Anatomical Adaptations of *Boerhavia* L. and *Commicarpus* Standl. (Nyctaginaceae) for Survival in Arid Environments of Namibia

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Members of the Nyctaginaceae Jussieu. are distributed throughout southern Africa. Eight species of the family occur naturally in arid parts of Namibia. These species have acquired the ability to survive and reproduce in these dry conditions. They are xerophytes, which have been described as drought evaders, avoiders, and drought-tolerant. In the Nyctaginaceae, *Boerhavia deserticola*, *B. hereroensis*, *Commicarpus helenae* and *C. squarrosus* are thought to be drought avoiders. In this study we investigated their stem, leaf and anthocarp anatomy for adaptations to arid environments. The results indicated that the four species are avoiders, with modifications of the trichomes, secretions, crystals, secondary growth, Kranz mesophyll, water storage cells, tannins, mucilage, inner and outer stomatal ledges, large-diameter xylem vessels, and the presence of sclerenchyma in their stems, leaves and anthocarps. These adaptations enable the plants to tolerate arid conditions, conserve water and maintain a high photosynthetic rate, and aid seed dispersal.

Key words: Adaptations, arid environment, avoiders, *Boerhavia*, *Commicarpus*, Namibia, xerophytes.

INTRODUCTION

The Nyctaginaceae Jussieu., commonly known as four-o'clocks, are a relatively small family capable of growing in gypsum-rich soil (Douglas and Manos, 2007). In southern Africa, five genera (*Boerhavia* L., *Commicarpus* Standl., *Mirabilis* L., *Phaeoptilum* Radlk., and *Pisonia* L.) occur abundantly in the taxon's southern African diversity centre, which is Namibia (Germishuizen and Meyer, 2003).

The Namibian climate is determined by the Subtropical High Pressure Zone, which pushes moist air from the Intertropical Convergence Zone back with dry air, resulting in a dry atmosphere and consequently few clouds (mean annual rainfall less than 600 mm), intense solar radiation, high daytime temperatures (>30°C) and high evapotranspiration (Mendelsohn et al., 2002). These arid conditions have been maintained for millions of years, resulting in shallow soils, low levels of soil nutrients and scarcity of water in most areas (Mendelsohn et al., 2002).

Boerhavia deserticola Codd., *B. hereroensis* Heimerl, *Commicarpus helenae* (Roem. & Schult.) Meikle var. *helenae* and *Commicarpus squarrosus* (Heimerl) Standl. are four perennial forbs of the Nyctaginaceae which successfully survive in the arid conditions of Namibia. *B. deserticola* and *B. hereroensis* grow in sandy and rocky places on hill slopes, dry streambeds and riverbanks in areas such as Karibib, Twyfelfontein, the Spitskop Mts. and Brandberg Mts. (Codd, 1966; Struwig and Siebert, 2009). *C. squarrosus* is often found in the same habitat as *B. hereroensis*, but C. *helenae* var. *helenae* is associated with stony soil or well-drained sandy, gravelly or loamy soil (Struwig and Siebert, 2009).

Plants adapted for survival in a dry habitat are known as xerophytes (Mauseth, 1988). Levitt (1956) classifies xerophytes as plants which are drought evaders, avoiders, or tolerant of drought. Evaders are either ephemerals that survive the dry conditions as seeds, or perennials that survive the unfavourable conditions through dormancy as bulbs or tubers. Avoiders have morphological, anatomical or physiological adaptations which reduce water loss, increase water uptake, store excessive quantities of water or enhance water translocation.

