

ANATOMY OF THE SOUTHERN AFRICAN *BOERHAVIA* AND *COMMICARPUS* SPECIES (NYCTAGINACEAE)

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Abstract

The Nyctaginaceae in southern Africa is represented by five genera of which *Boerhavia* L. and *Commicarpus* Standl. are the most species-rich. Stem, leaf and anthocarp material was collected *in situ* and examined with a scanning electron microscope and a light microscope. The anatomy of the leaf and anthocarp proved diagnostic at the generic level, but was uniform amongst the species of each genus. Kranz anatomy occurs around the minor veins in the leaves of *Boerhavia*, but in *Commicarpus* the minor veins are surrounded by large parenchyma cells. The anthocarp of *Boerhavia* has five ribs or three wings, with sclerenchyma within the ribs and the area between the ribs, whereas *Commicarpus* has ten ribs with sclerenchyma only present within the ribs. The number of chlorenchyma rows in the stems could be diagnostic and the outline of the sclerenchyma bundles in the anthocarp could divide the *Commicarpus* species into two groups, but more research needs to be done on these characters.

Introduction

The Nyctaginaceae consists of about 30 genera and 400 species (Douglas and Manos, 2007) mainly distributed in the tropical and subtropical areas of the New World (Bittrich and Kühn, 1993; Jordaan, 2000), with some genera extending into the temperate regions such as southern Africa (Thulin, 1994). Anatomy of this family is summarized by Metcalfe and Chalk (1950, 1979) and Bittrich and Kühn (1993) with numerous studies which focus on specific anatomical features in a few species (Mikesell and Popham, 1976; Vanvinckenroye *et al.*, 1993). The stem anatomy of the family is characterized by anomalous secondary growth and numerous studies have focused on this phenomenon (Rajput and Rao, 1998; Carlquist, 2004). Stomata are present in both the adaxial and abaxial epidermis (amphistomatic) or only in the abaxial epidermis (hypostomatic) (Bittrich and Kühn, 1993). The mesophyll is centric, dorsiventral or isobilateral and Kranz anatomy occurs in a few genera (Carolin *et al.*, 1978; Muhaidat *et al.*, 2007). Calcium oxalate crystals are present and tannin idioblasts occur in some genera (Edeoga and Ikem, 2002).

The structure of the anthocarp differs between genera. The wall of the anthocarp can either have wings or ridges that are either smooth or bear warts. The anthocarp wall is constructed of epidermis, sclerenchyma, parenchyma, vascular strands and columnar parenchyma cells, and raphide bundles are common (Willson and Spellenberg, 1977; Douglas and Manos, 2007).

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In southern Africa, south of the Zambezi River, that is, Botswana, Lesotho, southern Mozambique, Namibia, South Africa, Swaziland and Zimbabwe, five genera (*viz.*, *Boerhavia* L., *Commicarpus* Standl., *Mirabilis* L., *Phaeoptilum* Radlk. and *Pisonia* L.) occur (Germishuizen and Meyer, 2003). *Boerhavia* and *Commicarpus* are the most species-rich genera, totaling 16 species of which six are endemic to the region (Table 1).

Boerhavia and *Commicarpus* can be distinguished from each other morphologically as their habit, the shape of the flower and the anthocarp structure differ (Meikle, 1978). *Boerhavia* has a diffuse habit, the flowers have a bell-shaped perianth and the anthocarp has either 3-4 wings or 5 ribs and the surface may be smooth or covered with multicellular trichomes. *Commicarpus* has a scrambling or climbing habit, the flowers have a funnel-shaped perianth and the anthocarp has ten ribs covered with large, viscid and mucilaginous glands (Stannard, 1988). The anatomy of the genus *Boerhavia* has been studied extensively in the literature with *Boerhavia diffusa* L. var. *diffusa*, a South American species introduced to southern Africa (Codd, 1966; Bromilow, 2010), mostly used as the representative (Rajput and Rao, 1998; Edeoga and Ikem, 2002). The anatomy of *Commicarpus* however, was inadvertently included during studies of *Boerhavia repanda* Willd. or *Boerhavia chinensis* (L.) Aschers. & Schweinf., as both names are currently regarded as synonyms for *Commicarpus chinensis* (L.) Heimerl. subsp. *chinensis* (Das and Santakumari, 1978; Rajput and Rao, 1998).

