# A TAXONOMIC STUDY OF *CRYPTOLEPIS* (APOCYNACEAE) IN SOUTHERN AFRICA

by

# LIZE JOUBERT

Submitted in fulfilment of the requirements for the degree

# MAGISTER SCIENTIAE

in the Faculty of Natural and Agricultural Sciences, Department of Plant Sciences (Botany) at the University of the Free State Bloemfontein

# November 2007

Supervisor: DR. A.M. VENTER Co-supervisor: PROF. R.L. VERHOEVEN Co-supervisor: PROF. H.J.T. VENTER

# CONTENTS

1.	Intro	oduction and historical review	1		
2.	Materials and methods				
	2.1	Micromorphology of pollen and translators	8		
	2.2	Leaf epidermal surfaces and anatomy	9		
	2.3	Seed coat surfaces	10		
	2.4	Taxonomic treatment of genus and species	10		
	2.5	Floral morphology	14		
	2.6	Format of references	15		
3.	Leaf and floral terminology in Cryptolepis R.Br.				
	3.1	Colleters	16		
	3.2	Leaf venation	18		
	3.3	The inflorescence	22		
	3.4	Terminology and structure of the flower	22		
4.	Pollen and translators				
	4.1	Introduction	32		
	4.2	Results	35		
		4.2.1 Translator	35		
		4.2.2 Pollen	38		
	4.3	Discussion	47		
5.	Anatomy and micromorphology of leaf epidermal				
	surf	surfaces			
	5.1	Introduction	52		
	5.2	Results	53		
		<i>C. capensis</i> Schltr.	53		
		C. cryptolepioides (Schltr.) Bullock	57		
		C. decidua (Planch. ex Benth.) N.E.Br.	60		

		C. delagoensis Schltr.	63
		C. oblongifolia (Meisn.) Schltr.	67
		<i>C. obtusa</i> N.E.Br.	70
	5.3	Discussion	73
6.	Micromorphology of seed coat surfaces		
	6.1	Introduction	75
	6.2	Results	76
		C. capensis	76
		C. cryptolepioides	82
		C. decidua	87
		C. delagoensis	92
		C. oblongifolia	97
		C. obtusa	101
	6.3	Discussion	106
7.	Taxonomic treatment		
	7.1	Generic description of Cryptolepis in	
		southern Africa	109
	7.2	Key to the southern African Cryptolepis species	112
	7.3	Description of species	114
		C. capensis	114
		C. cryptolepioides	119
		C. decidua	124
		C. delagoensis	129
		C. oblongifolia	132
		C. obtusa	138

8.	Discussion and conclusions		
	8.1	Taxonomically important characteristics for	
		distinguishing the genus	143
	8.2	Taxonomically important characteristics for	
		distinguishing the southern African Cryptolepis	
		species	144
	8.3	Taxonomical position of C. decidua	147
References			149
Summary			164
Opsomming			166
Acknowledgements			
Addendum			

# **CHAPTER 1**

#### INTRODUCTION AND HISTORICAL REVIEW

The genus *Cryptolepis* R.Br. mainly consists of slender, woody climbers, but a small number of low growing shrubs and one tree species are also included. The generic name *Cryptolepis* is derived from *Kryptos* = 'hidden', and *Lepis* = 'a scale', which refers to the corona lobes that close off the corolla tube mouth and hide the anthers and stigma (Santapau and Irani, 1960; Stearn, 1991). Members of this genus occur throughout Africa, the island Socotra, India, southern China, Malaysia and Sri Lanka. Most of these regions are under-collected and some species are known from only one or two specimens. The majority of species occur in tropical forests or savanna, but a small number are restricted to semi-desert regions. *Cryptolepis* species are never a dominant part of the vegetation and, since most seemingly have little medicinal or any other economic value, they are usually overlooked.

*Cryptolepis* belongs to the family Apocynaceae, subfamily Periplocoideae. The type genus of the Periplocoideae, *Periploca* L., was first described in 1753 by Linnaeus, who placed it in the Order Pentandria Digynia. Robert Brown described the genus *Cryptolepis* in 1810 from a specimen collected in India by Buchanan Hamilton (Fig. 1.1). Though Brown (1810) never assigned a type species, the specimen on which he based the genus description, was later named *Crytolepis buchananii* by Roemer and Schultes (1819). This species is now considered to be the type species of the genus (Santapau and Irani, 1960).