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TABLE 1. Voucher specimens deposited in the National Herbarium Windhoek (WIND), Namibia, and the A.P. Goossens Herbarium, Potchefstroom, South Africa (PUC) (NP – National Park; NR – Nature Reserve)

Taxon	Voucher	Locality
Boerhavia coccinea var. *coccinea*	Struwig 55	Namibia. Okatjiho Farm
	Struwig 108	South Africa. Wyllie's Poort
	Struwig 120	South Africa. Mapungubwe NP
B. cordobensis	Struwig 112	South Africa. Mapungubwe NP
	Struwig 122	South Africa. Tsipise
	Struwig 132	South Africa. Klerksdorp
B. deserticola	Struwig 38	Namibia. Brandberg
	Struwig 42	Namibia. Twyfelfontein
	Struwig 43	Namibia. Sesfontein
B. diffusa var. *diffusa*	Struwig 88	South Africa. Mtuzini NR
	Struwig 117	South Africa. Mapungubwe NP
	Struwig 125	South Africa. Tzaneen
B. erecta	Struwig 23	South Africa. Potchefstroom
	Struwig 135	South Africa. Kruger NP
	Struwig 143	South Africa. Kruger NP
B. hereroensis	Struwig 34	Namibia. Karibib
	Struwig 35	Namibia. Klein Spitzkuppe
	Struwig 40	Namibia. Twyfelfontein Lodge
B. repens var. *repens*	Struwig 168	Namibia. Maltahöhe
	Struwig 170	Namibia. Maltahöhe
Commicarpus chinensis subsp. *natalensis*	Struwig 61	South Africa. Uhmlanga Rocks
	Struwig 62	South Africa. Richards Bay
	Struwig 63	South Africa. Richards Bay
C. decipiens	Struwig 47	Namibia. Tsumeb
	Struwig 51	Namibia. Klein Waterberg
	Struwig 176	Namibia. Omaruru
C. fallacissimus	Struwig 33	Namibia. Windhoek
	Struwig 46	Namibia. Joubert pass
C. fruticosus.	Struwig 59	Namibia. Naukluft Mountains
	Struwig 163	Namibia. Naukluft Mountains
	Struwig 164	Namibia. Naukluft Mountains
C. helenae var. *helenae*	Struwig 44	Namibia. Khowarib Rest Camp
	Struwig 141	South Africa. Kruger NP
	Struwig 183	Namibia. Otjimbingwe
C. pentandrus	Struwig 48	Namibia. Tsumeb
	Struwig 57	Namibia. Aris Farm
	Struwig 131	South Africa. Manyaka
C. pilosus	Struwig 109	South Africa. Waterpoort road
	Struwig 111	South Africa. Waterpoort road
	Struwig 114	South Africa. Mapungubwe NP
C. plumbagineus var. *plumbagineus*	Siebert 3969	South Africa. Kruger NP
	Struwig 106	South Africa. Louis Trichard
	Struwig 126	South Africa. Duiwelskloof
C. squarrosus	Struwig 36	Namibia. Klein Spitskuppe
	Struwig 39	Namibia. Brandberg
	Struwig 41	Namibia. Twyfelfontein

Tolerant plants can undergo dehydration without dying (Levitt, 1956).

The list of morphological, anatomical or physiological adaptations of avoiders is extensive and every species has its own unique set of adaptations (Woodell, 1973). The four Nyctaginaceae species mentioned are thought to be avoiders of desiccation. This paper reports the anatomical adaptations – trichomes, secretions, secondary growth, Kranz mesophyll (i.e., with the bundle sheath surrounded by radially arranged mesophyll cells; Mauseth, 1988), water storage cells, inner and outer stomatal ledges

and sclerenchyme – of the stem, leaf and anthocarp of *Boerhavia deserticola*, *B. hereroensis*, *Commicarpus helenae* var. *helenae* and *C. squarrosus*, which enable these species to survive in an arid environment. The phylogenetic implications of these adaptations are also briefly discussed.

MATERIALS AND METHODS

SAMPLING

Fresh stem, leaf and anthocarp material was collected on site in February 2009. Voucher specimens are deposited in the National Herbarium Windhoek (WIND), Namibia, and the A.P. Goossens Herbarium (PUC), Potchefstroom, South Africa (Tab. 1).

SCANNING ELECTRON MICROSCOPY

The stem, leaf and anthocarp material was stored in 70% ethanol and dehydrated in 90% and $2\times$ 100% ethanol successively for ten min each before critical-point drying. The plant material was then mounted on specimen stubs and sputter-coated with gold/palladium and examined with an FEI Quanta 200 ESEM scanning electron microscope.