Although the two genera and their species in southern Africa are sharply differentiated by their morphology, there is still a lack of knowledge about their anatomy. An anatomical study was required to determine whether additional taxonomic evidence could be obtained to aid in the delimitation of the genera and their species. The aim of this paper is to describe the stem, leaf and anthocarp anatomy of southern African *Boerhavia* and *Commicarpus* species for the first time and to report on the taxonomic significance of these characters.

Materials and Methods

Sampling: Stem, leaf and anthocarp material was collected *in situ* during 2009 and 2010 in Namibia and South Africa, as these two countries make up the southern African centre of diversity and together play host to all 16 taxa. Voucher specimens were deposited in the National Herbarium Windhoek (WIND), Namibia and the A.P. Goossens Herbarium (PUC), Potchefstroom, South Africa (Table 2).

Scanning electron microscopy: Stem, leaf and anthocarp material was stored in 70% ethanol and dehydrated once in 90% and twice in 100% ethanol successively for ten minutes before critical point drying. The plant material was then mounted on specimen stubs and sputter-coated with gold/palladium and examined with a FEI Quanta 200 environmental scanning electron microscope (ESEM).

Table 1. List of southern African *Boerhavia* and *Commicarpus* species and their distribution in southern Africa (*introduced aliens; ^Eendemic).

Species	Distribution in southern Africa
<i>Boerhavia coccinea</i> Mill. var. <i>coccinea</i>	Botswana, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe
* <i>Boerhavia cordobensis</i> Kuntze	Namibia, South Africa
^E <i>Boerhavia deserticola</i> Codd	Namibia
* <i>Boerhavia diffusa</i> L. var. <i>diffusa</i>	Botswana, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe
* <i>Boerhavia erecta</i> L.	Botswana, Mozambique, Namibia, South Africa, Zimbabwe
^E <i>Boerhavia hereroensis</i> Heimerl	Namibia, South Africa
<i>Boerhavia repens</i> L. var. <i>repens</i>	Botswana, Namibia, South Africa, Zimbabwe
<i>Commicarpus chinensis</i> (L.) Heimerl subsp. <i>natalensis</i> Meikle	South Africa, Mozambique
^E <i>Commicarpus decipiens</i> Meikle	Namibia
^E <i>Commicarpus fallacissimus</i> (Heimerl) Heimerl ex. Oberm. Schweick. & I. Verd.	Namibia, Botswana
^E <i>Commicarpus fruticosus</i> Pohn.	Namibia
<i>Commicarpus helenae</i> (Roem. & Schult.) Meikle var. <i>helenae</i>	Botswana, Namibia, South Africa
<i>Commicarpus pentandrus</i> (Burch.) Heimerl	Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe
<i>Commicarpus pilosus</i> (Heimerl) Meikle	Botswana, Namibia, South Africa, Zimbabwe
<i>Commicarpus plumbagineus</i> Standl. var. <i>plumbagineus</i>	Botswana, Mozambique, Namibia, South Africa, Swaziland, Zimbabwe
^E <i>Commicarpus squarrosus</i> Standl.	Namibia

Light microscopy: Stem, leaf and anthocarp material was fixed in 4% aqueous paraformaldehyde. Fixed material was then rinsed three times in 0.05 M cacodylate buffer for 15 minutes each and followed by three rinses with distilled water for 15 minutes each. The material was dehydrated in an ethanol series of 50%, 70%, 90% and twice in 100% ethanol for 15 minutes each followed by 15 minutes in 100% resin (L.R. White™ Wirsam/London Resin Company). This was followed by two changes in resin for one hour each and was left overnight at 20°C before being embedded and then polymerised overnight at 65°C. Embedded material was cut with a Reichert-Jung microtome and stained with 0.5% toluidine blue in 1% borax and 0.1% neufuchsin for 15 seconds. Micrographs were taken at 40x, 60x and 100x magnification with a Nikon Digital Camera DXM 1200 F, fitted on a Nikon Eclipse E 800 and a Nikon Digital Sight camera fitted on a Nikon Eclipse 80i light microscope.

