

## **Epicuticular wax and anatomical features of *Arthroaerua leubnitziae* (Kuntze) Schinz (*Amaranthaceae*) related to the ecological conditions in the Namib Desert**

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### **Abstract**

*The structure and arrangement of epicuticular wax on Arthroaerua leubnitziae shoots was investigated in relation to the anatomy of internodes with longitudinal ribs and furrows. Common xeromorphic features like stomata hidden in the furrows, papilla-like trichomes, and massively cutinized outer epidermal walls are water-saving adaptations to resist drought conditions, especially during occasional shortages of groundwater supply. A basal wax layer on the cuticle should prevent, besides intracuticular wax, excess water loss by cuticular transpiration. This basal wax layer is reinforced by polymeric aldehydes and withstands abrasion by wind-borne sand particles on the ribs, at least to some extent. The cuticle in the furrows is densely covered by epicuticular wax crystals which render the furrows highly water repellent. Water from fog droplets will therefore be unable to occlude the furrows and especially the stomata. This allows unhindered entrance of CO<sub>2</sub> in the intercellular spaces of the chlorenchyma and photosynthetic carbon gain can take place without risk of transpirational water loss under fog conditions. Epicuticular wax would therefore contribute to maintain a sufficient water status of Arthroaerua plants in the fog-belt of the Namib Desert.*

**Keywords:** *Arthroaerua leubnitziae*, epicuticular wax, xeromorphic adaptations, fog, water relations, Namib Desert.

### **Introduction**

The pencil bush, *Arthroaerua leubnitziae* (*Amaranthaceae*), is one of the endemic species in the Namib Desert. The main distribution area of this single representative of the genus *Arthroaerua* is the Outer Central Namib between the Ugab and Kuiseb riverbeds. The northern border of distribution is near Angra Fria (Loris *et*

*al.* 2004) whilst the dunes south of the Kuiseb probably impede a more southern distribution. Vouchers in the National Herbarium of Namibia (WIND) are from S 19°22.30, Hoanib riverbed, down to S 23°07.30, Rooibank at the Kuiseb riverbed (Kolberg pers. comm.)<sup>1</sup>. Report of another area of occurrence at Lüderitz (Merxmüller 1966-1972) is not substantiated by herbarium material and may be erroneous. The distribution area of *Arthroaerua* extends only exceptionally more than 60 km eastward from the coast. This borderline roughly coincides with the beginning of the eastern minimum zone which is characterized by extremely low precipitation (Hachfeld 2000, Hachfeld & Jürgens 2000). A list of biotopes in the Outer Namib where *Arthroaerua* occurs was given by Giess (1981). He mentioned depressions and washes, plains, hills or rocky outcrops, and riviërs, the dry riverbeds of ephemers. On the sand and gravel plains, especially with the soil type gypsisol, *Arthroaerua* is the dominant plant (Hachfeld 1996).

In most cases, the *Arthroaerua* plants are regularly flowering and fruiting, thus showing high vitality despite the rather hostile environment in the Namib desert. This especially indicates sufficient water supply to maintain photosynthesis and growth. Roots of *Arthroaerua* extend to a depth of 2-3 m where groundwater is available (Kutschera *et al.* 1997). Groundwater at this level is present along the rivers and numerous smaller drainage lines, in rock crevices or at the flanks of rocks where run-off from precipitation accumulates. In the plains, water retaining crusts of gypsum or limestone frequently occur to a depth of ca. 2 m. Water stored above these crusts obviously provides a long-lasting supply. It is the partly very local existence of groundwater which allows *Arthroaerua* plants to grow at rather different sites (Loris *et al.* 2004).

On the other hand, *Arthroaerua* is clearly restricted to the fog-belt of the Outer Namib desert. Despite this fact, there is little evidence of e.g. direct water use from fog via root uptake, since dew or fog moistens the substrate only to a depth of 2-3.5 cm (Walter 1973). First lateral roots emerging from the tap root, however, are formed to a depth of ca. 20 cm and are obviously unable to get use of this moistness. These roots rather provide access to water from exceptionally abundant rainfalls (Loris *et al.* 2004). Additionally, fog collection by the shoot systems of *Arthroaerua* is probably not very effective and uptake of water from water vapor by the shoots remains hypothetical (Loris 2002). Therefore, present knowledge about the influence of fog on the water economy of *Arthroaerua* is not very conclusive.

Preliminary observations showed the occurrence of epicuticular wax (EW) on the shoots of *Arthroaerua* and solubility characteristics of this EW layer indicated the presence of polymeric aldehydes as reported from other plants (Haas *et al.* 2001). Increasing evidence suggests this component to reinforce EW against stress of various origins. This may be of importance under the environmental conditions

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in the Namib Desert and especially with respect to fog; EW could be one of the prerequisites to maintain a sufficient water status of the plants. For better understanding these functional aspects, EW of *Arthroerua* and its relation to the special anatomy with alternating ribs and furrows (Zemke 1939) was investigated.

## Materials and Methods

### Plant material

Shoots of *Arthroerua leubnitziae* (Kuntze) Schinz (*Amaranthaceae*) were collected at the following transects and locations:

(1) Transect roughly in S-N direction, longitudinally extending ca. 220 km, at the beds of the greater rivers Kuiseb, Swakop, Omaruru, Messum, and Ugab, in a distance of some 10-20 km inward from the coast.

