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Dedicated to Prof. Dr. GÜNTHER NATHO
on the occasion of his 65th birthday

Psammophorous plants and other adaptations to desert ecosystems with high incidence of sandstorms

With 2 Colour Plates

Abstract

Sandstroms are an important climatic phenomenon of many deserts, causing major ecological problems for plant life. A number of features observed in desert plants allow survival under certain ecological constraints caused by wind-blown sand and related phenomena.

In this context, a peculiar adaptation to desert conditions, the "psammophorous" plants, are of special interest. Hitherto under-rated, many plant species possess specialized structures, enabling them to fix a protective layer of sand grains on parts of their surface. An analysis of the distribution, ecology, and structural peculiarities of psammophorous plants in the Namib and Karoo is presented.

It is proposed that strongly developed psammophory primarily has evolved as an adaptation to habitats which experience a high impact from wind blown sand, while the phenomenon in less well developed cases might be of relevance for the plant water budget, thermal energy balance, serve as protection against herbivores or have a mimetic function.

Zusammenfassung

Sandstürme stellen in nicht wenigen Wüstengebieten ein häufig auftretendes Ereignis dar. Sie bringen eine Vielzahl z. T. schwerwiegender ökologischer Probleme für pflanzliches Überleben in diesen Gebieten mit sich. Bei entsprechend belasteten Wüstenpflanzen kann ein breites Spektrum von strukturellen und phänologischen Merkmalen beobachtet werden, die das Überleben unter den ökologischen Zwängen, die durch windbewegten Sand und verwandte Phänomene verursacht werden, erlauben.

In diesem Zusammenhang sind die ,,psammophoren" Pflanzen, die hochspezielle Anpassungen an Wüstenbedingungen aufweisen, von besonderem Interesse. Es handelt sich hier um Pflanzenarten, die spezialisierte Strukturen für die Anheftung einer Schutzschicht aus Sand an Teilen ihrer Oberfläche besitzen. Es wird eine Analyse der Verbreitung, Ökologie und strukturellen Anpassungen psammophorer Pflanzen in der Namib und der Karoo vorgestellt.

Ausgeprägt entwickelte Psammophorie wird hier vor allem als eine Anpassung an stark sandstrahlbelastete Wüstenstandorte interpretiert, wohingegen das Phänomen bei weniger deutlicher Ausprägung auch für den Wasserhaushalt und die Energiebilanz der Pflanzen von funktionell-ökologischer Relevanz sein könnte. Weiterhin ist in zahlreichen Fällen die Annahme einer mimetischen Funktion bzw. eine Bedeutung als Fraßschutz gegen Herbivore naheliegend.

1. Introduction – the impact of sandstorms

In open desert landscapes as well as in coastal habitats high wind speeds frequently cause high transport rates of soil particles, including larger grain fractions such as sand and, sometimes, even smaller stones. The resulting particle stream involves a number of ecological effects, many of which cause major problems for desert organisms, especially for plants:

a) Plants can be burried under wind-blown sand.
b) Roots of plants can be exposed when aeolian erosion removes soil material.
c) Plants suffer from higher transpiration losses caused by high wind speed.
d) Plants get mechanically wounded by the sand-blasting effect.

Resulting features such as e.g. the predominance of grasses in dunefields and the formation of specific growth forms of wind-pruned plants are well known and have been mentioned already in early literature (e.g. WARMING & GRAEBNER 1918). A younger review of plant adaptations to sandy coastal and desert dune habitats is provided by DANIN 1991.

In contrast, the direct effects caused by high incidence of heavy sand-blasting and special morphological adaptations sheltering against the abrasive forces of sand-blasting have not been discussed hitherto. DANIN 1991 reports the observation of a layer of sand on some plants of sandy habitats, but does not follow up this phenomenon.

Apparently, adaptations to sandstorms are not evenly distributed in all deserts of the world. The Southern Namib Desert of Namibia and the South African Cape Province provide optimal conditions to study both, the impact of sandstorms and those structural and phenological features of plants which can be interpreted as an adaptive response to high incidence of sandstorms:

a) A steep temperature gradient between the cool coastal air (upwelling Benguela current) and the hot hinterland results in frequent high-speed air movements (LANCASTER 1990; LINDESAY & TYSON 1990).
b) Large amounts of sand and silt are generated by two important sources: The Orange River and the sandy beaches of the Atlantic Ocean (LANCASTER 1990).
c) Untypical for deserts, in the Southern Namib Desert high air humidity, low temperatures, and high incidence of fog support a rich vegetation in habitats, which, owing to extremely low rainfall, show extreme geographical desert features including the formation of dunes and the high ecological importance of sand-blasting (spatial combination of physical desert and biotic semi-desert).
d) The old age of the above described conditions in the Namib region (WARD et al. 1983; WARD & CORBETT 1990) provided sufficient time for the evolution of adaptations to sand-blasting.

This rare combination of factors provides good conditions to study the influence of sand-blasting on plants.

2. Material and methods

In course of a detailed mapping project of the flora and vegetation of the Namib region, numerous examples and localities of psammophorous plants have been recorded. Distribution data and habitat information from own field work was supplemented with information gained from literature and herbaria. Observations on permanent plots during a period of 15 years (1980 to 1994) and including all seasons allowed a better understanding of the dynamic aspects of psammophorous plants and sand cover.

In chapter 5.2 an alphabetical list of families with psammophorous plants (including author names) is given. For other species names the authorship is provided when the name is first mentioned. Specimens of our field work are housed in BTU, HBG, KOELN, NBG, WIND.