Table 2. 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 specimens	Locality
<i>Boerhavia coccinea</i> var. <i>coccinea</i>	Struwig 55	Namibia. Farm Okatjiho
	Struwig 108	South Africa. Wyllie's Poort
	Struwig 120	South Africa. Mapungubwe NP
<i>B. cordobensis</i>	Struwig 112	South Africa. Mapungubwe NP
	Struwig 122	South Africa. Tsipise
<i>B. deserticola</i>	Struwig 132	South Africa. Klerksdorp
	Struwig 38	Namibia. Brandberg
	Struwig 42	Namibia. Twyfelfontein
<i>B. diffusa</i> var. <i>diffusa</i>	Struwig 43	Namibia. Sesfontein
	Struwig 88	South Africa. Mtuzini NR
	Struwig 117	South Africa. Mapungubwe NP
<i>B. erecta</i>	Struwig 125	South Africa. Tzaneen
	Struwig 23	South Africa. Potchefstroom
	Struwig 135	South Africa. Kruger NP
<i>B. hereroensis</i>	Struwig 143	South Africa. Kruger NP
	Struwig 34	Namibia. Karibib
	Struwig 35	Namibia. Klein Spitzkuppe
<i>B. repens</i> var. <i>repens</i>	Struwig 40	Namibia. Twyfelfontein Lodge
	Struwig 168	Namibia. Maltahöhe
	Struwig 170	Namibia. Maltahöhe
<i>Commicarpus chinensis</i> subsp. <i>natalensis</i>	Struwig 61	South Africa. Uhmlanga Rocks
	Struwig 62	South Africa. Richards Bay
	Struwig 63	South Africa. Richards Bay
<i>C. decipiens</i>	Struwig 47	Namibia. Tsumeb
	Struwig 51	Namibia. Klein Waterberg
	Struwig 176	Namibia. Omaruru
<i>C. fallacissimus</i>	Struwig 33	Namibia. Windhoek
	Struwig 46	Namibia. Joubert pass
<i>C. fruticosus</i> .	Struwig 59	Namibia. Naukluft Mountains
	Struwig 163	Namibia. Naukluft Mountains
	Struwig 164	Namibia. Naukluft Mountains
<i>C. helenae</i> var. <i>helenae</i>	Struwig 44	Namibia. Khowarib Rest Camp
	Struwig 141	South Africa. Kruger NP
	Struwig 183	Namibia. Otjimbingwe
<i>C. pentandrus</i>	Struwig 48	Namibia. Tsumeb
	Struwig 57	Namibia. Aris Farm
	Struwig 131	South Africa. Manyaka
<i>C. pilosus</i>	Struwig 109	South Africa. Waterpoort road
	Struwig 111	South Africa. Waterpoort road
	Struwig 114	South Africa. Mapungubwe NP
<i>C. plumbagineus</i> var. <i>plumbagineus</i>	Siebert 3969	South Africa. Kruger NP
	Struwig 106	South Africa. Louis Trichardt
	Struwig 126	South Africa. Duiwelskloof
<i>C. squarrosus</i>	Struwig 36	Namibia. Klein Spitzkuppe
	Struwig 39	Namibia. Brandberg
	Struwig 41	Namibia. Twyfelfontein

Results

Trichomes: Trichomes are present in all the organs of both *Boerhavia* and *Commicarpus*, and vary in their size, length, distribution and abundance. The trichomes are uniserial and multicellular. The trichomes terminate in a head which is either globose (Fig. 1A) or clavate (Fig. 1B). The walls of the trichomes are impregnated with numerous crystalline granules (Fig. 1C). The head of the trichomes stain dark purple/blue with toluidine blue, which is an indication of dense cytoplasm (Fig. 1D). The trichomes secrete a substance which makes the organs extremely sticky.