(2) Transect in W-O direction at the catchment of the Tumas river – along a gradient from coast to inland – with sampling sites from 100 m a.s.l. near Swakopmund to 500 m a.s.l. inland to the border of the Khomas highland.

(3) Locations north of Swakopmund with special conditions, i.e. the salines and the so-called great lichen field (Schieferstein 1989) near Wlotzkas Baken, where *Arthroerua* is the only representative of higher plants growing in lichen fields.

The shoots comprised at least 4 successive internodes including the youngest one. In most cases, the material was collected from well developed plants of presumably medium age. If available, samples from younger plants were also taken. The wettability of the shoots was observed in the field and further tested in the laboratory.

### Scanning electron microscopy (SEM)

A first set of untreated specimens was prepared at the day of sampling. For examination of ribs and outer openings of furrows, small tangential sections of internodes were made, placed on conductive carbon adhesive tabs and air dried. To assess the action of wind-borne sand particles, preparation was done with respect to exposition, i.e. E or W exposed parts of the shoots. To enable inspection of the cavities, transverse sections of ca. 1 mm thickness were additionally prepared.

Furthermore, fresh shoots stored in plastic bags were transferred within few days to the laboratory in Hohenheim. This material was used either for chemical wax analyses (see below) or for SEM specimens designed to examine the solvent resistance of EW crystals which could indicate the presence of polymeric aldehydes. Shoots were therefore extracted with chloroform (30s at room temperature only, or additionally 20s at 60°C). After extraction, the samples were prepared as described for the untreated ones. All specimens were mounted on sample holders and coated with gold/palladium (30 nm) in a Balzers Union SCD 040 sputter coater. For examination, a Zeiss DSM 904 SEM was used.

## Analysis of cuticular waxes

Shoot parts (usually 6 per sample, containing internodes 2-4 counted from the apex) were extracted by dipping for 30s in „cold“ chloroform (room temperature) and subsequently for 20s in „hot“ chloroform (60°C). Wax extracts were analysed by thin layer chromatography (TLC) and gas chromatography (GC) as already described (Haas *et al.* 2003). The individual extracts were fractionated into compound classes by preparative TLC on silica gel G (Riedel-deHaen) with the solvents 1) *n*-hexane and 2) chloroform/*n*-hexane (75:25, v:v). Individual fractions were analysed by GC with a Shimadzu GC-17 A gas chromatograph equipped with a CP-Sil 8 CB capillary column (25 m x 0.32 mm, Varian-Chrompack), on-column injector and FID. Operating conditions of the chromatograph were: detector temperature 360°C, linear velocity of helium carrier gas 30 cm/s. The column temperature was initially set to 160°C for 2 min and then increased by 8°C/min to 340°C (or 360°C for esters). The fractions of primary alcohols were analysed as trimethylsilyl ethers after derivatization with N,O-bis-(trimethylsilyl)-acetamide/pyridine (1:1, v:v). Free fatty acids were converted to methyl esters by means of BF<sub>3</sub>/MeOH (14%, w:w). Appropriate internal standards were employed for each fraction. Approximate area values of extracted surfaces were calculated from main dimensions (length, diameter) of internodes, measured by use of a vernier calliper.

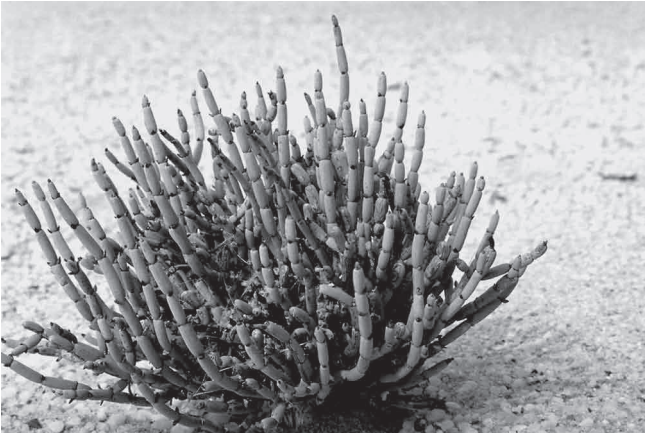
## Results

### Morphology and anatomy

The richly branched shrubs are usually not more than 1 m tall and up to 2 m in diameter. The terete shoots are markedly articulated (Figures 1, 2 & 3). Further branching of terminal shoots usually occurs at nodes 5-10 counted from the apex. The formation of inflorescences which ceases further growth of the particular shoot may induce branching immediately below the inflorescence axis.

Loss of shoots through browsing by animals like springboks (*Antidorcas marsupialis*) is rather scarce (if occurring at all), which indicates low palatability. This may be caused by the great number of calcium oxalate crystals in the cortex (Figure 4), combined with an unusually high sulphate content (Walter 1973). The presence of other deterrent substances is not known. Complex branching patterns frequently result either from occasional drying out of shoots or shoot tips, which may be initiated by e.g. severe attrition due to wind-borne sand particles, or from the above-mentioned formation of inflorescences (Figure 2). Furthermore, water stress leads to the development of comparatively short internodes and the irregular and scarce formation of new ones.

Younger shoot parts form only few scale-like leaves (Figure 3). These appear in early spring (together with the inflorescences) and are shed after some weeks.