The status of the family Apocynaceae and the subfamily Periplocoideae have varied considerably in the past. The family Apocynaceae was first described by Jussieu (1789). Brown (1810) split the family Asclepiadaceae from the Apocynaceae using pollen characteristics to distinguish between the two families, the Apocynaceae having single pollen grains and no translators, whereas the Asclepiadaceae have pollinia and translators (Brown, 1810; Endress, 2001; Endress and Bruyns, 2000). Brown (1810) further divided the Asclepiadaceae

into three subfamilies namely Asclepiadeae verae (now Asclepiadoideae), the Periploceae (now Periplocoideae) and the genus *Secamone* R.Br. by itself in an unnamed category which later became the Secamonoideae (Endress, 2001). Brown (1810) must have mistakenly placed *Cryptolepis* in the family Apocynaceae, since members of the genus *Cryptolepis* have translators and pollen tetrads. Later Bentham (1876) and Hooker (1883) placed *Cryptolepis* in the Asclepiadaceae (then Asclepiadeae).

Schlechter (1905a, 1924) proposed that the Asclepiadaceae, as described by Brown (1810), be subdivided into two families, namely Asclepiadaceae and Periplocaceae. This classification was supported by later authors such as Bullock (1956), Hutchinson (1973), Huber (1973), Dyer (1975), Arekal and Ramakrishna (1980), Kunze (1993, 1996), Swarupanandan *et al.* (1996), Omlor (1996) and Venter and Verhoeven (1997). *Cryptolepis* was placed in the Periplocaceae.

Schlechter (1924) separated the Asclepiadaceae and Periplocaceae on the basis of pollen characteristics. The Periplocaceae were characterized by pollen arranged in tetrads, these loosely deposited on spoon-like translators with a soft, sticky, amorphous viscidium (or sticky disc). The Asclepiadaceae, in contrast, were characterized by pollen grouped into pollinia, these attached via a caudicle to a clip-like corpusculum (Endress and Bruyns, 2000). Later studies by Schill and Jäkel (1978) and Verhoeven and Venter (1998) revealed that several Periplocoid genera have pollen tetrads gathered into pollinia. Endress (2001) further suggested that the translator stalk in the Periplocoideae is similar in cross-section to the clip-like corpusculum of the Asclepiadoideae and Secamonoideae, suggesting a close relationship between these families. Indeed, Kunze (1993) regarded the upper part of the adhesive disc and the stalk of the periplocoid translator as homologous with the corpusculum of the Asclepiadoideae and Secamonoideae.



Fig. 1.1 Type specimen of *Cryptolepis* R.Br. collected by Dr. Buchanan Hamilton and later named *C. buchananii* Roem. & Schult.

These and several other characteristics show a gradual transition from the Periplocoideae, through the Secamonoideae to the Asclepiadoideae, supporting a classification in which the family Asclepiadaceae is subdivided into three subfamilies namely Periplocoideae, Secamonoideae and Asclepiadoideae. However, several studies have revealed a similar gradual transition from the Apocynaceae through the Periplocoideae and Secamonoideae to the Asclepiadoideae (Endress, 2001). In *Apocynum* L., the type genus of the Apocynaceae, for instance, pollen is arranged in tetrads and the style-head produces a secretion that hardens to form simple strap-like translators that resemble those of the Periplocoideae (Nilsson *et al.*, 1993). Based on this apparent monophyly of the families Apocynaceae and Asclepiadaceae, Hallier (1905), Safwat (1962), Thorne (1992), Judd *et al.* (1994) and Takhtajan (1997) suggested that the two families be united into a single family, the Apocynaceae *sensu lato*.

Molecular studies by Sennblad and Bremer (1996) and Civeyrel et al. (1998) indicated that the Apocynaceae sensu stricto are paraphyletic and therefore do not represent a natural group. Based on a combination of morphological and molecular data, Endress and Bruyns (2000) suggested a classification in which the two families, Apocynaceae sensu stricto and Asclepiadaceae, are combined into the Apocynaceae sensu lato with five subfamilies namely the Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae and Asclepiadoideae. Subsequent molecular studies by Potgieter and Albert (2001) showed that the subfamilies Asclepiadoideae, Secamonoideae and Periplocoideae are well supported as monophyletic groups, but showed no support for the monophyly of the Apocynoideae and Rauvolfioideae as delimited by Endress and Bruyns (2000). Current morphological and molecular evidence therefore supports a single family, Apocynaceae sensu lato with three monophyletic subfamilies, Secamonoideae, Asclepiadoideae and Periplocoideae, but further research is needed to establish the relationship and phylogenetic circumscription of the subfamilies Apocynoideae and Rauvolfioideae in the Apocynaceae.