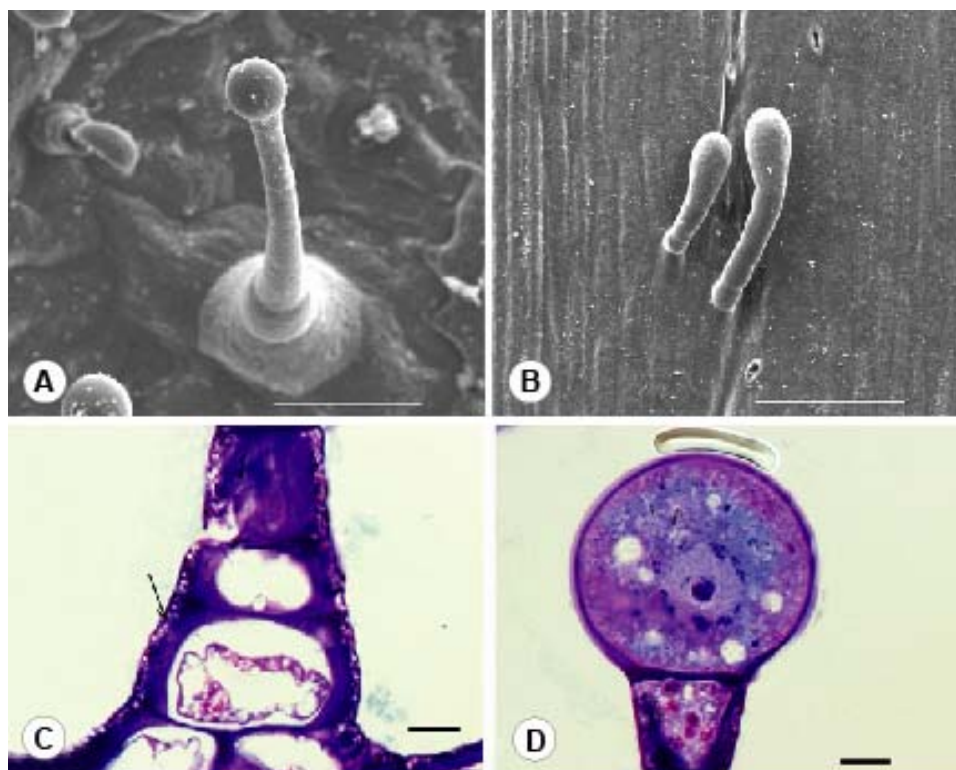


Fig. 1. A. Scanning electron micrograph of a trichome with a globose head of *Boerhavia hereroensis*. B. Scanning electron micrograph of a trichome with a clavate head of *Commicarpus fallacissimus*. C. Crystals in the cell wall of the trichome (indicated by the arrow) of *B. hereroensis*. D. Dense cytoplasm in the globose head of the trichome of *B. hereroensis*. Scale bars A: 50 μm ; B: 100 μm ; C-D: 10 μm .

Stem anatomy:

Boerhavia: The cell walls of the epidermis are thickened, especially the outer periclinal wall, which is impregnated with crystalline granules of varying thickness. The cuticle is thin. The epidermal cells are rounded and not of the same size, with some cells larger than others (Fig. 2A). The stomata are not sunken and the outer and inner periclinal walls of the guard cells are thickened but not cutinized. The collenchymatous hypodermis consists of 1-3 layers of cells. The

hypodermis does not form a continuous cylinder around the axis of the stem but is interrupted at the substomatal chambers. The chlorenchyma cells are spherical to brick-shaped and arranged in 2-4 rows with large and small intercellular spaces. The cells vary in size. The innermost cell layer of the cortex (starch sheath) consists of large cells with thickened walls. The primary xylem consists of vessel elements with a large diameter. All the stem sections show anomalous secondary growth. The secondary xylem and secondary phloem form clusters of thick walled fibres with conjunctive parenchyma in between (Fig. 2B). Consecutive cambial layers differentiate from phloem parenchyma cells which were formed by the preceding cambium. No rays are present. Medullary bundles form in the pith. Bundles of raphide crystals are present throughout the stem in no specific pattern.