3. Sandstorms in the Namib Desert

In the coastal Namib desert steep climatic gradients exist between the cool and moist oceanic air in contact with the upwelling Benguela current, and the hot desert plains further inland (LANCASTER 1990; LINDESAY & TYSON 1990; JÜRGENS et al. 1996). The steep gradient in temperature and the conflict between trade winds (from the east) and coastal winds (out of southern or southwestern direction) frequently cause extremely high wind speeds out of southern direction, reaching highest velocity in the hours of early afternoon.

Highest wind speeds are observed in the coastal parts of the Southern Namib between Lüderitz and Alexanderbay, reaching some 20 to 30 km inland (LANCASTER 1990). In this region the storm frequently transports large amounts of mineral soil particles, including coarser fractions like sand, pebbles, and even small stones. The material is generated mainly from the mouth of the Orange River and from along the sandy beaches of the Atlantic Ocean.

3.1 Dunes

One part of this mass transport takes place by means of barchan dunes (BESLER 1980), which, according to employees of Consolidated Diamond Mines (CDM) in the Southern Namib sometimes move 16 m per day, summing up to about 100 m per month. Barchans do not move everywhere, but merely follow certain streets or wind channels of limited width. Due to the high speed of the dunes, these streets normally are devoid of any perennial plant life, while in their vicinity plains without barchans are well vegetated.

The mobile barchans themselves do not carry perennial vegetation. However, other landscape units of the dunefields allow the existence of a limited number of plant species (SEELY 1990, 1991), mainly grasses and annuals, owing to less strong sand movement. However, the vegetation of dunes lies outside the focus of this article.

3.2. Habitats with strong sand-blasting

Another part of the mass transport concerns rocky or stony areas. Here the particle stream (jumping sand grains) moves quicker, because the sand grains are reflected by the rock surface (CHEPIL 1945; BESLER 1975, 1980).

Consequently no sand is deposited but a sand flow passes the area with high speed, involving considerable destructive energy. It is painfull for men to walk in such an area. Locality names such as "Hexenkessel" refer to the extreme conditions the early diamond prospectors in the Southern Namib had to suffer. Even rock is polished and streamlined by the permanent sand-blasting. Fig. 1 shows a streamlined black dolomite yardang near Grillental. The surface and shape of the rock has been formed according to the force of sand-blasting controlled by micro-wind-channels and by the distribution of harder quartz veines which protect the softer dolomite in their wind shadow. In the region near Grillental and Pomona sand-blasting results in an aerodynamic landscape, including large yardangs of many tenths of meters length. It is possible that the large surface diamonds of the Pomona region have been enriched and sorted by these extreme sandstorms, forming the residual when all softer stones are destroyed (and smaller stones blown away) by sand-blasting (pers. comm. CDM geologist JOHN WARD). Similar effects of sand-blasting can be observed in many inselbergs in the dunefields (e.g. Uri-Hauchab).

The impact caused by sand-blasting is correlated with altitude. Higher mountains are not affected by the sand-blasting. Similarly, on a scale of decimeters, there is a decreasing gradient of impact with increasing distance to the soil surface.

4. Adaptions of plants in sandstorm areas: a descriptive list and a first approach

Strong sand-blasting is lethal to most plant species. This could be documented several times by means of permanent observation plots in the Richtersveld. Example given a releve in the Annisvlakte near Kuboes was covered by numerous species including the perennial *Brownanthus schlichtianus* (SONDER) IHLENF. & BITTRICH (Mesembryanthemaceae). After strong sandstorms (east wind) in August/September 1994 all vegetation was killed and the plot was covered by microdunes formed by small stones (!). No surviving perennials could be documented in the vicinity with the single exception of a few plants of *Euphorbia gummifera* BOISS. which were heavily damaged on those parts exposed to the east wind (Fig. 8).

In spite of all these lethal effects, most of the sand-affected habitats of the Southern Namib carry perennial plant life because the joint effect of high air humidity, frequent fog events, mild temperature, and ephemeral rainfall provides sufficient humidity for plant life, in spite of the extreme physical desert conditions.

Vegetation is somewhat concentrated to safe sites in the wind shadow of rocks, but outside the safe sites, even in extremely exposed positions (e.g. on yardangs) perennial plants are found. Obviously these plants possess some adaptations enabling them to survive the impact of sandstorms.

In the following paragraphs 5 to 8 a number of structural and phenological peculiarities of these plants shall be described and interpreted and at least one example for each structure shall be named. Nearly all examples for the following enumeration have been observed in extreme sand-blasting-habitats of the Namib desert. Evidently, this does not necessarily imply that the described features form structural adaptations or survival strategies evolved *exlusively* for survival in sand-blasting environments. Some of them obviously can be interpreted as protective structures of more general functional importance, being successful in various environments.

5. Survival means of biogenic protective structures (tissues produced by the plant itself)

Specialized surface structures protect the plant at the periphery of its various organs.

5.1. Stem

A number of plant species has developed protective tissues at the stem surface, allowing survival of the stem after sandstorms, though leaves are more frequently destroyed in this group. Good examples are provided by Geraniaceae.

5.1.1. Bark

Pelargonium mirabile DINTER (= *Pelargonium crassicaule* L'HÉRIT.) looses leaves and flowers during sandstormes, while the stem is protected by the dark bark (Fig. 3 and 4).