4

The subfamily Periplocoideae comprises 190 species belonging to 32 genera (Venter and Verhoeven, 1997). These numbers have varied considerably in the past and lonta and Judd (2007) proposed the great diversity of the subfamily, morphological variability of closely related taxa, the lack of information on several poorly collected taxa and the small, complex flowers which are difficult to interpret from herbarium material, as probable causes for the instability of classification in the subfamily.

The Periplocoideae are restricted to the tropical and sub-tropical parts of the Old World where they are widely, though unevenly, distributed over Africa, Madagascar and Asia. *Cryptolepis*, *Raphionacme* Harv. and *Periploca* are the only genera that occur in both Africa and Asia. *Cryptolepis* occurs over the whole of sub-Sahara Africa, reaching across Somalia and Socotra into the southern parts of Asia (Venter *et al.*, 2006b). This wide distribution, together with relatively simple floral characters compared to other genera in the subfamily, suggests that *Cryptolepis* is one of the least specialized genera in the subfamily and possibly closely resembles the ancestral type (Good, 1952; Safwat, 1962).

*Cryptolepis*, consisting of 30 species, is the second largest genus in the subfamily, the largest being *Raphionacme* with 36 species (Venter, pers. com. Department of Plant Sciences, University of the Free State). The seemingly basal position of *Cryptolepis*, in addition to its large size in a subfamily that consists mainly of mono- or ditypic genera, could lend it considerable taxonomic and systematic significance. Determining the evolutionary history of the genus may shed some light on the phylogenetic relationship of the Apocynoideae with the Periplocoideae, and could eventually aid the development of a sound classification system for the Apocynaceae *sensu lato*. However, a complete taxonomic treatment is a prerequisite for determining the evolutionary history of the genus of the genus and at present no such study exists. All literature on the taxonomy of *Cryptolepis* is based on a regional perspective and no treatment includes all species.

Apart form the purely taxonomic need for a revision of the genus, growing interest in the phytochemistry of *Cryptolepis* necessitates the compilation of effective keys and a phylogenetic classification. The phytochemistry of the Periplocoideae is poorly studied, but in the recent past such studies have been done on three *Cryptolepis* species, namely *C. buchananii, C. sanguinolenta* (Lindl.) Schltr. and *C. oblongifolia* (Meisn.) Schltr. Some of these studies have focused on the antimicrobial and antiplasmodial (antimalarial) activities, as well as toxicity of compounds isolated from different *Cryptolepis* organs (Ansah *et al.,* 2005; Cimanga *et al.,* 1991, 1996a, 1996b, 1997; Dutta *et al.,* 1980; Paulo *et al.,* 1984; Shah and Khare, 1981). If any compound of medicinal or economic value is isolated from *Cryptolepis*, a sound taxonomic treatment of the genus will be of significant importance since chemotaxonomic data can only be effectively applied if correct species identification is possible. Further chemotaxonomic research should be based on phylogenetic species relationships.

Several changes in the number and names of species occurred since several genera such as Curroria Planch. (Brown, 1902; Venter and Verhoeven, 1997), Ectadiopsis Benth. (Schlechter, 1896), Mitolepis Balf.f. (Venter and Verhoeven, 1997) and Socotranthus Kuntze (Venter and Verhoeven, 1997) have been declared synonymous with Cryptolepis. A number of new species, Cryptolepis vemenensis Venter & R.L.Verh. (Venter and Verhoeven, 1999), C. nugaalensis Venter & Thulin (Venter et al., 2006b) and C. somaliensis Venter & Thulin (Venter et al., 2006b), have been described in recent years. Others, such as C. albicans Jum. & H.Perrier of Madagascar (now Pentopetia albicans (Jum. & H.Perrier) Klack.) have been moved to other genera (Klackenberg, 1999). The urgent need for a sound taxonomic treatment of the genus Cryptolepis is illustrated by the chemotaxonomic analysis of the genus by Paulo and Houghton (2003) wherein confusion occurs as to the correct classification of the genus within the Periplocoideae. The same publication contains discussions on the distribution of Cryptolepis species such as C. pendulina (Venter & D.V.Field) P.I.Forst., C. gravi P.I.Forst., C. nymanii (Schuman) P.I.Forst., C. papillata

6

P.I.Forst. and *C. lancifolia* P.I.Forst., which had already been placed in synonomy with other genera by Venter and Field (1989) and Venter and Verhoeven (2001).