LIGHT MICROSCOPY

Stem, leaf and anthocarp material was fixed in 4% aqueous paraformaldehyde. Fixed material was then washed three times in distilled water for 15 min each wash. The material was dehydrated in an ethanol series of 50%, 70%, 90% and $2\times$ 100% ethanol for 15 min each followed by 15 min in 100% resin (L.R. White^{TM} Wirsam/London Resin Company). This was followed by two changes in resin for 1 h each. Then the material was left overnight at 20°C before being embedded and cured overnight at 65°C. Embedded material was cut with a Reichert Jung microtome and stained with 0.5% toluidine blue in 1% borax and 0.16% cresyl fast violet in water with 20% ethanol for two min each stain. Sections were also stained for pectinaceous substances in 0.02% ruthenium red in water for 10 min, and for lipids in Sudan black B in 70% ethanol for 30 min. Micrographs were taken with a Nikon Digital Sight camera fitted on a Nikon Eclipse 80i light microscope at $40\times$, $60\times$ and $100\times$.

X-RAY MICROANALYSIS

The composition of the crystals observed in the leaves, stems and anthocarps was determined by element analysis with an FEI Quanta 200 ESEM with an integrated Oxford Inca X-sight EDS system operating at 15 kV.

RESULTS

STEM

Trichomes

The trichomes of both the *Boerhavia* and *Commicarpus* species are uniserial, multicellular, glandular trichomes with either globose heads (Fig. 1a), as in *B. deserticola* and *B. hereroensis*, or both globose and club-shaped (Fig. 1b), as in C. *helenae* var. *helenae* and *C. squarrosus*. The trichome walls are impregnated with numerous crystals. The trichome heads stain darkly with toluidine blue, which is an indication of dense cytoplasm, and can secrete a substance which makes the stems extremely adhesive.

Epidermis

The outer periclinal epidermal cell walls of the four species are thickened and impregnated with a thick layer of crystals, followed by thin cuticle (Fig. 1c). The stomata are not sunken and the outer and inner periclinal walls of the guard cells are thickened. Small inner and large outer ledges are present. A collenchymatous hypodermis rich in pectin is present and consists of one or two cell layers. Round to brick-shaped chlorenchyma cells are arranged in two to five rows with large and small intercellular spaces. The innermost cell layer of the cortex consists of large cells with thickened walls (endodermis) (Fig. 1d).

Conducting tissue and secondary growth

The xylem consists of large-diameter vessel elements. Although these four species are forbs, secondary growth occurs and is anomalous in that the secondary xylem and phloem develop in concentric rings around the axis of the stem. The xylem and phloem form clusters with thick-walled fibres in between (Fig. 1d). Consecutive cambium differentiates from phloem parenchyma cells which were formed by the preceding cambium. No rays are present. Medullary bundles form in the pith.

Crystals

Bundles of raphide crystals are present in the cortex and the pith in no specific pattern.