5.1.2. Wax layers

Species of *Sarcocaulon* (bushman candle; Geraniaceae) are well known because of their stems possessing a thick wax layer. This wax layer has previously been interpreted as protective tissue against transpiration losses (von WILLERT et al. 1991) but it additionally also serves for survival in sand-blasting environments, e.g. in *Sarcocaulon patersonii* (DC.) G. DON f. (Fig. 5).

5.1.3 Thickened outer cell walls of epidermal cells

Arthraerua leubnitziae (KUNTZE) SCHINZ (Fig. 17; Amaranthaceae) provides a good example, although occurring exclusively in the Central and Northern Namib. The stems of the plants often suffer from sandstorms out of easterly directions. Cross sections (SEM) do not only show the position of the stomata at the basis of deep longitudinal foldings (pers. comm. K. LORIS, Stuttgart), but also reveal an extraordinary thick outer cell wall (>100 µm) of the epidermis.

5.1.4. Hairs

Few plants possess a dense layer of hairs sheltering the stem surface, e.g. *Monechma mollissimum* (NEES) P.G.MEY. (Acanthaceae).

5.2. Leaf

A number of plant species has developed protective tissues at the leaf surface, allowing survival of the whole plant with leaves.

5.2.1. Hairs

Many plants of sandy desert habitats and coastal dunes show dense hair layers [e.g. *Didelta carnosa* (L. f.) AITON var. *tomentosa* (LESS.) ROESSLER].

5.2.2 Protection by bladder cells

Many Mesembryanthemaceae of cheap-investment strategy possess thin-walled bladder cell idioblasts which serve as temporal water reserves (VON WILLERT et al. 1991). Obviously these soft structures are able to survive strong sand-blasting. Even after partial destruction the collapsed bladder cells serve as protective structure (JÜRGENS 1986). Similar structures have been described from Chenopodiaceae with bladder hairs (VOLKENS 1887).

5.2.3 Protection by nested leaf generations

In many cases leaves of subsequent nodes are grouped in a nested arrangement. Consequently the inner leaves are protected by the outer leaves and protective structures of the epidermis can be limited to the outer parts of the leaves (*Crassula muscosa* L.).

5.2.3.1 Dead leaves

In a large number of Mesembryanthemaceae the young leaf pair is protected during the dry season by the dead remnants of the pair of the older leaf generation. Species of the genera *Conophytum* and *Argyroderma* (Mesembryanthemaceae) present examples for this structure.

5.2.3.2 Living leaves

Bud-like rosettes and/or compact growth-forms are generally interpreted as being functional against transpiration losses during the dry season. The compact column-like leaf arrangement of many species of *Crassula* (e.g. *Crassula columnaris* THUNB.) is frequently observed in sandstorm habitats of the Southern Namib.

5.2.4 Thickened outer cell walls of epidermal cells

As described for the stem epidermis of *Arthraerua leubnitziae,* also the outer cell walls of the leaf epidermis can be thickened considerably. An example is found in *Dracophilus dealbatus* (N. E. BR.) WALGATE (Mesembryanthemaceae).

5.3 Whole organs

More complex or holistic structural adaptations involve consistency, structure and position or the three-dimensional orientation of whole organs. E.g. the leaves of *Monsonia ignorata* MERXM. & A. SCHREIB. (Geraniaceae), a small geophyte of the Central Namib dunefield, are in strictly horizontal orientation a few mm above the soil surface, so in a layer of extreme sand-blasting. The horizontal orientation, ensured by stabilizing foldings of the leaf blade, results in minimum exposure to the particle stream, flowing horizontally as well. Only the leaf margin, which shows special protective structures, experiences a strong impact.

6. Survival by means of abiotic protective structures

Abiotic protective structures are utilized or manipulated or made available by special efforts of the plant. The most common abiotic structures are sand-layers fixed to the surface of the plant (= psammophorous plants). Psammophorous plants are able to fix a layer of soil particles on their surface for at least a certain period of the ontogeny of the organ (for more detail see chapter 9.).

6.1. Psammophorous plants with sand-layers on the leaf

The best examples are found in the dicot genera *Psammophora* (four spp., e.g. *P. modesta*, Fig. 9 and *P. nissenii,* Fig. 10–12) and *Arenifera* (*A. pillansii;* both genera of Mesembryanthemaceae), and among the monocots in *Chlorophytum viscosum* (Fig. 14), *Trachyandra divaricata, Ornithogalum psammophorum,* and some other geophytic Asparagales.

6.2 Psammophorous plants with sand-layers on the stem

Good examples are provided by Asteraceae *(Helichrysum, Ifloga)*, Acanthaceae *(Monechma),* Scrophulariaceae *(Sutera)*, while unusual forms are found in Euphorbiaceae (*Euphorbia gummifera*; Fig. 8).

6.3 Use of the soil as protective structure (= sunken growth forms)

Growth forms which are more or less sunken into the soil surface are of remarkable importance in sandstorm affected regions of the Southern Namib desert. Examples of Mesembryanthemaceae are *Fenestraria rhopalophylla* (SCHLTR. & DIELS) N. E. Br. (Fig. 13 from MARLOTH 1908 and Fig. 16), *Cheiridopsis verrucosa* L. BOLUS and *Psammophora nissenii* (Fig. 10; the latter one also being psammophorous). Other examples are *Crassula mesembrianthemopsis* DINTER (Crassulaceae), *Euphorbia tuberculata* JACQ. (Euphorbiaceae), and many geophytic life-forms such as e.g. *Bulbine* spp. (Asphodelaceae).