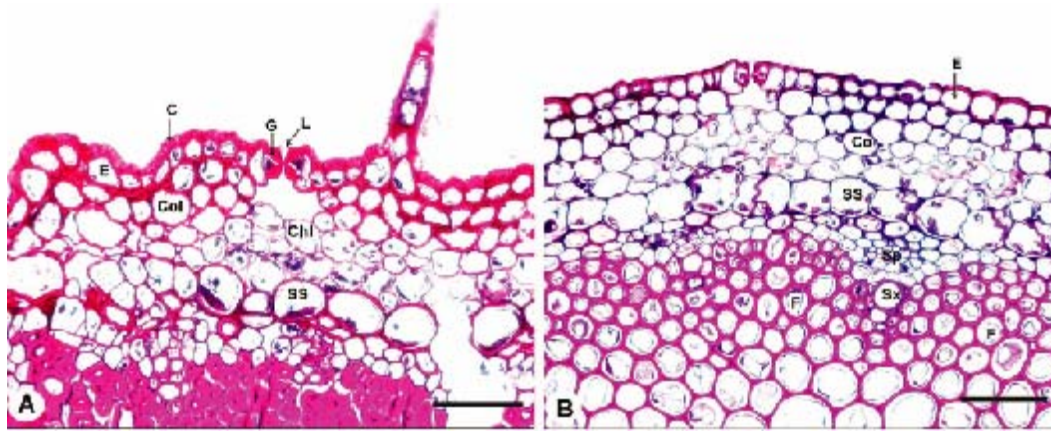


Fig. 2. A. Light micrograph of a cross section through a portion of a stem of *Boerhavia deserticola*. (C= crystals, Chl= chlorenchyma, Col= collenchymas, E= epidermis, G= guard cell of stoma, L= outer ledge of guard cell, SS= starch sheath). B. Light micrograph of a cross section through a portion of a stem of *Boerhavia diffusa* var. *diffusa* showing secondary growth. (Co= cortex, E= epidermis, F= fibre, Sp= secondary phloem, Sx= secondary xylem). Bars = 50 µm.

Commicarpus: The structure of the stem corresponds with that which was described for *Boerhavia*, except that the chlorenchyma cells are arranged in 3-6 rows.

Leaf anatomy:

Boerhavia: The epidermal cells are large, irregular in shape and the walls are thickened, especially the dome-shaped outer periclinal wall, which is not cutinized. The outer periclinal wall is impregnated with crystalline granules which are more numerous on the abaxial surface than the adaxial surface (Fig. 3A). The cuticle is thin. Tannin idioblasts are sometimes present in the epidermis of either or both surfaces (Fig. 3A). The stomata are present on both leaf surfaces (amphistomatic) and the structure is the same as described for the stem. The mesophyll consists of palisade and spongy parenchyma cells which are irregular in shape. The minor veins are surrounded by atriplicoid Kranz anatomy (that is, the veins are surrounded by a layer of Kranz cells which in turn are surrounded by palisade cells) (Fig. 3B). The main veins are not surrounded by Kranz anatomy and the vessels have a large diameter. Throughout the mesophyll, bundles of

raphide crystals are present in no specific pattern (Fig. 3C) and small druse crystals are present inside the palisade cells.

