such dune field in between the East Gariiep Centre and the Southern Cape. However, the pattern of coolest temperature in the winter months clearly separates the three partial areas of this interesting pattern of disjunction (Fig. 18). These warmer lowland pockets could have

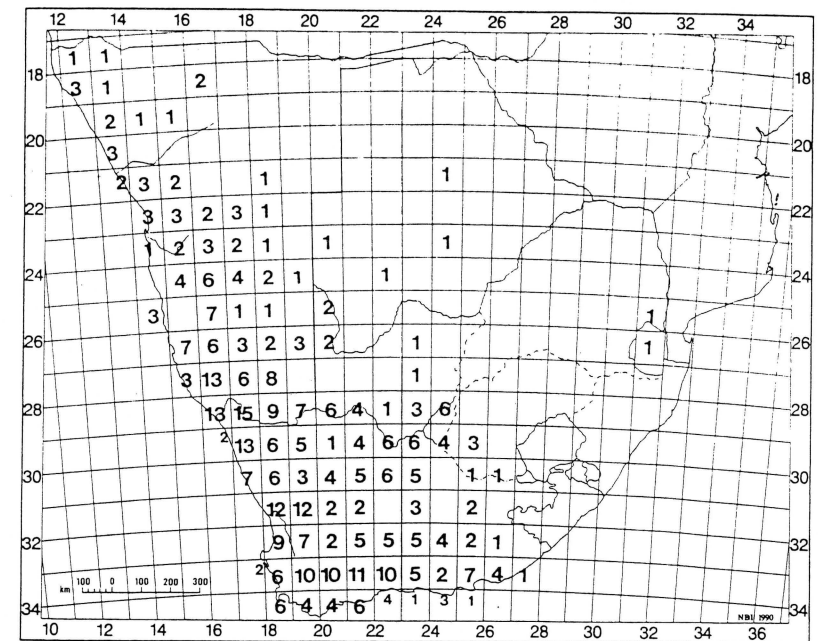


Figure 12. Centre of diversity (number of species per degree square) of *Zygophyllum* (Zygophyllaceae). At the species level, the genus is fragmented into a winter rainfall group well separated from species of the summer rainfall group.

been the only existing areas where the tropical arid taxa of the Nama Karoo could survive during the last glaciation, ca 18 000 years ago. Survival in relatively small refuge areas would also explain some patterns of the Succulent Karoo, e.g. the concentration of numerous peculiar taxa in some centres of endemism like the Knersvlakte and parts of the Little Karoo. Isolation in refuge areas might have been expressed stronger in the past: centres of evolution of convergent life and growth form series represented by different genera of Mesembryanthemaceae in ecologically similar soil catenas of Knersvlakte and

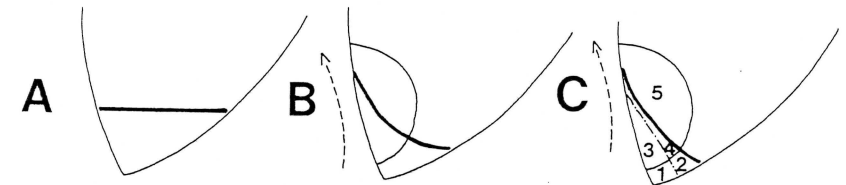
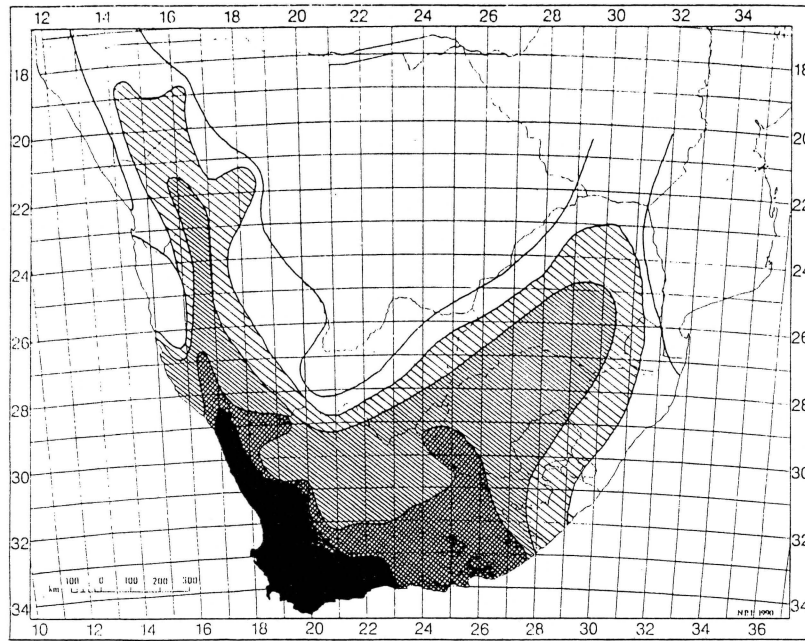


Figure 13. Schematic illustration of one possible hypothesis of the fragmentation of parts of the flora of Southern Africa. Thick line = limitation between tropical and temperate region; arrow = formation of Benguela current; thin line = limitation of arid region; dotted line = limitation between winter rainfall and summer rainfall region (further explanation in the text).