Obviously survival of these plants could simply be attributed to the safe site inhabited by the plant. However, use of this safe site is only possible because of numerous additional structural peculiarities of the plants, e.g. possession of translucent windows which allow the entrance of light and photosynthesis below the soil surface level. Therefore, sunken growth forms can be seen as a variation in the utilization of sand as a protective structure against sandstorms.

7. Survival in safe sites

In another group adaptations of the plant allow the utilization of safe sites, which normally are not in the growth-form range of the systematic group.

7.1 Safe micro-sites, provided by the habitat and used by the plant

Several plant species are able to use micro-habitats e.g. in the wind shadow of minute ridges formed by quartz veines. The Fig. 2 shows an individual of *Zygophyllum prismatocarpum* E. MEY. ex SOND. This species normally shows upright growth up to two meters height. In the sandstorm channel close to Grillental the plants are forced into horizontal growth behind sheltering rock ridges. Nevertheless the plant as a whole obviously is not avoiding the sand-blasting, as the wood at the basis of the stem is heavily polished by sand-blasting.

7.2 Survival by acrotonous upright growth forms

Sandstorm affected habitats often show typical growth form patterns, including higher upright growth in systematic groups, which normally are very small, prostrate or creeping. For example all those members of the genus *Brownanthus,* which occur in the winter rainfall Karoo of Northern Namaqualand and the Southern Namib, form very low cushions [*B. marlothii* (PAX) SCHWANTES, *B. namibensis* (MARLOTH) BULLOCK, *B. pubescens* (N. E. BR. ex MAAS) BULLOCK] or low shrubs with prostrate, often rooting branches *(B. schlichtianus).*

B. marlothii and *B. namibensis* regularly occur in sandstorm affected habitats. Both species show a very dense periphery (cushion) and possess a special protective structure of stem and leaves formed by bladder cell idioblasts. Looking at the plants growing somewhat higher, *B. schlichtianus,* rarely exposed to sandstorms, is showing prostrate or creeping growth, while *B. arenosus* (SCHINZ) IHLENF. & BITTRICH (Fig. 7), growing in sandstorm habitats, shows upright growth form. The here described preference of upright growth in the lowest plant parts is a structural feature often very well visible in all members of a plant community in sandstorm affected habitats. These upright growth forms allow a rapid passage of the leaves through the zone of highest sand-blasting next to the soil surface during ontogeny.

8. Protection owing to escape in time (short living organs or life-forms with periodic shoot reduction)

Cheap and short-living structures such as the leaves and flowers of *Sarcocaulon multifidum* E. MEY. ex KUNTH (Fig. 6) may be of advantage in sandstorm affected habitats due to a better resulting carbon budget. Furthermore, it may be of advantage for short-lived organs, as well as for ephemerals and annuals, that sand transport is inhibited after the seasonal rain falls, in comparison to the properties of a dry soil surface during most of the year. Unfortunately, the relative importance of short-lived structures in sandstorm habitats cannot be tested easily, as short-lived structures are an important structural adaption to arid habitats in general.

9. Detailed observations in psammophorous plants

9.1. Definitions

Above-ground parts of plants can carry a thin layer of soil material. But not in all cases such a layer of soil particles matches the definition of psammophorous plants. If the particle size is very low, this phenomenon is commonly not regarded as a special feature but referred to as dust pollution of the surface (ELLER 1979). In other cases the particle size ranges from coarse silt to coarse sand and can be called sand-layer in a wider sense. These sand layers on plant surfaces can be observed under various circumstances:

(a) Accidental sand covers of irregular occurrence, plants without sand-fixing structures

These sand layers of often ephemeral character can be observed in many species when plants are exposed to extreme deposition of sand, e.g. along sandy or silty roads. Even surfaces with the astonishing "self-cleaning properties" reported by BARTHLOTT 1990 will not be cleaned in arid climates. If the plants do not support the fixing of sand actively and if the occurrence is of irregular or random character and merely represents an ephemeral event in the life of the plant, this phenomenon is not in the scope of this article.

(b) Sand cover of regular occurrence, plants without sand-fixing structures

Passive coverage by sand can occur regularly under certain conditions. E.g. plants of sandy beaches or coastal dunes often carry a more or less dense layer of sand grains, owing to the sticky nature of the coastal sand, which is often coated with hygroscopic salts and various organic compounds. Sand covers of this nature do occur regularly in the life of these plants, but do not form an effective shelter, because stronger sandstorms remove the loosely fixed sand from the plant surface. Nevertheless it can not be exluded that these regularly occurring sand layers have some biological effect.

(c) Psammophorous plants, regular occurrence of actively fixed sand layers

In contrast to the aforementioned groups true psammophorous plants show regular occurrence of a sand cover (at least on parts of their surface and at least during certain ontogenetic stages) owing to **active fixing** of the sand to the plants surface **by means of special structural features**. As a first approach, psammophorous plants can be identified (in the field) by the fact that their sand layers cannot be easily removed, e.g. by running water. This strategy of actively fixing sand by means of special surface properties is called by us psammophory (oral proposal by D. MÜLLER-DOBLIES in 1991).

The limits of this definition are reached, when, due to man-made environmental changes, plants with sticky surfaces experience sand or dust deposition, while under natural conditions these plants would not be exposed to sand or dust-storms. This is the case e.g. along gravel roads in savanna or forest regions. Therefore it is not possible to identify a psammophorous plant by artificial exposure of e.g. greenhouse plants to sand. For example, *Lychnis viscaria* L. is not a psammophorous plant (although the sticky portions of the stems are very well able to fix sand) because in the natural environment sand is very rarely fixed by this plant (however: insects).