LEAF

Epidermis

Both the abaxial and adaxial leaf surfaces of the *Boerhavia* species are densely covered by uniserial, multicellular, glandular trichomes of various lengths, with globose heads. The trichomes on the surfaces of the two *Commicarpus* species are less
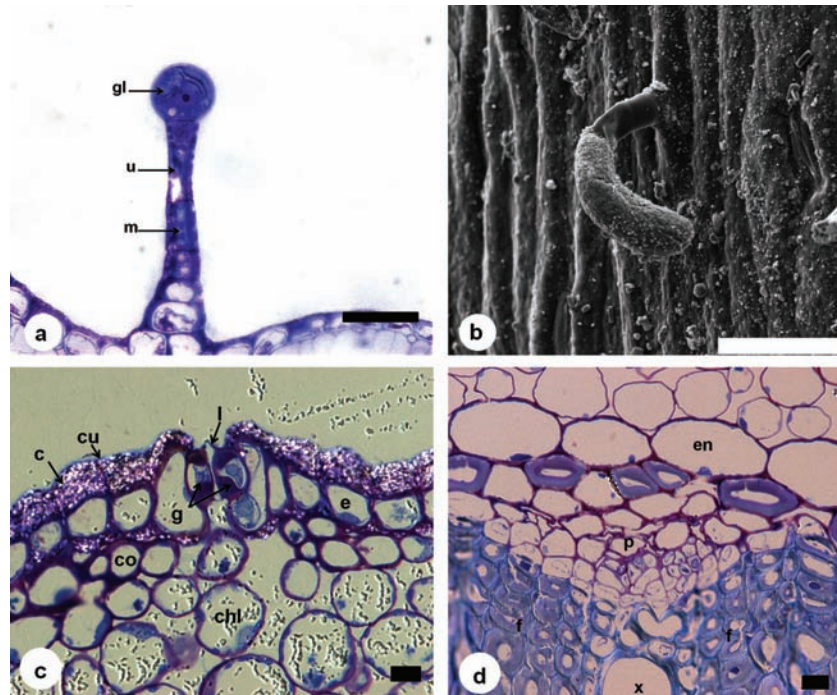
Fig. 1. Scanning electron and light micrographs of *Boerhavia* and *Commicarpus* stems. (**a**) light micrograph of trichome with globose head in *B. hereroensis*. gl – globose head; u – uniserial; m – multicellular. Bar = 50 µm, (**b**) Scanning electron micrograph of trichome with club-shaped head in *C. squarrosus*. Bar = 50 µm, (**c**) Light micrograph of C. *helenae* var. *helenae* stem showing stoma with thickened periclinal walls and epidermis impregnated with crystals. c – crystals; chl – chlorenchyma; co – cortex; cu – cuticula; e – epidermis; g – guard cells; l – ledges. Bar = 10 µm, (**d**) Light micrograph of *B. deserticola* stem showing secondary growth. en – endodermis; f – fibres; p – phloem; x – xylem. Bar = 10 µm.
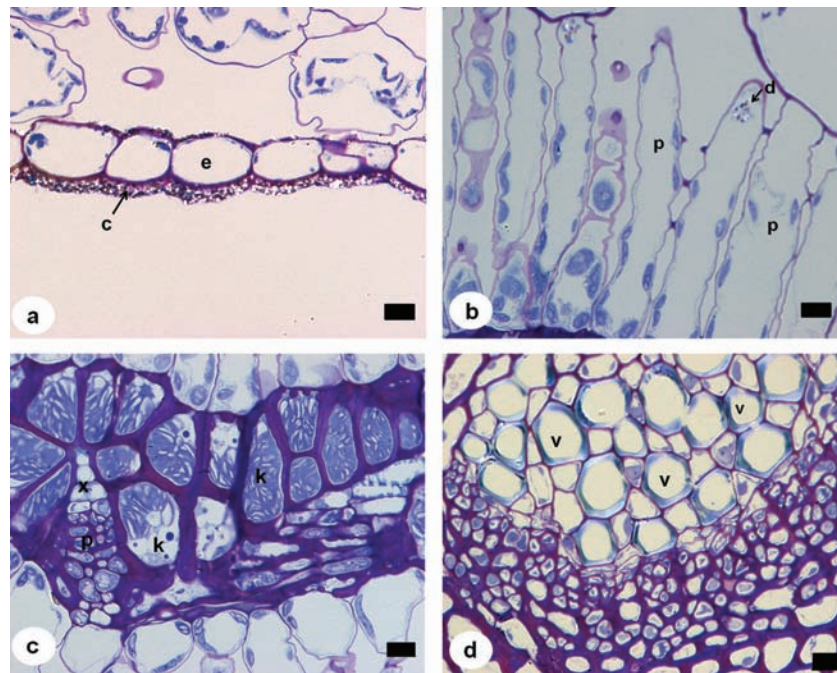