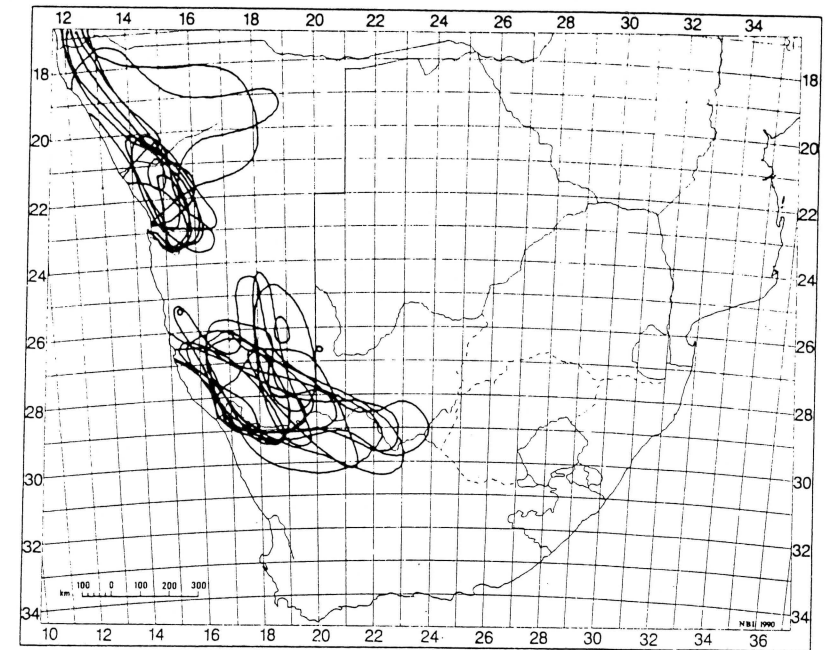
**Figure 14.** Rough illustration of the joint area of a number of taxa linking the Cape Floristic Region to a wider area along the highlands in Northwestern and Northeastern direction, including 18 species: *Adiantum capillus-veneris*, *Bulbine frutescens*, *Cheilanthes capensis*, *Chrysocoma ciliata*, *Cotyledon*, *Crassula*, *Delosperma*, *Ehrhardta calycina*, *Felicia filifolia*, *Frankenia pulverulenta*, *Gazania krebsiana*, *Hermannia cuneifolia*, *Helichrysum asperum*, *Hypertelis salsoloides*, *Ifloga verticillata*, *Oncosiphon piluliferum*, *Othonna*, *Sutherlandia frutescens*. Black = 100%, squares = >ca 80%, dense stripes = >ca 50%, wide stripes = >ca 10%.

Little Karoo (Jürgens, 1986) are today more or less linked by continuous presence of Succulent Karoo.

#### Recent migrations

It is an open question whether in the Namib region migration of arid taxa and/or desertification processes take place today. Acocks (1953) reported strong desertification in the eastern Karoo. However, Hoffman and Cowling (1990) and Hoffman (1991) present evidence that there is no strong process of desertification. While desert growth is generally accepted for the Sahara, palaeosciences do not report an expansion of the Namib desert during the last decennia or millenia.

However, at least two plant species with very long lifespans provide hints that the Namib Desert might also be growing. *Aloe dichotoma* possesses populations with normal demographic structure (some dead and old individuals, large number of younger adults and young plants) along the eastern margin of its area (e.g. near Pofadder), while populations in the more arid western margin (e.g. Northeastern Richtersveld) show very few young individuals or even no establishment of young plants at all. In these cases, young plants