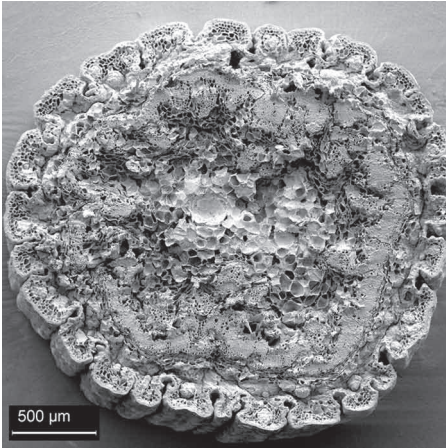


**Figure 1:** Young plant of *Arthroa leubnitziae*, showing upright terete shoots with pronounced articulation and acute tips („pencil bush“), emerging from highly branched basal parts. Size 16 cm in diameter.

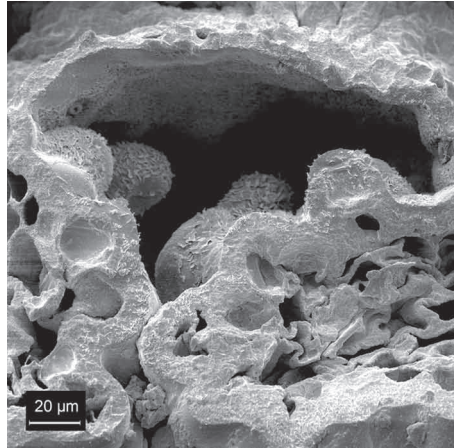
**Figure 2:** Uppermost part of a shoot system, showing dense clustering of branches with comparatively short internodes and partly dead tips, others still flowering.



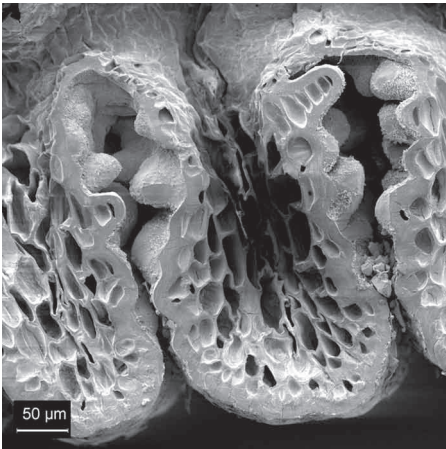
**Figure 3:** *Arthroa* shoots with internodes of medium length, showing fine striation due to ribs and furrows, scale-like leaves, and inflorescence axes after abscission of fruits.



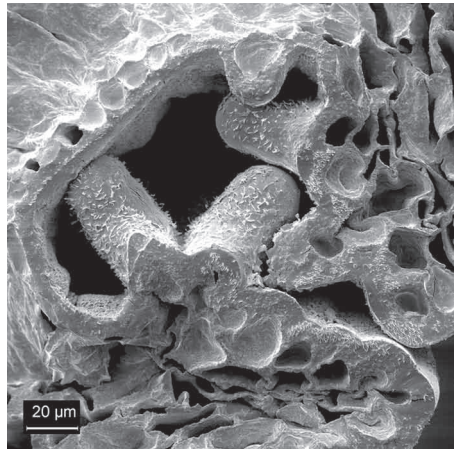
**Figure 4:** Low-magnification SEM micrograph of internode in transverse section with ribs and furrows. Note conspicuous globoid crystal idioblasts in the cortical tissues.



**Figure 5:** Inner cavity of a furrow, showing stomata and reduced thickness of epidermal cell walls adjacent to the chlorenchyma. Note dust particles retained by papilla-like trichomes in the outer furrow part (lower left).



**Figure 6:** Ribs and furrows in transverse section with few-celled papilla-like trichomes, collenchyma of ribs, and collapsed chlorenchyma adjacent to the inner furrow parts. Outer epidermal walls heavily thickened and cutinized.

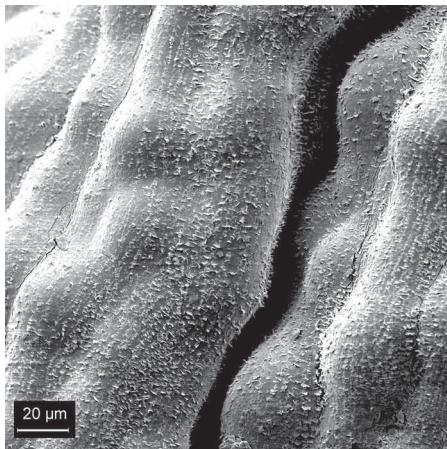


**Figure 7:** Papilla-like trichomes extending in the inner cavity of a furrow. Note EW crystals on the trichomes and intracuticular wax crystallized on cutting surfaces of cutinized outer epidermal cell walls.