The aim of the current study is to provide a taxonomic revision of the six *Cryptolepis* species that are indigenous to the southern African sub-region. The study further aims at identifying characteristics that may be used to effectively delimit the *Cryptolepis* species and the compilation of a taxonomic key for species identification. This study is introductory to a full monograph on the 30 species of *Cryptolepis*.

# CHAPTER 2 MATERIALS AND METHODS

## 2.1 Micromorphology of pollen and translators

Fresh flowers, preserved in 3% phosphate-buffered glutaraldehyde, or flowers collected from herbarium vouchers, rehydrated in 3% phosphate-buffered glutaraldehyde for 48 hours, were used to obtain pollen and translators. The flowers were dissected and the anthers and translators removed.

For transmission elecron microscopy anthers were postfixed in 2% osmium tetroxide, dehydrated in an alcohol series and embedded in Spurr's low-viscosity resin. Sections were cut using a LKB Ultrotome III microtome and glass knives, stained with uranyl acetate followed by lead citrate, and exmined with a Philips CM 100 electron microscope at 60 kV.

For scanning elecron microscopy (SEM) pollen was removed from the anther thecae in 100% alcohol and the rest of the anther material discarded. Pollen was washed into centrifuge tubes with glacial acetic acid and prepared according to the acetolysis method of Erdtman (1960) and Hesse and Waha (1989). The acetolysed pollen was prepared according to the method of Reitsma (1969) by rinsing in acetic acid, washing twice with water, followed by alcohol, before being mounted on stubs, air-dried and sputter coated with gold. The pollen samples were studied and photographed using a Jeol Winsem 6400 or Shimadzu Superscan SSX-550 scanning electron microscope at 10 kV and a working distance of 17 mm.

The remainder of the acetolysed pollen material was mounted in glycerine jelly and sealed with paraffin wax for light microscopy studies. Samples were examined with an Olympus AX70 photo microscope. Where available, at least 30 pollen tetrads of each specimen were investigated and the tetrad length and width were measured. Pollen tetrad measurements are given as average values for length and width followed by the standard deviation for each measurement as well as the minimum and maximum measurements. The length to width ratio of all tetrads were calculated and the mean length to width ratios are given in Table 4.2.

Translators were mounted on stubs using double sided tape and sputter coated, then photographed and measured with the Jeol Winsem 6400 or Shimadzu Superscan SSX-550 Scanning Electron Microscope at 10 kV and a working distance of 17 mm. Translator measurements are given in Table 4.1.

# 2.2 Leaf epidermal surfaces and anatomy

Fresh leaves, preserved in 3% phosphate-buffered glutaraldehyde, or leaves collected from herbarium vouchers, rehydrated for 48 hours in 3% phosphate-buffered glutaraldehyde, were used for studying the epidermal surface with a SEM and the leaf anatomy using a light microscope.

For epidermal surface studies, leaf samples were cut into 5 x 5 mm pieces and dehydrated in an alcohol series. The dehydrated leaf samples were critical point dried, mounted on stubs with epoxy glue and painted at the corners with silver paint to improve conductivity. The samples were then sputter coated and studied with the Jeol Winsem 6400 or Shimadzu Superscan SSX-550 scanning electron microscope at 10 kV and a working distance of 17 mm.

For anatomical studies, glutaraldehyde fixed leaf samples were rinsed in phosphate buffer, dehydrated in an alcohol series and embedded in Spurr's low-viscosity resin. Sections were made using a LKB Ultrotome III microtome and glass knifes. Sections (3–5  $\mu$ m) were affixed to microscope slides by heating at 100°C until the water evaporated, and stained for three minutes with 1% Toluidine blue in 1% borax. Sections were rinsed with distilled water, and air

dried before the coverslips were mounted, whereafter they were examined with an Olympus AX70 photomicroscope.

Descriptions of leaf anatomy and surface morphology follow the terminology of Metcalfe (1979) and Wilkinson (1979).

#### 2.3 Seed coat surfaces

Dry seeds, obtained from mature fruit on herbarium specimens, were mounted on stubs with epoxy glue and painted on the tip with silver paint. The seeds were sputter coated and photographed using a Jeol Winsem 6400 scanning electron microscope at 10 kV and a working distance of 25 mm. Seed coat surface descriptions follow the terminology of Boesewinkel and Bouman (1984) and Barthlott (1981).