Hence, this definition includes a structural and an environmental portion. Furthermore, various degrees of psammophory can be distinguished.

In literature, psammophorous plants have rarely been mentioned. First notice of the phenomenon was taken when the genera *Psammophora* DINTER & SCHWANTES and *Arenifera* A. G. J. HERRE (both Mesembryanthemaceae) were desribed (BOLUS 1927, 1930; HERRE 1948; DINTER 1923; DINTER & SCHWANTES 1926a, b, 1927). These publications do not provide analytical data with respect to the functional and ecological meaning of the adaption. At this time, psammophorous plants have not even been understood as a life-form group or strategy type, because only these very few examples of the two above-mentioned genera were known. DANIN (1991) reports the observation of a layer of sand on some plants of sandy habitats, but he does not follow up this phenomenon as well. The hypothesis of a mimetic function has recently been brought forward by BARTHLOTT (1992) for *Psammophora modesta* (DINTER & BERGER) DINTER & SCHWANTES, but no evidence is added. NEINHUIS et al. (this volume) study the anatomical epidermal structures of sand-fixing leaf surfaces of some geophytic monocots of Southern Africa in detail, revealing a wide spectrum of anatomical types, defined by origin, distribution and function of sand-fixing structures. Ecological and ecophysiological literature has been ignoring the phenomenon up to today.

9.2 Systematic position of psammophorous plants

Species list of psammophorous plants:
(* = Mediterranean Region, all others: Namib Region)

Acanthaceae
Monechma cleomoides (S.Moore) C.B.CL.
[syn. *M. arenicola* (ENGL.) C.B.CL.]
Monechma mollissimum (NEES) P.G.MEY.
Monechma spartioides (T.ANDERS). C.B.CL.
Petalidium angustitubum P.G.MAY

Aizoaceae
Limeum arenicolum SCHELLENB.
Limeum viscosum (GAY) FENZL

Amaryllidaceae
(taxonomy in MÜLLER-DOBLIES & MÜLLER-DOBLIES 1985 and 1994a)
Bokkeveldia watermeyeri (L. Bolus) D. & U.M.-D.
B. w. subsp. *botterkloofensis* D. & U.M.-D.
Brunsvigia sp.
Namaquanula bruce-bayeri D. & U.M.-D.
Namaquanula etesionamibensis D. & U.M.-D.
Strumaria bidentata SCHINZ
Strumaria hardyana D. & U.M.-D.

Anthericaceae
Chlorophytum viscosum KUNTH (Fig. 14)

Asphodelaceae
Trachyandra bulbinifolia DINTER (OBERM.) p.p.
Trachyandra divaricata (JACQ.) KUNTH.

Asteraceae
Helichrysum gariepinum DC.
Helichrysum pumilio (O.HOFFM.) HILLIARD & B.L.BURTT
Helichrysum roseo-niveum MARLOTH & O.HOFFM.
Ifloga verticillata (L.f.) FENZL
**Ifloga spicata* (FORSSK.) SCH.BIP.
Lasiopogon glomerulatus (HARV.) HILLIARD
Leysera tenella DC.

Caryophyllaceae
**Silene succulenta* FORSSK.
**Silene villosa*
**Spergularia purpurea* (PERS.) G.DON f. and spp.

Colchicaceae
Hexacyrtis dickiana DINTER

Euphorbiaceae
Euphorbia gummifera BOISS. (Fig. 8)

Hyacinthaceae
(taxonomy in MÜLLER-DOBLIES 1994b and 1996)
Albuca aspera U.M-D.
Albuca bontebokensis U.M-D.
Albuca bruce-bayeri U.M-D.
Albuca crudenii ARCHIBALD
Albuca dinteri U.M-D.
Albuca etesiogaripensis U.M-D.
Albuca foetida U.M-D.
Albuca glandulosa BAKER
Albuca jacquinii U.M-D.
Albuca shawii BAKER
Albuca spiralis L.f.
Albuca viscosa L.f.
Albuca viscosella U.M-D.
Dipcadi vaginatum BAKER
Dipcadi dinteri BAKER
Ornithogalum sabulosum U. & D.M-D.
Ornithogalum psammophorum U. & D.M-D.
Ornithogalum scabrocostatum U. & D.M.-D.
Ornithogalum karachabpoortense U. & D.M-D.

Iridaceae
Babiana sp.

Mesembryanthemaceae
Arenifera pillansii (L.BOLUS) A.G.J.HERRE
Psammophora herrei L.BOLUS
Psammophora longifola L.BOLUS
Psammophora modesta (DINTER & BERGER) DINTER & SCHWANTES (Fig.9)
Psammophora nissenii (DINTER) DINTER & SCHWANTES (Fig. 10–12)

Scrophulariaceae
Nemesia viscosa E. MEY. ex. BENTH.
Peliostomum viscosum E. MEY. ex BENTH.
Sutera fruticosa (BENTH.) HIERN
Sutera maxii HIERN
Sutera pallida (PILG.) OVERKOTT & ROESSLER
Sutera sessilifolia (DIELS) HIERN
Sutera tristis (L.f.) HIERN

Zygophyllaceae
**Fagonia arabica* L.
**Fagonia glutinosa* DELILE

9.3 Quantitative degrees of psammophory in relation to the systematic position

The best developed examples of psammophory are observed in five species of Mesembryanthemaceae (in *Psammophora*, Fig. 9–12 and in the monotypic *Arenifera*). A comparable thickness of the sand layer is reached in *Chlorophytum viscosum* KUNTH (Fig. 14). These six species with strongest expression of the phenomenon all occur in the Southern Namib with a concentration in the Sperrgebiet.