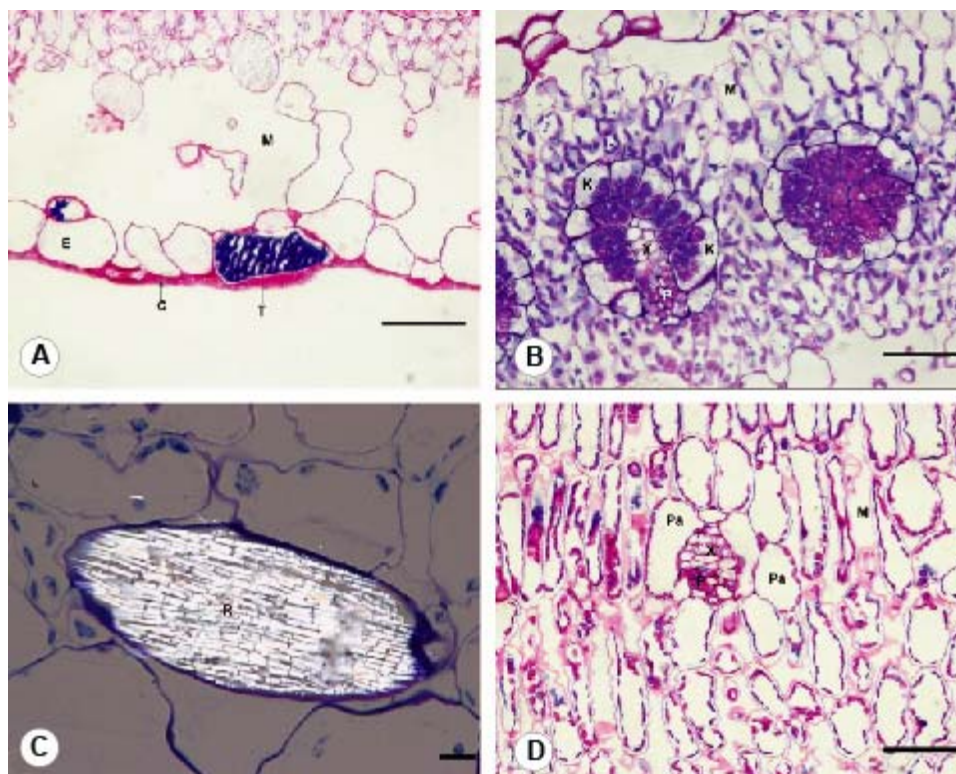


Fig. 3. A. Micrograph of the abaxial leaf surface of *Boerhavia erecta* (C= crystals, E= abaxial epidermis, M= mesophyll, T= tannin). B. Kranz anatomy (K) around the minor veins of *Boerhavia coccinea* var. *coccinea*. (M= mesophyll, P= phloem, X= xylem). C. Raphide crystals (R) in the mesophyll of *Boerhavia hereroensis*. D. Parenchyma cells (Pa) around the minor veins of *Commicarpus pilosus* (M= mesophyll, P= phloem, X= xylem). Bars A, B, D = 50 μ m; C = 10 μ m.

Commicarpus: The structure of the leaf is the same as described for *Boerhavia*, except that the minor veins are not surrounded by Kranz anatomy but with large parenchyma cells (Fig. 3D), and tannin idioblasts are absent from the epidermal cells.

Anthocarp anatomy:

Boerhavia: The anthocarps of the different species have five ribs, except for *B. cordobensis*, which has three wings and *B. erecta* which has five wings. The outer epidermal cells are irregularly brick-shaped to round (Fig. 4A). The outer periclinal wall of the epidermal cells is thickened and impregnated with a thick layer of crystalline granules. The cuticle is thin. The epidermis overlays 3-5 rows of parenchyma cells which are followed by 3-8 rows of sclerenchyma. The sclerenchyma occurs within the ribs and the area between the ribs. Below the epidermis of the ribs, columnar cells sometimes occur which become mucilaginous. Five or six

vascular bundles occur near the sclerenchyma in the ribs. The inner epidermal cells are brick-shaped and the outer periclinal wall is thickened, although not as much as that of the outer epidermis. Bundles of raphide crystals are present throughout the anthocarp in no specific pattern.