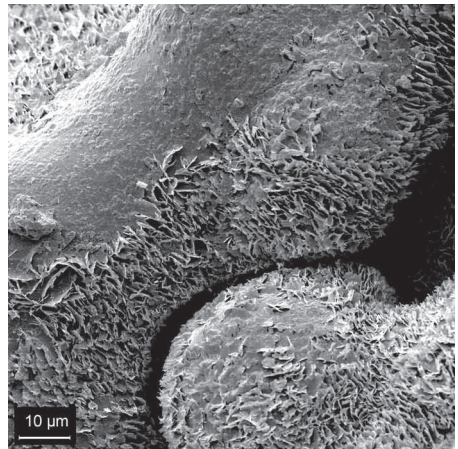
Therefore, the green branches are practically the sole photosynthetic organs of *Arthroerua* plants. The internodes superficially show a fine striation due to some 25 or more longitudinal ribs alternating with furrows. As seen by low-magnification SEM of transverse sections, these furrows widen inwards to form a channel like cavity (Figure 4). Closer SEM examinations at higher magnification reveal further anatomical features and details of EW (Figures 5-17). Stomata are restricted to the epidermis within the furrows and especially the cavities and are never found on the ribs (Figure 5). Unicellular or few-celled trichomes resembling papillae extend in the furrows and in the inner cavities as well (Figures 6, 7). These trichomes prevent dust particles from further entrance in the cavities (Figures 5, 6). The massively thickened outer walls of epidermal cells including the trichomes are completely cutinized and cutinization also extends in the anticlinal walls. The formation of wax crystals on cutting surfaces in the cutinized regions indicates a considerable content of intracuticular wax (Figures 7, 12). Below the epidermis, the ribs consist of collenchyma which contains no chloroplasts. Adjacent to the inner cavities, chlorenchyma is developed which extends ca. 4 cell layers centripetally, forming an almost complete cylinder.

### Epicuticular wax micromorphology

EW crystals occur in low density on the epidermis of ribs (Figure 8). However, the number of wax crystals markedly increases at the margins of the furrows (Figure 9) and this covering is present in the slits, too. A very dense arrangement of wax



**Figure 8:** Surface view of outer furrow part and adjacent ribs with EW crystals.

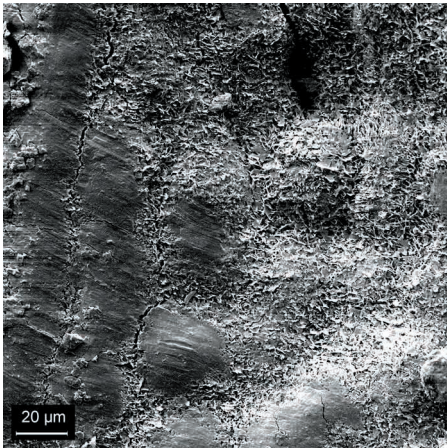


**Figure 9:** Well preserved EW platelet crystals at the margins of a furrow and abrasive damage on the elevated surfaces of adjacent epidermal cells.

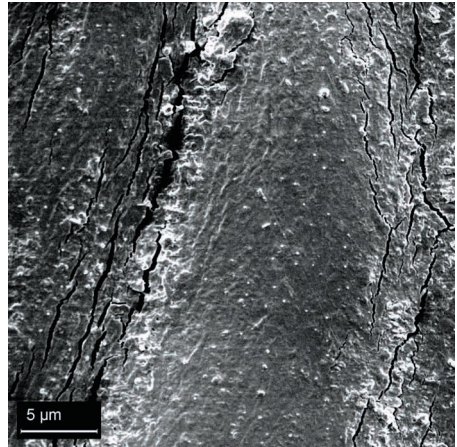
crystals is observed in the cavities, especially around the stomata (Figure 12). Even the guard cells are covered with crystals which may obscure the stomatal slit (Figure 13). The crystals are oriented more or less perpendicular to the cuticle surface but show no pattern of orientation otherwise. The wax crystals are lobed platelets with dissected margins and irregular outlines (Figure 14). They are interconnected with adjacent ones at varying angles. Concerning these micromorphological characteristics, the platelets may be termed membraneous platelets (Barthlott *et al.* 1998). Such membraneous platelets also form a dense covering on the leaves (Figure 15).

### Abrasion of wax crystals

Abrasive damage was frequently observed on the surface of internodes. This is indicated by a particularly sharp border with intact crystals at the margins of furrows and their absence on elevations of adjacent epidermal cells (Figure 9). Absence of crystals is also to be noted on the elevations of cells on the ribs while the depressions over the anticlinal walls show crystals with little damage (Figure 10). Signs of drastic abrasion are the parallel scars caused by wind-borne sand particles which not only abrade the EW crystals but scratch the underlying wax layer, too. On previously damaged parts, however, smooth surfaces with minute crystals indicate subsequent wax secretion and recrystallization (Figure 11).

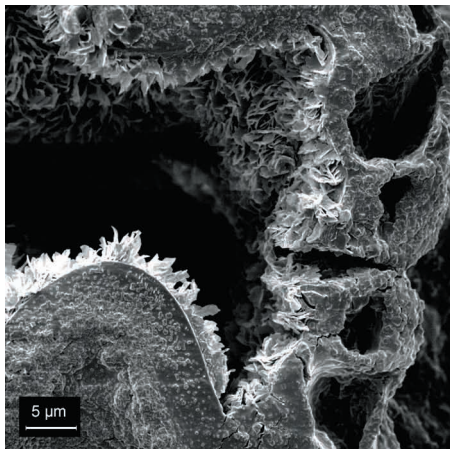


**Figure 10:** Abrasive damage on the elevated surface of a rib (left), showing loss of EW crystals and parallel scars caused by wind-borne sand particles in the basal wax layer.

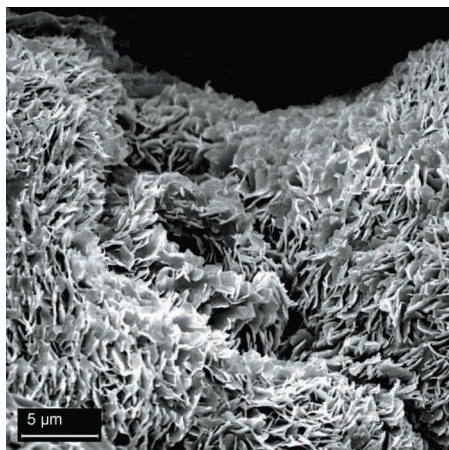


**Figure 11:** Abraded rib surface with regeneration of minute wax crystals from the basal wax layer (fissures are preparation artifacts).