Fig. 2. Light micrographs of *Boerhavia* and *Commicarpus* leaves. (**a**) Abaxial leaf surface of *C. squarrosus*. e – epidermis; c – crystals, (**b**) Palisade cells – beneath adaxial epidermis of *B. hereroensis* (p) with druse crystals (d), (**c**) Kranz mesophyll (k) around minor veins of *B. hereroensis*. p – phloem; x – xylem, (**d**) Wide vessels (v) in vascular bundles of *B. hereroensis*. Bars = 10 µm.
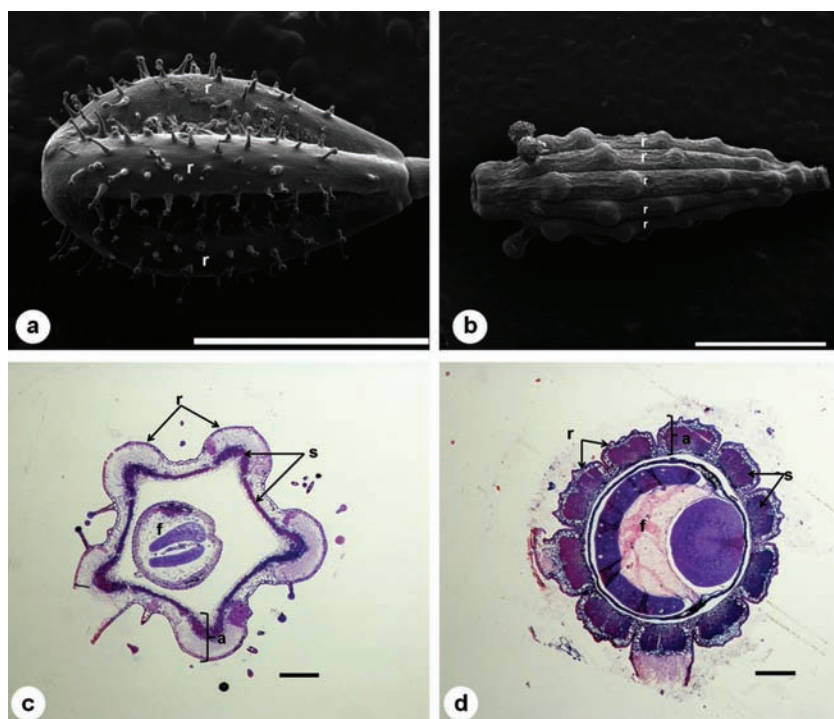
Fig. 3. Scanning electron and light micrographs of *Boerhavia* and *Commicarpus* anthocarps. (**a**) Anthocarp of *B. hereroensis* covered with multicellular trichomes. r – ribs. Bar = 500 μm, (**b**) Glabrous anthocarp of *C. squarrosus*. r – ribs. Bar = 1 mm, (**c**) Light micrograph of anthocarp of *B. hereroensis*. a – anthocarp; f – fruit; r – ribs; s – schlerenchyma. Bar = 100 μm, (**d**) Light micrograph of anthocarp of *C. squarrosus*. a – anthocarp; f – fruit; r – ribs; s – schlerenchyma. Bar = 100 μm.

dense. The structure of the stomata is the same as described for the stem and occurs on both the adaxial and abaxial surfaces. The epidermal cells are large, with thickened outer periclinal walls impregnated with a layer of crystals (Fig. 2a). This layer is thicker on the abaxial than on the adaxial surface. The cuticle is thin. Tannin idioblasts occur in the abaxial epidermis in the two *Boerhavia* species but not in the two *Commicarpus* species. The tannins fill the entire cell and have a coarsely granular appearance.

Mesophyll

The mesophyll of the *Boerhavia* and *Commicarpus* species consists of one or two rows of elongated palisade cells (Fig. 2b) as well as spongy cells which are irregular in shape.

Conducting tissue

The minor veins of the *Boerhavia* species have atriplicoid Kranz mesophyll (Fig. 2c); that is, the veins are surrounded by a layer of Kranz cells (which are bundle sheath cells with large chloroplasts), in turn surrounded by palisade cells. The

cells between the veins are sometimes also Kranz cells and not palisade cells (Fig. 2c). The main vein of the *Boerhavia* species is surrounded by mesophyll cells. Kranz mesophyll is not present in the *Commicarpus* species. The vessel elements of the main veins in both *Boerhavia* and *Commicarpus* species are of large diameter (Fig. 2d).