Looking at taxa with somewhat lower thickness of the sand layer Scrophulariaceae, Asteraceae, Acanthaceae and Aizoaceae can be mentioned. All these families provide a number of psammophorous species. In these families the genera *Sutera, Helichrysum, Monechma* and *Limeum* show highest number of psammophorous species. Species of *Silene* (fide M. VESTE, Bielefeld) and *Ifloga* provide examples for psammophory in the Mediterranean Region of the Holarctic Kingdom.

On a third level numerous species of Amaryllidaceae and Hyacinthaceae have to be mentioned, which in several cases fix sand only in limited parts of their surface (compare NEINHUIS & al. this volume).

9.4 Psammophory in relation to structure and life history of the plant

9.4.1 Psammophory and life-forms

Psammophorous plants are found primarily in low life-forms, preferentially in nano- and micro-chamaephytes (JÜRGENS 1986: 236; e.g. *Arenifera pillansii*), subterraneous chamaephytes (*Psammophora nissenii*; Fig. 10–12) and small geophytes (e.g. *Chlorophytum viscosum*; Fig. 14), while in psammophorous meso- to mega-chamaephytes or even nano-phanerophytes (*Monechma* spp.) normally only the youngest leaves or the stem bases are sand-fixing.

9.4.2 Position of sand layers (sand fixing structures) in the plants architecture

Sand layers do not occur in all parts of psammophorous plants. Three patterns are frequently observed:

(a) Parts of the plant that are close to the soil surface are more often and/or more densely covered with sand than upper parts of the plants.
(b) Plant surfaces that face towards the periphery of the plant are more often and/or more densely covered by sand layers than surfaces that face towards the centre of the plant. For example the leaves of *Chlorophytum viscosum* (Fig. 14) carry sand only on the outer surface and the edge of the leaves.
(c) In many species preferentially or exclusively the edges of the leaves are covered by a sand layer (many geophytic monocots).

9.4.3 Anatomical patterns of psammophory

A variety of different structures is fixing sand on plant surfaces. Various types of hairs and various patterns of epidermis produce sticky substances which fix sand. While sand particles fixed to hairs allow passage of air, obviously the presence of an uninterrupted glutinous layer on the surface of assimilating organs would cause severe problems with respect to the gas exchange.

Especially in leaves in many cases only the edges of the leaf or certain linear or spotted patterns of the plants surface, sometimes elevated areas, possess sticky properties and fix sand. These structures could be owing to the necessity of sufficient free gas exchange.

The importance of the problem is very obvious in the genus *Psammophora* where young leaves produce a glutinous layer covering almost the whole leaf surface (Fig. 11). Here the distribution of stomata is limited to certain spots, where two to four stomata are concentrated at the bottom of a pitlike structure (Fig. 12). The same arrangement can be observed in the genus *Arenifera*. After a number of weeks this glutinous liquid gets hard.

9.4.4 Sand layers in the life history of the plant

Younger parts are more often and/or more densely covered by sand layers while older parts tend to loose a part of the sand cover. This sequence can be observed e.g. in species of *Psammophora* and *Monechma* where only the younger leaves possess a sticky wax layer, while in older ones the wax looses the ability to fix sand and other particles.

9.5 Phytogeographic distribution of psammophorous species

Plant species possessing a layer of sand on parts of their surface occur in many parts of the world, but they are a particularly well developed constituent of the flora of the arid regions of southern Africa. There is phytogeographical centre of psammophorous plant in the Southern Namib desert, although the life-form group as a whole has a much wider range of distribution in various regions with sparse or low vegetation units.

The concentration of the phenomenon in the Southern Namib is most obvious in the six strongest developed examples of psammophory, i.e. the genera *Psammophora* (all four spp.), *Arenifera* (monotypic) and *Chlorophytum viscosum*.

Other species, with less well developed sand layers, show a phytogeographic concentration in the whole Namib region, including Namaqualand and the Karoo. Only few species have been observed outside these southern African deserts and semideserts. For example psammophorous species of *Ifloga, Silene,* and *Fagonia* are known from the Holarctic Kingdom, occurring on sandy patches and dunes along the coasts of the Mediterranean Sea.

It is too early to make conclusive statements, because it has to be expected that many more psammophorous species will be recognized in the future. Nevertheless the concentration to (a) the Southern Namib desert region, (b) the arid regions of Southern Africa as a whole, and (c) other regions with sparse or low vegetation units will possibly remain the basal pattern.

10. Discussion: The ecological niche of psammophorous plants

Although psammophorous plants are found in a wide spectrum of habitats, typical sites can be named which support a high species diversity or a high density of individuals of psammophorous taxa (compare chapter 5). These habitat preferences and the phytogeographical patterns (chapter 5) in combination with structural, phenological and ontogenetical observations allow the proposal of a few first hypotheses with respect to the possible ecological niche of psammophory. A number of hypotheses can be considered:

10.1 Mimesis

Strongly developed psammophory surely involves a mimetic effect, as mentioned by BARTHLOTT 1992 in an article on mimicry. The fact that soil material of the surrounding habitat is fixed to the surface makes the plants well camouflaged in its environment. But the biological importance of this effect in relation to herbivorous animals has never been tested.

10.2 Mechanical protective structure against herbivorous and phytophagous animals

Similarly it is very likely that dense sand layers on a plant surface reduce the attractiveness of a plant to herbivorous animals. They also could reduce the ability of many phytophagous insects to physically reach the plants surface, but the biological importance of these effects has not yet been established.