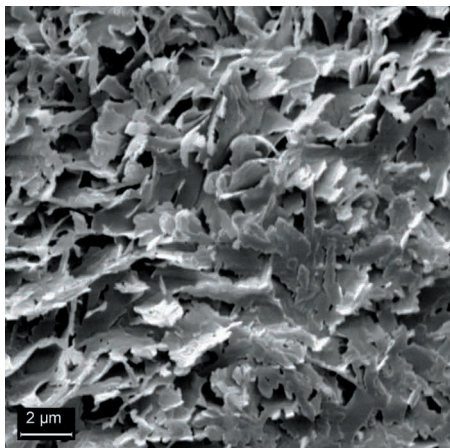




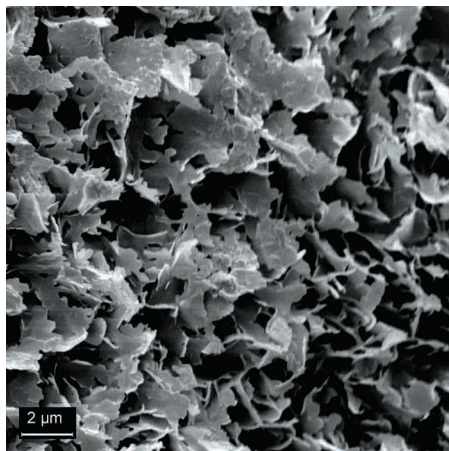
**Figure 12:** Inner part of a furrow with stoma in transverse section, showing dense covering with EW platelets on the cuticle. Note crystallization of intracuticular wax on cutting surfaces.



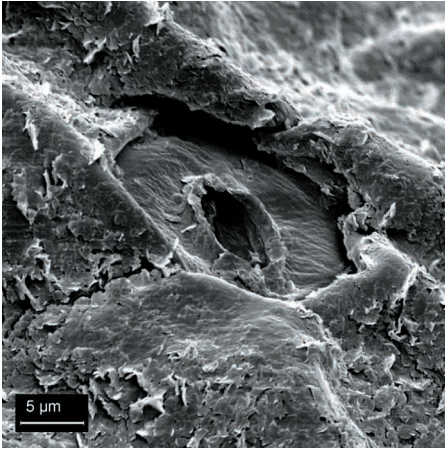
**Figure 13:** Dense covering with EW platelets on the guard cells of a stoma and the surrounding epidermis in the inner furrow cavity.



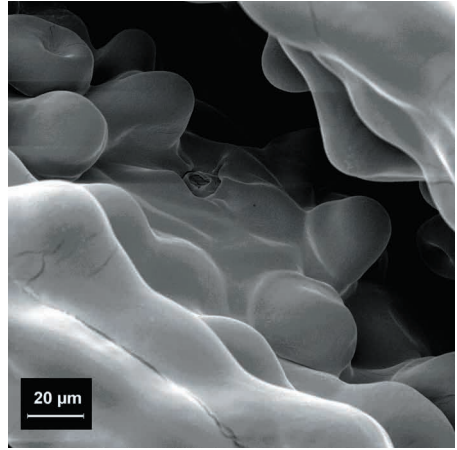
**Figure 14:** EW crystals at higher magnification. The platelets are irregularly lobed with dissected margins and partly interconnected with adjacent ones.



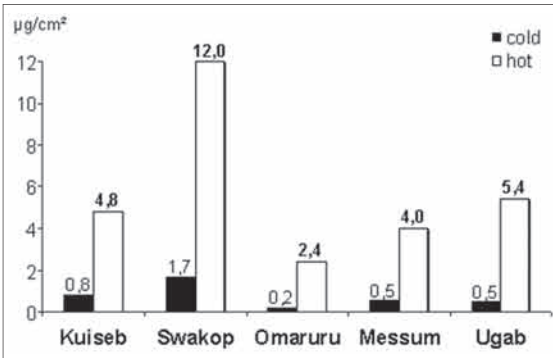
**Figure 15:** EW platelets of the leaf surface, similar in shape as on the internodes.



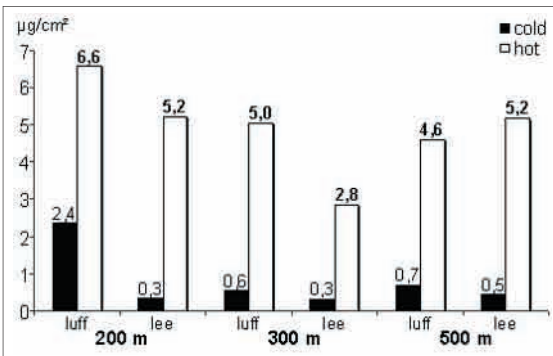
**Figure 16:** Effect of treatment with cold chloroform (room temperature) on the EW microstructure: Remnants of wax crystals and the basal layer with fissures and perforations.



**Figure 17:** Complete removal of EW by extraction with hot chloroform (60°C), leading to a smooth cuticle surface.



**Figure 18:** EW yields (μg/cm<sup>2</sup>) from sub-sequent extraction steps (cold/hot) of *Arthroaerua* plants in samples of transect 1.