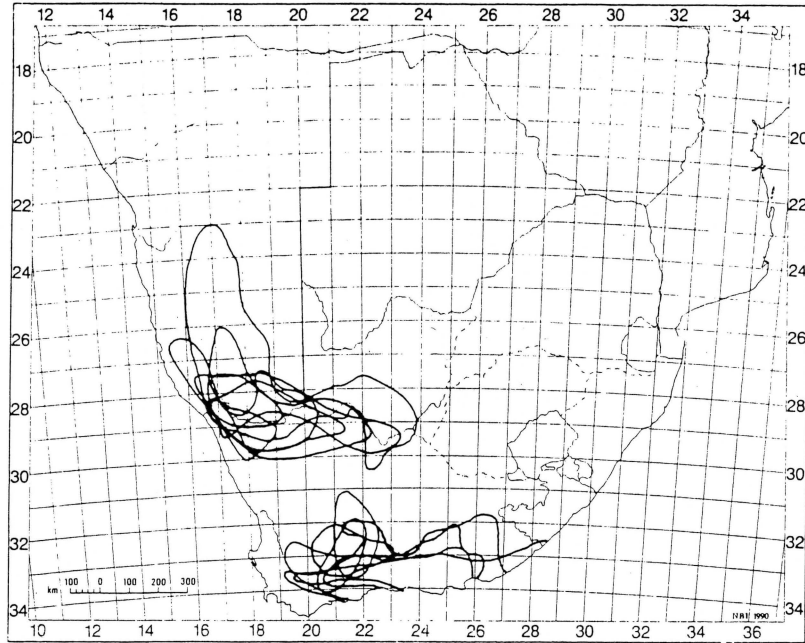


**Figure 15.** Disjunct distribution between East Gariiep District and Central Namib Desert, including: *Asclepias buchenaviana*, *Aristida parvula*, *Commiphora namaensis*, *Euphorbia gariepina*, *Heliotropium tubulosum*, *Indigofera argyroides*, *Indigofera disjuncta* var. *disjuncta*, *Rogeria longiflora*, *Stipagrostis hochstetteriana* var. *secalina*, *Sutera maxii*, *Tetragonia reduplicata*, similar vicariant species: *Euphorbia gregaria* versus *E. damarana*, *Helichrysum gariepinum* versus *H. roseo-niveum*. Similar: *Antheophora ramosa*, *Cheilanthes dinteri*, *Euphorbia avasmontana*, *Monechma genistifolium*.

are only found in nearby sites with additional water supply as e.g. by runoff from rocky surfaces, a clear indication of an aridification of the climate. Still further westwards, i.e. in even more arid climate, large populations of dead plants of *Aloe dichotoma* can be found (e.g. east of the Tsaukeib mountains), while living plants are missing completely.

In a similar way, different populations of the monotypic gymnosperm *Welwitschia mirabilis* show a remarkable difference in the demographic structure of different populations: In the proper Namib desert establishment of young plants is extremely rare or completely absent, only populations in sparse savanna much further inland in a more humid region show a normal demographic structure with numerous young plants. This is best expressed in the South Angolan inland, where *Welwitschia* occurs at a rainfall of 250–350 mm in millions of healthy individuals evenly distributed over the grassy plains (indicating independence from underground water) or even occurring in continuous dappled shade in thick scrub (Whellan, 1965). Therefore, the hypothesis has been proposed (Jürgens, 1992) that the old desert *Welwitschia* are relict populations established long ago. This hypothesis is supported by the observation that young *Welwitschia* rapidly form a cork layer around the stem, giving protection against the frequent fires of a savanna habitat





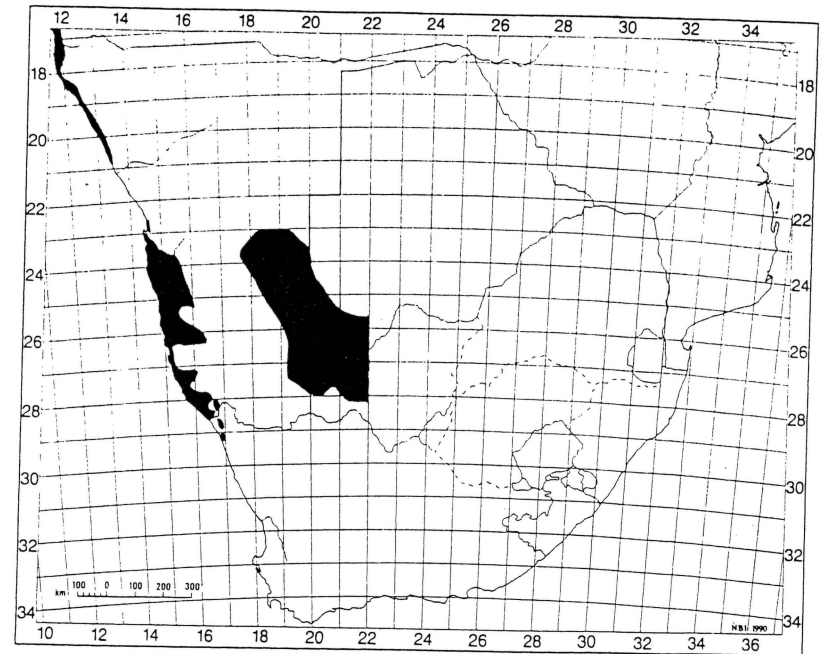
**Figure 16.** Disjunct distribution between East Gariep District and Southern Karoo, including: *Acanthopsis disperma*, *Anacampseros papyracea*, *Carissa haematocarpa*, *Menodora juncea*, *Nymania capensis*, *Pelargonium* sect. *Glaucophyllum*, *Schotia afra*. Similar: *Berkheya spinosissima*, *Chasmatophyllum*, *Crassula corallina* ssp. *corallina*, *Crassula exilis*, *Felicia hirsuta*, *Mestoklema*, *Microloma armatum*, *Trichodiadema*.