#### 2.4 Taxonomic treatment of genus and species

Only *Cryptolepis* species indigenous to the southern African sub-region were included in the present study. This region consists of South Africa with nine provinces, Namibia, Botswana, Lesotho and Swaziland (Fig. 2.1).

Where possible fresh material was collected and herbarium vouchers were prepared. Detailed observations of the habitat as well as vegetative and floral characteristics of the species were made. Herbarium specimens on loan from southern African herbaria, as well as from the major herbaria of Europe and the U.S.A. were also studied. All existing type specimens were examined, type literature was confirmed and synonyms were declared. Where holotypes were missing, like those destroyed in the bombing of Berlin (B) during the Second World War, isotypes or syntypes were located and lectotypes declared from these. Where no types could be found neotypes were declared.



Fig. 2.1 Countries and provinces of southern Africa. B: Botswana, LE: Lesotho, NA: Namibia, S: Swaziland. Provinces of South Africa: EC: Eastern Cape, G: Gauteng, KZN: KwaZulu-Natal, L: Limpopo, MP: Mpumalanga, NC: Northern Cape, NW: North West, WC: Western Cape. Scale bar = 400 km.

Literature used in the description of species includes the following:

Leaf shape descriptions follow Systematics Association Committee for Descriptive Biological Terminology (1962) and Lawrence (1951).

Spelling of author names follow Brummitt and Powell (1992).

Spelling and abbreviations of taxonomic literature cited as in Stafleu and Cowan (1976).

Nomenclatural citation and designation of type material follow the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000).

Herbaria acronyms are given as in Holmgren et al. (1990).

Localities of all specimens cited were located in and are arranged according to the quarter-degree reference system of Edwards and Leistner (1971), Leistner and Morris (1976) and the Reader's Digest Atlas (Walton, 1984).

Associated species and author names follow Germishuizen and Meyer (2003).

Specimens from the following herbaria were examined:

- B Herbarium, Botanischer Garten und Botanisches Museum Berlin-Dahlem,
  Berlin, Germany.
- BLFU Geo Potts Herbarium, Department of Plant Sciences, University of the Free State, Bloemfontein, South Africa.
- BOL Bolus Herbarium, University of Cape Town, Rondebosch, South Africa.
- BM Herbarium, Botany Department, The Natural History Museum, London, England.
- BR Herbarium, Nationale Plantentuin van België, Domein van Bouchout, Meise, Belgium.
- COI Herbarium, Botanical Institute, University of Coimbra, Coimbra, Portugal.
- G Herbarium Conservatoire et Jardin botaniques de la Ville de Genève, Genève, Switzerland. (G-DC).
- GRA Herbarium, Botanical Research Institute, Grahamstown, South Africa.
- J C.E. Moss Herbarium, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa.

- K Herbarium, Royal Botanic Gardens, Kew, Richmond, England.
- KMG Herbarium, McGregor Museum, Kimberley, South Africa.
- M Herbarium, Botanische Staatssammlung, München, Germany.
- MO Saint Louis Herbarium, Missouri Botanical Garden, Missouri, U.S.A.
- NBG Compton Herbarium, National Botanical Gardens of South Africa, Claremont, South Africa.
- NH Natal Herbarium, Botanical Research Unit, Durban, South Africa.
- NU Herbarium, Botany Department, University of Natal, Pietermaritzburg, South Africa.
- PRE National Herbarium, National Biodiversity Institute, Pretoria, South Africa.
- PRU H.G.W.J. Schweickerdt Herbarium, Botany Department, University of Pretoria, Pretoria, South Africa.
- SAM Herbarium of the South African Museum, incorporated in National Botanical Gardens (NBG), Claremont, South Africa.

SRGH National Herbarium and Botanic Garden, Harare, Zimbabwe.

- STE Stellenbosch Herbarium, National Botanical Institute, Stellenbosch, South Africa (now incorporated into NBG).
- W Herbarium, Department of Botany, Naturhistorisches Museum Wien, Vienna, Austria.

WIND National Herbarium of Namibia, Windhoek, Namibia.

Z Herbarium, Institut für Systematische Botanik, Universität Zürich, Zürich, Switzerland.