Crystals

Throughout the mesophyll, bundles of raphide crystals are present in no specific pattern, and small druse crystals are present inside the palisade cells (Fig. 2b).

ANTHOCARP

Anthocarp surface

The anthocarp surface of *B. hereroensis* is covered with uniserial, multicellular, glandular trichomes with globose heads (Fig. 3a). The anthocarp surface of *B. deserticola* either is glabrous or else the grooves between the ribs are covered by uniserial, multicellular, glandular trichomes with globose heads. The anthocarp surfaces of the two *Commicarpus* species are glabrous (Fig. 3b).

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Anthocarp interior

The epidermis is impregnated with a thick layer of crystals in both the *Boerhavia* and *Commicarpus* species. In the *Boerhavia* species, sclerenchyma occurs both within and between the ribs (Fig. 3c). In the *Commicarpus* species, ten ribs are present, with sclerenchyma tissue only within the ribs (Fig. 3d). Columnar cells in the tissue of the ribs becomes mucilaginous; the mucilage is released from the anthocarp, especially when wet.

X-RAY MICROANALYSIS

The crystals occurring in the leaves and anthocarps of both the *Boerhavia* and *Commicarpus* species consist mainly of calcium, carbon and oxygen (Tab. 2). Small amounts of magnesium, aluminium, chlorine and potassium are present on the leaf surface of the *Boerhavia* species; the same elements also occur on the surface of the *Commicarpus* species, except that sulphur is present rather than aluminium.

DISCUSSION

The leaves, stems and anthocarps of *Boerhavia* and *Commicarpus* species show few characters traditionally considered xeromorphic. Relatively thin cuticles and uncutinized outer periclinal walls characterize the epidermal cells. Furthermore, the mesophyll of *Commicarpus* species has little mechanical support tissue and relatively large intercellular air spaces. Most of the features observed are typical of the family Nyctaginaceae. Nevertheless, the investigated species are well able to survive in their extreme environment. The combination of typical family characteristics may confer advantages for survival in a xeric environment. Two noteworthy features are Kranz mesophyll in the *Boerhavia* species and the presence of crystalline inclusions in the outer epidermal cell walls. These crystals may play a significant role in reducing excessive heat loads as well as reflecting harmful UV light. Some workers are of the opinion that the excess heat load may be more of a limiting factor in desert environments than lack of water; similarly, the C_4 photosynthesis that apparently occurs in *Boerhavia* species, as reflected in the presence of Kranz mesophyll, helps plants to prevent photorespiration under high temperature (MacAdam, 2009). C_4 photosynthesis would be more an adaptation to high temperatures than to drought.

CHARACTERS ALLOWING PLANTS TO SURVIVE IN HARSH ARID CONDITIONS

The presence of dense nonliving hairs is often regarded as a xeromorphic feature (Fahn, 1986).

TABLE 2. Composition of crystals (% weight) occurring in the anthocarp and leaves of *Boerhavia* and *Commicarpus* species

Taxon and plant organ	Element	% weight
Boerhavia sp. anthocarp	C	21
	Ca	13
	O	64
	K	1
Boerhavia sp. leaf	C	15
	Ca	30
	O	52
	Al	1
	Cl	1
	K	1
	Mg	1
Commicarpus sp. anthocarp	C	23
	Ca	19
	O	55
	K	1
	Si	1
Commicarpus sp. leaf	C	22
	Ca	12
	O	64
	K	1
	Cl	1
	Mg	1
	S	1

However, many xerophytes do not have a layer of dense hairs and seem to do quite well without them (Cutler et al., 2008).