**Figure 19:** Comparison of EW yields (μg/cm<sup>2</sup>) from sub-sequent extraction steps (cold/hot) of luff and lee samples in *Arthroaerua* plants growing at different elevations in transect 2.

## Effect of solvent treatments

Treatment of internodes with „cold“ chloroform (room temperature) results in a drastic disturbance of wax micromorphology, loss of the majority of crystals and very reduced size of remaining ones (Figure 16). The solvent treatment also reveals the basal layer of EW. This layer with the remnants of crystals is partly broken into flakes and shows many fissures and perforations. The dense covering of guard cells with crystals is removed almost completely. Entire dissolution of wax is achieved with „hot“ chloroform (60°C) revealing a very smooth cuticle surface (Figure 17).

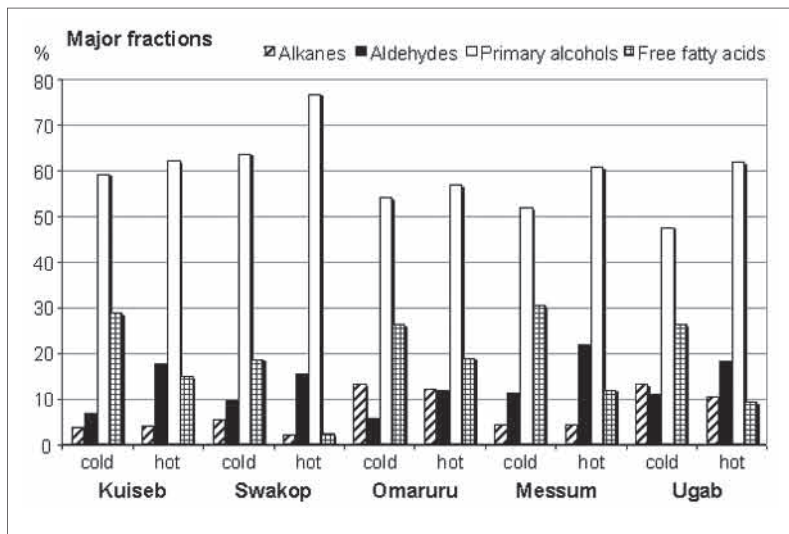
## Wax amounts and chemical composition

EW extracted from the shoots amounts from 2.6 to 13.7  $\mu\text{g}/\text{cm}^2$  (mean 6.6  $\mu\text{g}/\text{cm}^2$ ). This high variability is probably due to considerable variation between individual plants and may also be related to the rather approximate measurements of surface areas which particularly not include the areas in the furrows. No clear tendencies within or between transects are noticeable (Figures 18, 19) and inconsistent results are also obtained comparing shoots from luff and lee sides in plants of transect 2. The partly higher wax amounts in the luff samples may be caused by pronounced regeneration of the basal wax layer on abraded surfaces. Similar EW yields without any regularity were obtained from samples collected in the special locations (salines and lichen fields) and from some young plants (data not shown).

Comparatively small percentages of the total wax amounts are extracted with „cold“ chloroform, i.e. in the range of 7.4 to 31.7% (mean 14.1%). The much greater part of EW is obtained by the following extraction using „hot“ chloroform which yields 68.3-92.6% (mean 85.9%).

EW of *Arthroerua* consists of alkanes, esters, aldehydes, primary alcohols, and free fatty acids. These compound classes are common in plant waxes. Primary alcohols are invariably dominating in the compound class compositions of *Arthroerua* waxes (Figure 20). They are usually present in relative amounts of 50 to 80% (mean 67%). Aldehydes, free fatty acids, and alkanes are found in diverging percentages, esters are always a minor fraction. Free fatty acids are usually present in higher percentages in the first extracts while those of aldehydes increase in the second extracts. This increase of aldehyde percentages in extracts with hot solvent indicates the presence of polymeric aldehydes which are converted to monomers by cleavage of the polymer bonds (Haas *et al.* 2001).

The chain length distributions of the compound classes are in the range as usually found in plant waxes: Alkanes  $\text{C}_{21}$ - $\text{C}_{35}$ , main constituent  $\text{C}_{29}$ ; esters  $\text{C}_{38}$ - $\text{C}_{58}$ , main constituent  $\text{C}_{52}$ . Primary alcohols, aldehydes, and free fatty acids show  $\text{C}_{30}$  as major chain length in profiles ranging from  $\text{C}_{24}$ - $\text{C}_{32}$  (primary alcohols, alde-