# 2.5 Floral morphology

Where possible fresh flowers were dissected in the field and studied using a hand lens. SEM studies were carried out from fresh flowers preserved in 3% phosphate-buffered glutaraldehyde or flowers collected from herbarium vouchers, rehydrated in 3% phosphate-buffered glutaraldehyde for 48 hours and dissected. The dissected flowers were dehydrated in an alcohol series and critical point dried. The dried specimens were mounted on stubs with epoxy glue, painted at the corners with silver paint and sputter coated. These specimens were then examined and photographed using a Jeol Winsem 6400 scanning electron microscope at 10 kV and a working distance of 25 mm.

For light microscopy flowers were fixed in 3% phosphate-buffered glutaraldehyde, postfixed in 2% osmium tetroxide, dehydrated in an alcohol series and embeded in Spurr's low-viscosity resin. Sections were made using a LKB Ultrotome III microtome and glass knives. Sections (3–5 µm) were affixed to microscope slides by heating at 100°C until the water evaporated, and stained for three minutes with 1% toluidine blue in 1% borax. Sections were rinsed with distilled water, and air dried before the coverslips were mounted, whereafter they were examined with an Olympus AX70 photomicroscope.

Flower samples for studying with a dissection microscope, were collected from herbarium vouchers and rehydrated by heating in a diluted soapy solution. The flowers were dissected and mounted on specimen cards using herbarium glue. These samples were studied and floral parts measured using an Olympus SZ-40 stereomicroscope.

# 2.6 Format of references

References are given according to the specifications of the South African Journal of Botany. The list of references is arranged alphabetically and chronologically, making use of a, b, c etc. if an author published more than one publication during a given year. If the same author has published both on his own and as senior author with others the solo publications are listed first, followed by publications with one co-author. Thereafter publications with more than one co-author are listed. These are not arranged alphabetically, but chronologically to ease comparison with references given in the text, in which only the name of the first author, followed by *et al.* and the publication date are given (e.g. Jones *et al.*, 2000). Journal titles are given according to Alkire (2005).

# **CHAPTER 3**

## LEAF AND FLORAL TERMINOLOGY IN CRYPTOLEPIS

This chapter is aimed at explaining the specialized terminology used for the description and discussion of *Cryptolepis*.

### 3.1 Colleters

Colleters are taxonomically important in several families, including the Apocynaceae (Thomas, 1991; Thomas and Dave, 1991). Several types of colleters have been described (Thomas, 1991), but those occurring in the Apocynoideae are usually of the standard type, being conical and often dentate at the tip (Figs. 3.1 a, b). The colleter consists of a central core of parenchyma cells, ensheathed by radially elongated epithelial cells and covered by a thin cuticle (Fig. 3.1 d). In *Cryptolepis* standard type colleters occur in the leaf axils, at the bases of bracts on the inflorescences and as pairs at the inner margins of sepal bases (Figs. 3.1 a, b). Colleters are often associated with unicellular trichomes and in one of the southern African species, *C. decidua*, the colleters at the sepal bases are replaced by dense tufts of trichomes (Fig. 3.1 c). Thomas and Dave (1991) found that colleters did not function as nectaries and Thomas (1991) suggests that colleters may secrete a mucilaginous or resinous substance which covers and protects developing meristems.





<image>

(C)

(d)

(b)

Fig. 3.1 (a) *C. obtusa:* Upper surfaces of sepals showing paired dentate colleters at sepal margins. (b) *C. capensis:* Paired dentate colleters at inner sepal bases. (c) *C. decidua:* Upper surface of sepals showing clusters of trichomes at sepal bases and two apocarpous, semi-inferior ovaries. (d) Light micrograph of *C. obtusa* colleter, showing central core of parenchyma cells, ensheathed by radially elongated epithelial cells. col: colleters, e: epithelial cells, o: ovaries, p: parenchyma cells, s: sepal, t: unicellular trichomes. Scale bars: (a, b, c) = 100 µm, (d) = 20µm. ((a, d) *Venter, H.J.T. 9299*, (b) *Joubert, L. 31*, (c) *Verhoeven, R.L. 165*)

# 3.2 Leaf venation

The terminology of Hickey (1979) was used for the description of leaf venation. The following definitions of certain venation characteristics are quoted from Hickey (1979):

### Venation type

Venation types found in *Cryptolepis* fall under the Hyphodromous or Camptodromous venation divisions (Fig. 3.2 a). Hyphodromous venation is defined as a venation pattern in which all but the primary vein is absent, rudimentary, or concealed within a coriaceous or fleshy mesophyll. Camptodromous venation is defined as a venation type in which secondary veins do not terminate at the leaf margin, and includes Brochidodromous, Cladodromous, Eucamptodromous and Reticulodromous venation (Fig. 3.2 a). Brochidodromous venation is defined as a venation type in which the secondary veins are joined together in a series of prominent arches. In Eucamptodromous venation the secondaries are upturned and gradually diminish apically inside the margin, connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops. Reticulodromous venation is characterized by secondaries losing their identity toward the leaf margin by repeated branching into a vein reticulum.