(van Jaarsveld, 1990). Another supporting finding is the transpiration rate at the southern (arid) margin of the distribution area deeply fragmented into a number of genetically isolated populations in river valley systems (Kuisseb, Swakop): here, the phreatophyte *Welwitschia mirabilis* with its deep tap root transpires 1 litre of water per m<sup>2</sup> leaf surface area (von Willert *et al.*, 1991; von Willert and Wagner-Douglas, 1994), unusually high for desert plants. It is expected that future research will bring to light further evidence for a relatively recent expansion of the Namib Desert.

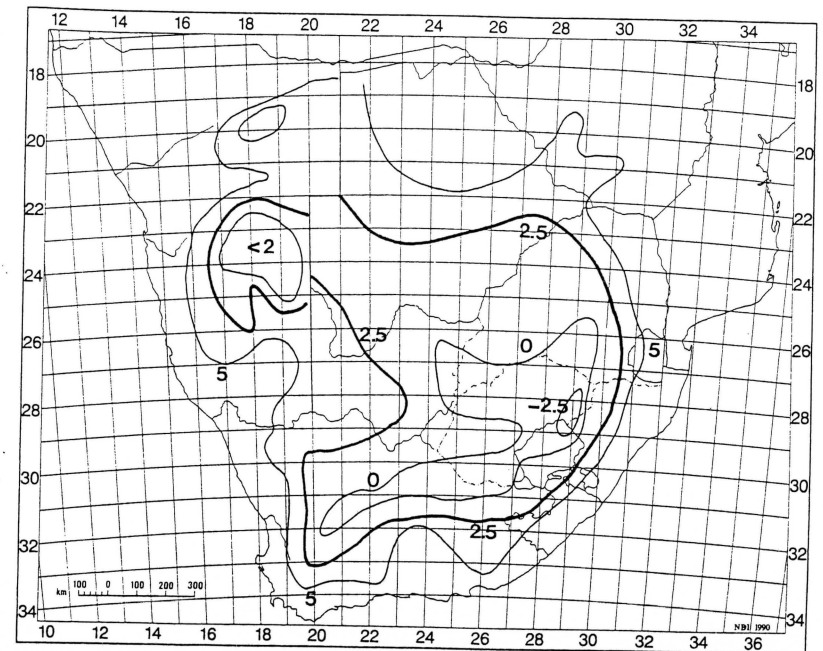
**Discussion: Stability and biodiversity in African arid regions**

Compared to the species-poor Sahara Desert, the arid regions of the Mandeb-Circle (Somalia, Ethiopia, Yemen), the Southern African Nama Karoo and especially the Succulent Karoo (Hilton-Taylor, 1994) show high to extremely high biodiversity. With respect to the Succulent Karoo this is interpreted as a result of the formation of a temperate winter rainfall regime not more than 5 Mio years ago, an event, which, interacting with the varied topography, led to intensive speciation, e.g. in Mesembryanthemaceae

**Figure 18.** Mean minima of temperature in July (South Africa) or in the coolest winter month (Namibia), respectively.



**Figure 17.** Position of major dunefields of Namib Desert and Kalahari.



(Ihlenfeldt, 1994b). With respect to the Mandeb Circle and to the Nama Karoo it is not yet possible to establish the relative quantity of contribution of younger speciation versus survival of old taxa. However, the high frequency of genera with very few species of isolated and limited distribution such as e.g. *Welwitschia*, *Moringa*, *Tribulocarpus*, *Wellstedtia* and *Sesamothamnus* makes it obvious that survival of old elements plays an important role in contributing to the biodiversity of arid summer rainfall regions. This statement is true especially with respect to tropical rocky habitats, e.g. in mountainous regions. In contrast, regions with zonal habitats (in the sense of Walter and Breckle, 1991: 130 ff.), e.g. deep sandy substrates in the Kalahari, are relatively poor in species diversity and in, probably, old disjunct taxa. This may be due to a greater role of competition in relatively uniform zonal habitats. Compared to these, rocky habitats do not only provide a higher ecological diversity, but, at the same time, they perpetuate the presence of arid conditions even during more humid periods, because they form edaphically arid sites. This also contributes to the explanation of the fact that the centres of disjunct patterns in Figs 2 to 4 are not situated in the extremely arid regions, but in the arid savanna biome.

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