The *Boerhavia* and *Commicarpus* species do not have hairs or nonglandular trichomes, but various densities of glandular trichomes. The trichomes of the species studied are present on both the stems and leaves, being most dense on the *Boerhavia* species. These trichomes produce a secretion which makes the stems and leaves sticky. The exact functions of the trichomes present on the *Boerhavia* and *Commicarpus* species are unknown and need to be determined by experimental work, but until such work can be done we may speculate about the following possible functions. Fernandes (1994) and Handley et al. (2005) reported that trichomes protected against herbivory and oviposition, as trichomes immobilized and trapped insects and also lessened the ability of insect eggs to stick to the leaf surface. In an arid environment it is of the utmost importance to deter herbivores, as any injury to plant parts may lead to massive water loss.

Hairs or nonglandular trichomes are traditionally thought to protect against water loss, as they decrease air movement at the leaf surface and increase the thickness of the boundary layer (Fahn and Cutler, 1992; Hanley et al., 2007). The densely arranged glandular trichomes may have a similar effect, and their significant length may increase the thickness of the boundary layer substantially.

Some authors assign more value to the ability of nonglandular trichomes or hairs to reduce the heat load than to their ability to reduce transpiration directly by increasing the boundary layer (Metcalf and Chalk, 1983; Fahn, 1986). Nonglandular trichomes rather reduce leaf temperature, and consequently indirectly lower the transpiration rate, by increasing the amount of sunlight reflected from the leaf surface (Fahn and Cutler, 1992; Gibson, 1998; Weryszko-Chmielewska and Chernetskyy, 2005). Whether the glandular trichomes of *Boerhavia* and *Commicarpus* are capable of significantly reflecting sunlight is unknown. The secretory product itself may be of more value in this regard. For example, the resinous material secreted by glandular trichomes of some xerophytes forms a shiny layer that reflects sunlight (Dell and McComb, 1974; Werker and Fahn, 1981). In our species the problem needs further investigation.

Trichomes in *Centaurea scabiosa* L. and *Leontodon hispidus* L. act as a calcium sink, as a portion of the calcium that arrives at the epidermis is diverted into the trichomes (De Silva et al., 1996), a function that could also be attributed to the studied species, in which the trichome walls are impregnated with crystals.

X-ray microanalysis showed that the crystals consist of up to 30% calcium. The calcium probably derives from soils rich in $CaSO_4 \cdot H_2O$, a gypsum found mainly in arid to semi-arid climates with low precipitation (Grotzinger et al., 2007). The family is known to grow on gypsum-rich soil (Douglas and Manos, 2007), and calcium oxalate crystals are found in the family (Metcalf and Chalk, 1950). The crystals of our species may be of calcium oxalate composition.

Crystals have many functions in plants. Here we enumerate the functions that may be performed by the ones in the studied species. Crystals accumulate excess calcium (Franceschi, 2001), thereby maintaining the ionic balance within cells (Franceschi, 2001; Ruiz, 2003). Crystals also play a role in the defense mechanism against herbivores, as they cause irritation, interfere with digestion, and abrade insects' mandibles (Finely, 1999; Korth et al., 2006). Crystals in the epidermis may reflect sunlight, cooling the surface (Franceschi, 2001) and impeding transmission of sunlight to the underlying tissue (Fahn and Cutler, 1992). Crystals in the epidermis may also give structural support (Franceschi and Horner, 1980) to stems, leaves and anthocarps.

The periclinal walls of the stoma guard cells are thickened to reduce evaporation of water from the guard cells (Jordaan, 1989). The stomata contain inner and outer ledges which protrude towards the pore and may lengthen the diffusion path through the guard cells, thereby reducing water loss through transpiration (Mauseth, 1988). Stomata are present on both surfaces of the leaf, which shortens the distance of carbon dioxide diffusion to the mesophyll cells and therefore increases photosynthesis, especially under favourable environmental conditions (Mauseth, 1988; Gibson, 1998). The presence of stomata on both leaf surfaces may indicate a high rate of photosynthesis when sufficient moisture is available. Amphistomatous leaves are very common in plants that grow in arid environments (Parkhurst, 1978).