10.3 Protective structure against excessive radiation

The sand layer will surely reduce the spectrum of radiation reaching the plant organs. This spectrum, however, and the resulting energy budget of the plant and its sand-layer have not been investigated. Psammophory shows no concentration to hot inland regions or hot microhabitats, but occurs more frequently in rather temperate regions.

10.4 Production of turbulences for thermal energy balance (cooling)

The effect might be of some importance in some cases e.g. fixing of sand exclusively along non-homogenous structural patterns on leaf surfaces (linear, only at margin etc.) But no evidence for this phenomenon has been brought foreward up to now, see also final remark under 10.3.

10.5 Water condensation at the surface

Depending on the grain size composition of the "sand-layer" and depending on its pollution with salts, an increase of water condensation on the plants leaf is possible. Perhaps dewfall on the outer sand grains is increased due to rapid cooling of these sand grains after sunset. Although no evidence for ecological importance of these possible effects has been provided up to now, the phytogeographical concentrations of psammophory in the coastal Succulent Karoo Biome with its high air humidity is obvious. Further research on this phenomenon is recommended.

10.6 Structure for water storage and protection of water accumulated over night

In addition to 10.5 sand-layers could be responsable for storage of water accumulated overnight by dewfall or rain for a prolonged period of time during the day. Water, stored in the sand layer, could allow longer photosynthesis and prolonged water-uptake in species, possessing the ability of water uptake via epidermis (BARTHLOTT & CAPESIUS 1974).

10.7 Protective structure against water losses by transpiration

Comparable to sunken or hidden stomata, a sand-layer will also reduce the steepness of the water vapour pressure deficit gradient near the stomata. This effect is increased, if 10.6 takes place.

10.8 Protective structure against physical destruction by sand-blasting

Especially taxa with very dense sand-layers like *Psammophora, Arenifera,* and *Chlorophytum* show a clear positive correlation with phytogeographical region and habitats of high importance of sandstorms. Inside this region psammophorous taxa are concentrated to habitats with strong impact from sand-blasting. In these habitats lethal destruction of non-psammophours plants by sandstorms has been observed by the author (see chapter 4).

10.9 No direct adaptive value, but secondary side-effect of other adaptions

It should also be considered that, at least in some cases, the existence of a sand-layer might not be of adaptive value, but merely a side-effect of other phenomena or of the history of the taxon. For example the development of glands (with sticky excretes) during evolutionary processes might lead to the fixing of sand as a secondary side-effect of only little ecological or biological significance. Similarly, increasing aridity or increasing wind speeds could result in deposition of sand on the surface of plant species which earlier did not develop a sand-layer because of lack of aeolian-transported sand.

11. Summary

In summary it is obvious that a number of possible effects might be of some adaptive value, but only little evidence is existing, allowing a final decision about the biological and/or ecological significance of the various described features. A few points have to be highlighted:

* Psammophory shows a wide distribution including extreme deserts and more densely vegetated semideserts of Succulent Karoo and Nama Karoo, but also grasslands and open savannes. Therefore it is highly unlikely that one single ecological challenge is correlated with the phenomenon.
* The phytogeographical centres of psammophory strongly support a high importance of sand-layers as a protective structure against the effects of sandstorms.
* The relatively high importance of psammophory in various parts of the Succulent Karoo south of the actual sandstorm regions could possibly support the hypothesis that psammophory involves some effect in relation to the water budget of the plant.
* No ecophysiological evidence for any of these hypotheses exists.
* Numerous other structural features of desert plants should be discussed with respect to their possible values as an adaption to sand-blasting. E.g. structures such as the scales of *Anacampseros papyracea* E. MEY (Fig. 15) and migrant lichens such as *Xanthoparmelia convoluta* could be reinterpreted in this new light.

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Plate I

Fig. 1
Yardang of black dolomite rock streamlined by strong sand-blasting in the diamond Sperrgebiet near Grillental south of Lüderitz

Fig. 2
Plants of *Zygophyllum primatocarpum* E.Mey. ex SOND., which normally grow strictly upright (2 m high), are forced into horizontal growth in the shelter behind rocks (detail from Fig. 1)

Fig. 3 and 4
Pelargonium mirabile DINTER with intact leaves and flowers (Fig. 3) and demolished leaves after a sandstorm (Fig. 4). The stem is protected by a thick dark bark

Fig. 5
The thick wax layer on the stem of *Sarcocaulon patersonii* (DC.) G. DON f. probably serves for survival in sand-blasting environments

Fig. 6
The cheap and short-living flowers of *Sarcocaulon* [illegible] E. MEY. ex KUNTH may be of advantage in sandstorm-affected habitats, forming part of an adequate investment strategy

Fig. 7
Survival by acrotonous upright growth forms, allowing rapid passage of the leaves through the zone of highest sand-blasting next to the soil surface. Figure shows (from left to right) *Euphorbia tuberculata* JACQ., *Othonna* cf. *sedifolia* DC., and four subsequent ontogenetical stages of *Brownanthus arenosus* (SCHINZ) IHLENF. & BITTRICH, the latter species showing upright growth in contrast to low growth forms or prostrate growth in other species of the genus

Fig. 8
Euphorbia gummifera BOISS., wounded by sand-blasting, has lost large quantities of latex which temporarily serves as a sticky surface (diamond Sperrgebiet near Grillental south of Lüderitz)