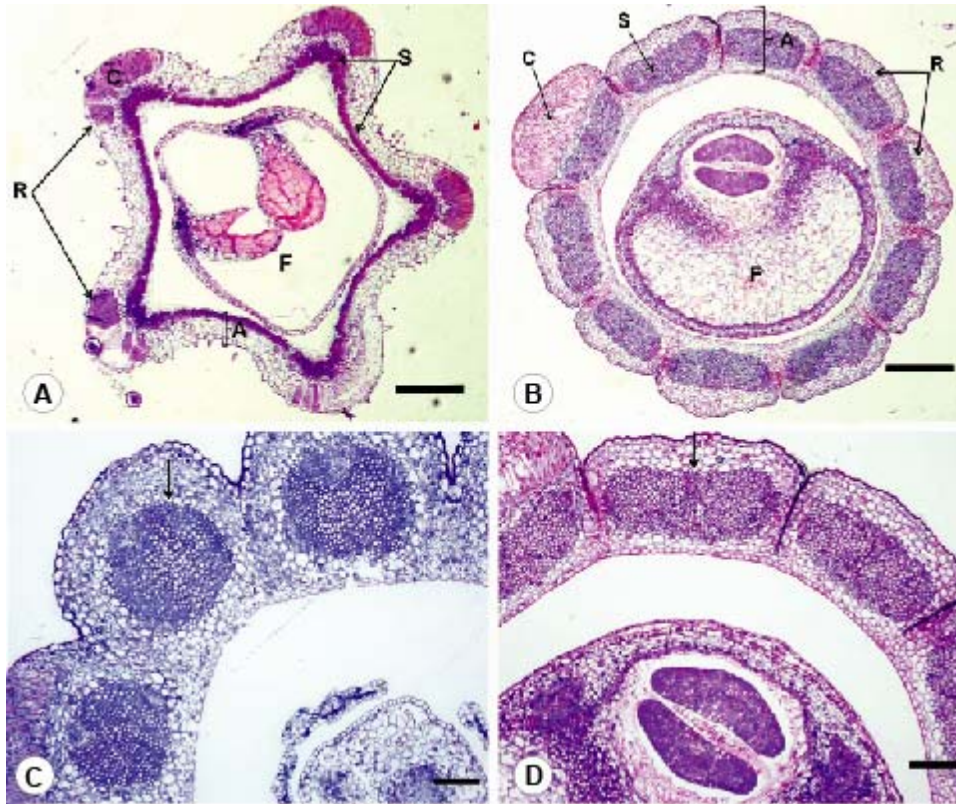


Fig. 4. Light micrograph of a cross section through the anthocarp of *Boerhavia* and *Commicarpus* species. A. Anthocarp of *Boerhavia diffusa* var. *diffusa*. B. Anthocarp of *Commicarpus pilosus*. (A= anthocarp wall, C= columnar cells, F=fruit, R= rib, S=sclerenchyma). C. Sclerenchyma bundle (sclerenchyma indicated by the arrow) with a round outline D. Sclerenchyma bundle with an elongated outline. Bars A: 0.3 mm; B: 0.3 mm; C-D; 100 μ m.

Commicarpus: The anthocarp has 10 ribs (Fig. 4B) and the epidermis is followed by 2-5 rows of parenchyma cells. The sclerenchyma occurs in a bundle within the ribs and, unlike *Boerhavia*, is not present in the area between the ribs. The sclerenchyma bundle is either round (Fig. 4C) or elongated sideways in outline (Fig. 4D). Five vascular bundles occur in the ribs near the sclerenchyma bundle, although it may appear as if two bundles have fused. Towards the inside of the rib the sclerenchyma bundle is followed by 3 rows of parenchyma cells and the inner epidermis. The area between the ribs consists of 3-6 rows of parenchyma cells.

Discussion

Careful observations of the anatomy of the different species suggested that the anatomy within a genus is uniform and can therefore not be used to distinguish among the different species. Several studies had previously shown the importance of certain anatomical characters to distinguish among the genera of the Nyctaginaceae (Fadeyi *et al.*, 1989; Edeoga and Ikem, 2002), and this is also the case for *Boerhavia* and *Commicarpus* in southern Africa.