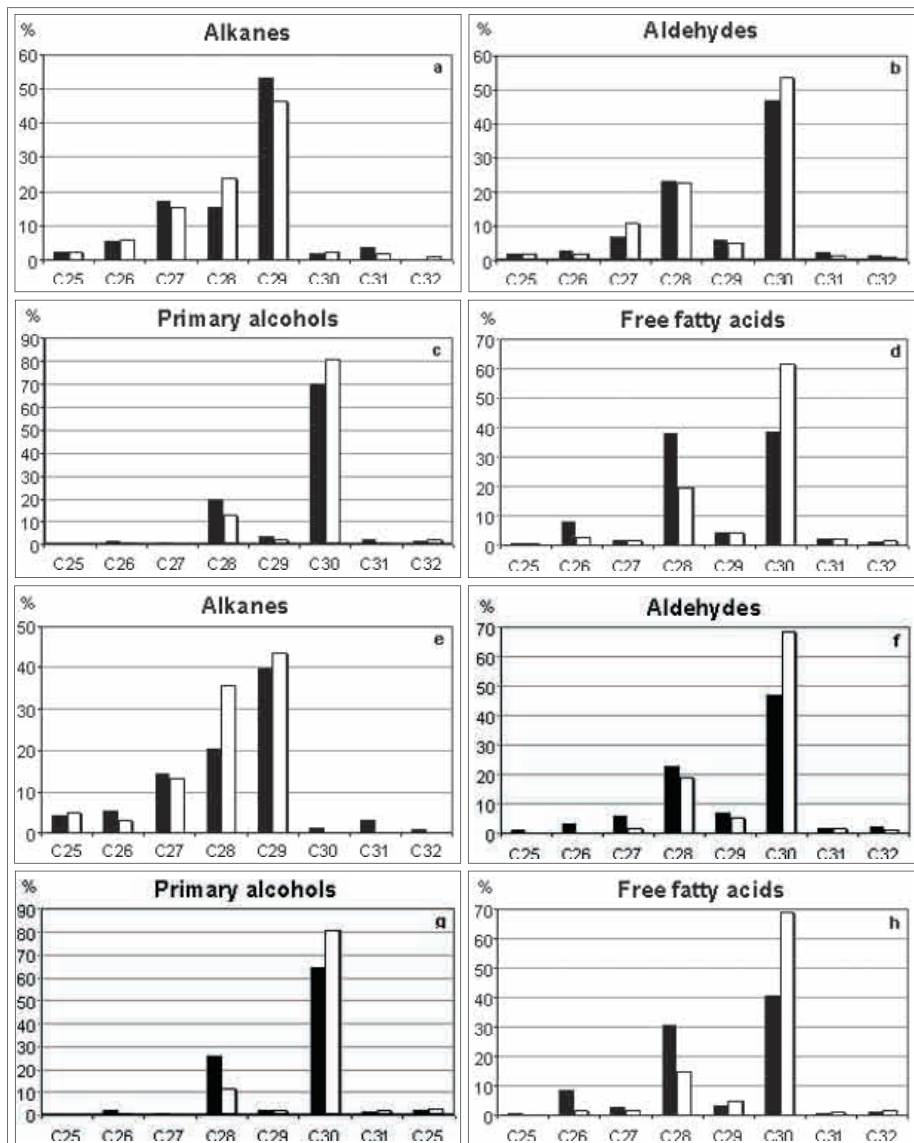
**Figure 20:** Percentages of major fractions from EW obtained by subsequent extraction steps (cold/hot) in the samples of transect 1.

hydes) or  $C_{14}$ - $C_{36}$  (free fatty acids). Profiles of primary alcohols, aldehydes and free fatty acids are clearly alternating, i.e. the even-numbered homologues predominate (Figure 21). Alkanes are normally dominated by odd-numbered ones. In the case of *Arthroaerua*, however, the alkanes show unusual high percentages of even-numbered homologues (especially  $C_{28}$ ) and the profiles are therefore not alternating. Furthermore, the samples from habitats not too far from the coast (all of transect 1; transect 2 up to 300 m a.s.l.) additionally contain branched alkanes with chain lengths  $C_{25}$ - $C_{29}$ . With few exceptions, the relative proportion of  $C_{30}$  as a major homologue of primary alcohols, aldehydes, and free fatty acids is increased in the second extracts.

## Discussion

### Xeromorphic features

*Arthroaerua leubnitziae* cannot be accounted clearly to one of the major xeromorphic adaptation types. There are similarities to switch shrubs of the *Retama* type (Larcher 2003) with green shoots as main photosynthetic organs and inconspicuous, ephemeric leaves. Other features, especially the articulation of shoots would point to succulent halophytes like articulated *Chenopodiaceae* (e.g. *Arthrocnemum*, *Salicornia*). However, succulence of the shoots is of little importance since true water-storing parenchyma is missing and gas exchange measurements do not



**Figure 21:** Variability in the chain length distributions of major wax fractions obtained by subsequent extraction steps (■ cold, □ hot) from two representative samples (a – d: Kuiseb, transect 1; e – h: Tumas, 200 m a.s.l., transect 2).

indicate CAM-characteristics (Loris & Pfiz pers. comm.)<sup>2</sup>. Walter (1973) has characterized *Arthroaerua* as a non-succulent sulphate halophyte due to its high sulphate content (besides sodium chloride). He stated that *Arthroaerua* requires continuous water supply provided at the riviers. Access to the groundwater is achieved by the deep-reaching tap root system. Not surprising, we noted an exceptionally bad state of many *Arthroaerua* plants at the Omaruru river, which is probably related to partly interrupted groundwater flow caused by the Omdel dam. Since the groundwater level depends on rainfalls of unpredictable frequency and abundance (Hachfeld 2000), occasional shortage is not uncommon in other parts of the Namib Desert, too. This is documented at least for some periods of exceptional drought (Walter 1973, Loris *et al.* 2004). Under conditions of unfavourable water supply and risk of high transpirational water loss, well known anatomical adaptations enable limiting of transpiration. Such adaptations are also developed in *Arthroaerua*:

- Stomata are hidden in the furrows which provide spaces of high relative air humidity. Escape of water vapor is decreased by the numerous papilla-like trichomes with resemble interlocking teeth. Functionally similar furrows with stomata restricted to these cavities are also present in shoots of e.g. *Retama raetam* (Fahn & Cutler 1992).
- The outer epidermal walls are thickened and completely cutinized. They obviously contain a considerable quantity of intracuticular wax which even crystallizes on cutting surfaces. Water permeability of the cuticularized layer, i.e. cuticular transpiration, should be reduced effectively by these means and the basal EW layer on the cuticle could further contribute to prevent water loss.
- Leaves as further potential sites of transpiration are scale-like and mostly absent.