### Orders of venation

Venation is differentiated into a series of size classes (Fig. 3.3). In *Cryptolepis* the primary veins (1°) are the thickest veins of the leaf, occurring singly as the midvein. Secondary veins (2°) are the next smaller size class that arise from the primaries. Intersecondary veins have a thickness intermediate between that of the second and third order veins, generally originating from the medial primary vein, interspersed among the secondary veins, and having a course parallel, or nearly so, to them. Two types of intersecondary veins may be discerned, namely simple intersecondary which consist of a single vein segment and composite

intersecondary which consist of coalesced tertiary vein segments for over 50% of its length.

Tertiary veins (3°) are the next finest branches of the secondary veins and those branches of equal thickness from the primaries. Arrangement of the tertiary veins is termed percurrent if the tertiaries from opposite secondaries join. The next finer order of veins originating from the tertiaries and those of equal size from lower order veins is known as the quaternary (4°) venation and the veins originating from these and those of equal size from lower orders are the quinternaries (5°). Quaternary and quinternary venation may also be referred to as higher order venation. Veinlets are the freely ending ultimate veins of the leaf and veins of the same order which occasionally cross areoles to become connected distally.

Areoles are the smallest areas of the leaf tissue surrounded by veins which, taken together, form a continuous field over most of the area of the leaf (Fig. 3.2b). Thus, smaller areas occasionally formed when veinlets cross their areoles are excluded. Any order of venation in a leaf from the primary to the highest order below that of freely ending veinlets can form one or more sides of an areole. However, only the order represented by the veinlets will intrude, or occasionally cross, the islets formed by the non-freely ending veins. The appearance and characteristics of the areoles are termed areolation. Development of the areoles may be one of the following: well developed with meshes of relatively consistent size and shape; imperfect with meshes of irregular shape, more or less variable in size; incompletely closed meshes with one or more sides of the mesh not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape; areolation lacking, as in hyphodromous or succulent leaves.

19



Fig. 3.2 Leaf architectural features: (a) Types of venation. (b) Areole development. (From Hickey, 1979)



Fig. 3.3 Leaf architectural features: orders of venation and vein configuration. (From Hickey, 1979)

### 3.3 The inflorescence

The flowers may be solitary or occur in simple to complex cymose inflorescences. The inflorescences vary from lax (Fig. 3.4 a), sub-compact to compact (Fig. 3.5). The cymes may be composed of monochasiums or dichasiums with branches terminating in monochasiums. At every branching point in the inflorescence paired bracts occur with dentate colleters at their bases.

### 3.4 Terminology and structure of the flower

The Apocynaceae has highly modified flowers with many specialized features. As a result a unique terminology has been developed to accurately describe the different structures in the subfamilies and genera.

The flowers of *Cryptolepis* are pentamerous, actinomorphic, bisexual. The sepals are free, narrowly ovate to ovate, glabrous or with fimbriate margins. Colleters are present at the sepal bases. These colleters are usually single, conical to dentate structures and one colleter is present at each inner margin of a sepal, resulting in ten paired colleters arranged around the sepal bases of a flower (Figs. 3.1 a, b). Occasionally colleters are absent and trichomes occur in dense clusters along the sepal bases, with no clearly discernable organization (Fig. 3.1 c).

Figs. 3.6, 3.7 a and b show the floral morphology of *Cryptolepis*. The corolla consists of a tube and lobes that, in the southern African *Cryptolepis* species are always longer than the tube. When in bud the corolla lobes are dextrorsely contorted (Fig. 3.8 a). The degree of contortion varies from full-turn helically twisted (Fig. 3.4 a) to half-turn helically twisted or only slightly turned (Fig. 3.5). The corolla tube is differentiated into an upper and a lower portion. The lower tube consists of the congenitally fused corolla, stamens and nectaries (Venter and Verhoeven, 2001). The stamens and nectaries are therefore epipetalous.