Plate II

Fig. 9
Psammophora modesta (DINTER & BERGER) DINTER & SCHWANTES, covered with a dense sand layer

Fig. 10
Leaf tips of *Psammophora nissenii* (DINTER) DINTER & SCHWANTES, camouflaged by a sand layer

Fig. 11
A close-up view of a young leaf of *Psammophora nissenii* grown in the greenhouse, i.e. in an environment without sandstorms. The leaf surface is covered by a sticky fluid substance, which is not yet fixing soil particles

Fig. 12
(Detail from Fig. 11). Few weeks later the sticky fluid substance became solid (mark the cell borders). Stomata are only found in a special arrangement in groups of 2 to 5 at the bottom of deep chimneys (sunken stomata)

Fig. 13
Fenestraria rhopalophylla (SCHLTR. & DIELS) N. E. BR., a subterranean growth form, receiving light for photosynthesis through a transparent window at the leaf tip (from MARLOTH 1908)

Fig. 14
Chlorophytum viscosum KUNTH, carrying a dense sand layer at the basal parts pointing towards the periphery of the plant

Fig. 15
Anacampseros papyracea E.Mey., with leaf scales forming a shelter against sandstorms

Fig. 16
Fenestraria rhopalophylla (SCHLTR. & DIELS) N. E. BR.

Fig. 17
Arthraerua leubnitziae (KUNTZE) SCHINZ (small bushes) and *Xanthoparmelia convoluta* (KREMP.) HALE in a sandstorm habitat of the Central Namib desert north of Laguneberg. Note the accumulation of lichens in the windsheltered habitats

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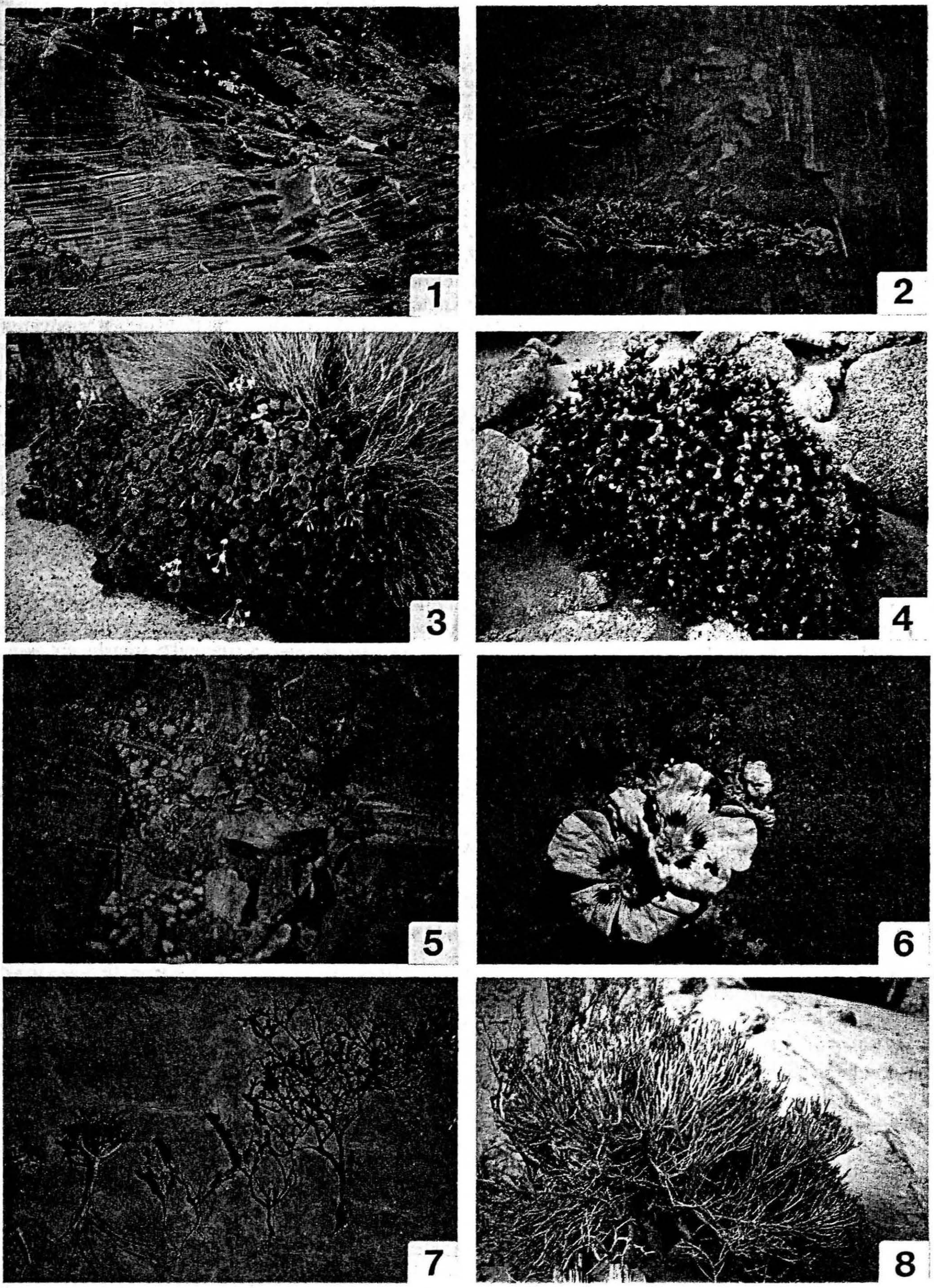

Plate I, explanations on p. 357