In periods of discontinuous water supply, *Arthroaerua* should therefore be able to minimize water loss from both stomatal and cuticular transpiration, at least when stomata are closed.

### **Epicuticular wax**

Species of *Amaranthaceae* are usually devoid of EW crystals (Engel & Barthlott 1988, Barthlott 1994). *Arthroaerua leubnitziae* may be one of the few species of this plant family with EW crystals. The ecological conditions of the Namib Desert obviously afford such an adaptation. From crystal micromorphology and chemical composition, waxes of *Arthroaerua* show no unusual features. However, a basal wax layer is present which contains polymeric aldehydes.

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Polymeric aldehydes are insoluble in organic solvents at room temperature but dissolve at elevated temperatures by cleavage of the polymer bonds. Their existence in EW is indicated up to now by i) only partial dissolution of wax structures with cold chloroform, ii) substantial aldehyde contents in extracts of a subsequent extraction step using hot chloroform and iii) complete removal of EW by the second extraction step (Haas *et al.* 2001). In *Arthroerua*, the micromorphological examinations show a considerable part of EW unaffected by the treatment with cold chloroform. Whilst platelet crystals are removed to a great extent, the basal wax layer remains on the cuticle surface. This layer and crystal remnants are completely dissolved with hot chloroform. These second extracts contain by far the major part of EW and show increased relative aldehyde contents. Therefore, the 2-step solubility indicates the presence of polymeric aldehydes in the EW of *Arthroerua*.

Polymeric aldehydes obviously enhance the stability of EW structures. They could reinforce the basal wax layer against the action of wind-borne sand particles, at least to some extent. Enhanced proportions of C<sub>30</sub> as major chain length in the wax compound classes are found in the basal layer and may further provide higher stability. By these means, the basal layer would be able to maintain its functions in partly preventing water loss of epidermis cells on the ribs and reducing the wettability of surfaces. Additionally, some regeneration of this layer after attrition takes place. The platelet crystals in the furrows need no special reinforcement against erosive damage and therefore contain practically no polymeric aldehydes.

Total EW amounts are with ca. 2.6-13.7µg/cm<sup>2</sup> in a rather moderate range, particularly sufficient to reduce the wettability. On the other hand, an obviously considerable content of intracuticular wax (as indicated by crystallization on cutting surfaces) acts as an effective barrier against water movement across the cuticle thus reducing cuticular transpiration to a tolerable level (Haas & Schönherr 1979, Schönherr 1976, Schreiber & Riederer 1996).

## **Arthroerua and fog**

*Arthroerua leubnitziae* is clearly confined to the fog zone of the Namib Desert (Hachfeld 2000) which indicates a relationship between fog and water economy of the plants. Fog is observed at ca. 100 days per year, lasting often from the evening till late morning. During this time, relative air humidity is at 100%, combined with comparatively low temperatures. This implies that no transpiration takes place. However, such moderate conditions are not observed on days without fog. Additionally, during a few days per year very hot and dry foehn-like fallwinds from the highlands enter the plains of the Outer Namib and cause considerable drying out.

Direct use of fog in the Namib Desert is suspected if shoots act like fog collectors as shown for *Asclepias buchenaviana*, syn. *Gomphocarpus filiformis* (E. Mey.) Dietr. (Loris *et al.* 2004). This possibility seems unimportant in the case of *Ar-*

*thraerua*. To our observations, the shoot systems are rather ineffective fog collectors and there are no roots in the upper soil regions which would be able to take up the water transferred to the soil.

On the other hand, shoots of *Arthroaerua* are more or less unwettable under fog conditions. The water repellency is provided by the EW crystals on the rib surfaces and is maintained when the crystals are eroded and the basal wax layer is exposed. Water from fog droplets is forced to drain off and therefore, this water repellency prevents the establishment of a continuous water film. Most important, water will be unable to enter the furrows by capillary forces due to the surface tension of water and highly water repellent surfaces in the furrows caused by the dense covering with EW crystals. Furthermore, fog droplets even of the smallest theoretical size, i.e. 10µm in diameter (Richter 1998) cannot enter the furrows due to the small spaces of ca. 1-5µm between the papillae (Figures 5, 6 & 7). Hence, no occlusion of the furrows and particularly the stomata by liquid water occurs (see also Schönherr & Bucovac 1971, Schönherr & Ziegler 1975). This provides unhindered entrance of gaseous CO<sub>2</sub> in the intercellular spaces of the chlorenchyma. Photosynthetic carbon gain therefore can take place under fog conditions without risk of water loss by transpiration. Under these circumstances, EW plays a substantial role in the water economy of *Arthroaerua* and the beneficial effects of fog are at least in part related to this fact.

Additionally, an interesting possibility is proposed by Loris *et al.* (2004). Measurements of water movement in *Arthroaerua* plants with artificial conditions of fog indicate that water is absorbed by the shoots and obviously transferred to the root. The mechanism of water uptake would be some kind of reversed transpiration. These observations, however, need to be substantiated by further data. Fog could well influence water relations in *Arthroaerua* and contribute to the ability of growth and development of plants in the Namib Desert.

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