The trichomes of the Nyctaginaceae are described as glandular and uniserial with ellipsoidal, clavate or spherical terminal cells, or stellate, as in the tribe Leucastereae or branched as in *Pisonia* (Metcalf and Chalk, 1965). Fadeyi *et al.*, (1989) described the trichome morphology of four *Boerhavia* species which occur in Nigeria as variable in their morphology, distribution and abundance and they are generally uniserial and multicellular with an acute apex or the trichomes terminate in a large apical cell. The trichomes of the southern African *Boerhavia* and *Commicarpus* are uniserial and multicellular with globose or clubshaped heads and their size, length, distribution and abundance vary considerably between and within genera and species, so much so that trichomes could not be used to distinguish between the two genera nor species.

The structure of the stem and leaves of *Boerhavia* correspond to the descriptions given by Metcalfe and Chalk (1950, 1983). Current results show that *Commicarpus* has more rows of chlorenchyma than *Boerhavia*, but this character needs further investigation to determine whether it is diagnostic. The anatomy of the leaves of *Boerhavia* and *Commicarpus* differ as *Boerhavia* has Kranz anatomy around the minor veins, which is absent in *Commicarpus*. This corresponds to the finding of Muhaidat *et al.* (2007) who investigated *Commicarpus plumbagineus* Standl., *Boerhavia coccinea* Mill. and *Boerhavia dominii* Meikle & Hewson for the presence of Kranz anatomy in a study investigating the Kranz anatomy and biochemistry of C₄ eudicots. The presence or absence of Kranz anatomy is therefore a diagnostic character to distinguish between *Boerhavia* and *Commicarpus*.

Tannin idioblasts and raphides are recorded for the family by various authors (Bittrich and Kühn, 1993; Edeoga and Ikem, 2002). The tannin idioblasts are absent in *Commicarpus* leaves, but due to the fact that they are not always present in the epidermal cells of *Boerhavia* leaves either, this character cannot reliably be used to distinguish between the two genera. The distribution of the raphides is not in a specific pattern and of no taxonomic value.

Anthocarp morphology is the character by which most genera can be distinguished within the family (Douglas and Manos, 2007) and, likewise, the anthocarp anatomy of the southern African species of *Boerhavia* and *Commicarpus* differ significantly. *Boerhavia* has five-ribbed or three- to five-winged anthocarps with sclerenchyma present within the rib and the area between the ribs. *Commicarpus* has ten ribs with sclerenchyma only present within the rib, and the sclerenchyma bundles can either be round (as in *C. decipiens*, *C. pentandrus*, *C. plumbagineus* var. *plumbagineus* and *C. squarrosus*) or elongated (as in *C. chinensis* subsp. *natalensis*, *C. fallacissimus*, *C. fruticosus*, *C. pilosus* and *C. helenae* var. *helenae*) in outline. However, the reliability of the outline of the sclerenchyma bundles still needs to be investigated further at

different developmental stages of the anthocarp before it can be considered as a diagnostic character with which to divide the *Commicarpus* species into two groups. This distinction could be used in later studies to understand the phylogeny of the genus in southern Africa.

The following key is therefore proposed:

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|-----|--|--------------------|
| 1a. | Anthocarp five ribbed or three- to five-winged; sclerenchyma present within the rib and the area between the ribs; minor veins of the leaves surrounded by Kranz anatomy | <i>Boerhavia</i> |
| 1b. | Anthocarp ten ribbed; sclerenchyma only present in the rib area; minor veins of the leaves surrounded by parenchyma cells | <i>Commicarpus</i> |

Conclusion

The anatomy of the southern African *Boerhavia* and *Commicarpus* species has been described for the first time. The leaf and especially the anthocarp anatomy can be used to distinguish between the two genera, but the anatomy at the species level is uniform and uninformative. However, this study provides evidence that the number of chlorenchyma rows in the stems may be a diagnostic character and that the shape of the sclerenchyma bundles in the anthocarp can possibly be used to divide *Commicarpus* in two groups which can later be used to understand the phylogeny of the genus in southern Africa.

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