Collenchyma gives mechanical support to growing organs by thickening the walls, and protects against sunlight and water loss (Cutter, 1978; Mauseth, 1988). A collenchymatous hypodermis is not regarded as a xeromorphic feature in this case, as it is a basic support structure present in many young mesophytic stems as well. Older stems of *Boerhavia* and *Commicarpus* species that have undergone anomalous secondary growth have massive amounts of fibres, and although a family feature, this may have ecological implications for the water economy of the plant. This is further discussed in the section on conducting tissue and secondary growth.

The mesophyll of the *Boerhavia* and *Commicarpus* species consists of palisade cells and spongy mesophyll. The palisade cells increase the internal leaf surface and therefore the photosynthetic rate (Rhizopoulou and Psaras, 2003), while the spongy mesophyll enhances the circulation of carbon dioxide throughout the leaf to maintain a high rate of photosynthesis (Mauseth, 1988) and to distribute light evenly as it is reflected repeatedly through the intercellular spaces. It has also been suggested that large intercellular air spaces may reduce leaf temperature by scattering the infrared radiation that reaches the mesophyll (McClendon, 1984).

Tannins occur only in the epidermal cells of the *Boerhavia* species; it may protect the underlying mesophyll cells against excess sunlight and ultraviolet radiation (Salatino et al., 1988). Tannins can also deter herbivores, as the protein-precipitating action of the tannins renders the plant indigestible, unpalatable and of poor nutritional value (Salatino et al., 1988).

The vessels in the vascular bundles are wide, increasing conductivity (Zwieniecki et al., 2001). Such vessels are vulnerable to cavitation, however, especially in an arid environment (Baas, 1986). Kranz mesophyll corresponds with C_4 photosynthesis (Fahn and Cutler, 1992), which enables species to increase their light, water and nitrogen use and therefore productivity (Long, 1999). The anomalous secondary growth results in the production of massive amounts of fibres, which give mechanical support to the stem. In addition, according to Gaff and Carr (1961) the apoplastic water stored in the thick

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cell walls and cell lumina may act as reservoirs and protect against dehydration by presenting a buffer to symplastic water loss. The phloem is also encapsulated by these fibres, which protect the phloem from drying. The phloem can therefore be active for many years (Mauseth, 1988).

An anthocarp is a structure comprising a fruit enclosed in a persistent perianth. The anthocarp of the *Boerhavia* species has five ribs, ten in the *Commicarpus* species. The columnar cells of the ribs become mucilaginous, and the mucoid substance is released especially when the anthocarps are wet (Spellenberg, 2004). The mucoid substance is sticky and may assist in seed dispersal by animals (Wilson and Spellenberg, 1977; Spellenberg, 2004), or it might anchor the seed to the soil to allow the radicle to penetrate the soil (van der Pijl, 1983). The ribs and the sclerenchyma present in the ribs give mechanical support to the anthocarp. The ribs and sclerenchyma therefore prevent the anthocarp structure from collapsing when the mucoid substance is released, and protect the seed inside the fruit against damage.

PHYLOGENETIC IMPLICATIONS

The Nyctaginaceae originated in the Neotropics (Douglas and Manos, 2007). Genera occur in both tropical and desert habitats (Douglas and Manos, 2007; Douglas and Spellenberg, 2010). It is not certain whether the family originated in a tropical or desert environment, so it cannot be determined whether the adaptations as discussed above are apomorphic or synapomorphic. Further studies of the adaptations in the family are therefore required. *Phaeoptilum spinosum* Radlk., an endemic of southern Africa, is one of the basal lineages in the family (Douglas and Manos, 2007). Comparison of its anatomy with that of southern African *Boerhavia* and *Commicarpus* species should shed some light on possible synapomorphies, but this necessitates a detailed anatomical study of all three genera.

CONCLUSION

The stems, leaves and anthocarps of *Boerhavia deserticola*, *B. hereroensis*, *Commicarpus helenae* var. *helenae* and *C. squarrosus* have some anatomical adaptations which favour its survival in the desert conditions of Namibia by conserving water, reducing the heat load, maintaining a high photosynthetic rate when water is available, and aiding seed dispersal. It is unknown whether the cytoplasm of these species may withstand dehydration. We classify the four species of the Nyctaginaceae as drought avoiders.

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