22

The pocket-like nectaries alternate with the stamens (Fig. 3.9 b). The nectar pockets, in which the nectar accumulates, occur at the level where the filaments arise from the corolla. This ring of nectary pockets also marks the upper limit of the lower corolla tube and the beginning of the upper corolla tube (Fig. 3.9 b) (Venter and Verhoeven, 2001).

In *Cryptolepis* the upper corolla tube is campanulate and arises by postgenital fusion of the corolla (Fig. 3.8 b) (Venter and Verhoeven, 2001). Kunze (2005) poses the question why members of the Apocynaceae, a highly evolved clade in the sympetalous Gentianales, would develop the less derived choripetalous ontogeny, only to form a tube by postgenital fusion. The answer to this question lies in the development of a corolline corona in the upper corolla tube. According to Kunze (2005) a corolline corona only develops in postgenitally fused tubes of the Apocynaceae. Postgenital fusion is a prerequisite for the development of a corolline corona initiation requires the presence of meristematic tissue along the petal margins. In congenitally fused tubes the meristematic bases of the petals fuse laterally to form an annular meristematic zone which elongates to from the tube and can not give rise to a corolline corona (Kunze, 2005).

In *Cryptolepis* the primary corona arises around the middle of the upper corolla tube, some distance above the stamen insertion, and alternates with the corolla lobes (Figs. 3.7 a; 3.8 b). The origin of the corona is often well marked by the presence of a spongy coronal foot at the base of each corona lobe. Usually the corona lobes are clavate and included in the corolla tube. The apices of these corona lobes may touch or fit tightly to form a dome over the style-head, closing off the lower corolla tube. In such cases the lower corolla tube is only accessible through openings between the corona bases (Figs. 3.4 b; 3.5). These openings are situated directly above the nectar pockets of the lower corolla tube. The corona lobes are rarely filiform and may be slightly exserted from the mouth of the corolla tube. In such cases the corona lobes do not touch to form a closed dome-like structure as described above.

In some *Cryptolepis* species a secondary corona is present in the corolla lobe sinuses (Fig. 3.5). The secondary corona occurs in the form of pockets in the corolla lobe sinuses, characteristic of postgenital fusion of the corolla tube (Kunze, 2005). Occasionally filiform lobes may arise from the pocket margins (personal observation); however, none of the southern African species exhibit this characteristic.

The stamens, alternating with the corolla lobes, are inserted at the base of the upper corolla tube. The filaments are short, carrying simple anthers (Figs. 3.9 a, b). The anthers connive over the style-head with their connective apices touching and their bases fused to the margin of the style-head, thus forming the gynostegium (Venter and Verhoeven, 2001). Each anther consists of two thecae, each with two locules (Fig. 3.8 b) and a connective that is elongated beyond the thecae to form a small, lobular to deltoid terminal appendage (Venter and Verhoeven, 2001) (Fig. 3.9 a).

The gynoecium consists of two apocarpous, semi-inferior ovaries (Figs. 3.1 c; 3.7 a). The two short styles unite terminally to from a compound style, which gives rise to a pentagonal style-head. The style-head is divided into three zones, namely the upper, marginal and lower zones. Alternating with the stamens are five grooves in the style-head (Fig. 3.7 a). The epithelial cells of each groove secrete a substance which hardens to form a translator (Fig. 3.7 b). The translators of *Cryptolepis* consist of a sticky or adhesive disc which is secreted on the lower zone of the style head. The sticky disc is connected to a spoon-shaped receptacle on the upper zone via a short stipe or stalk. Two adjacent anther thecae shed their pollen onto the receptacle of a single translator. The sticky disc of each translator is situated directly above a nectar pocket so that the translator is attached to any insect attempting to reach the nectar, which then pulls the translator away from the style-head and carries it to the next flower.

All elements of the *Cryptolepis* flower serve to optimise pollination efficiency. The secondary corona lobes direct insects along the corolla lobes, down to the

openings left by the bases of the primary corona, directly to the nectar pockets, which are located below the position of the sticky pads of the translators (Figs. 3.4 b; 3.5; 3.7 b).



<image><image>

Fig. 3.4 *C. capensis* (a) Lax inflorescence with bud, showing full turn helically twisted corolla lobes, and mature flower with reflexed corolla lobes. (b) Mature flower showing corona lobe apices fitting tightly to form a closed dome (d) over the gynostegium and openings (op) between corona bases. ((a, b) *Joubert, L. 31*)



Fig. 3.5 Compact inflorescence of *C. oblongifolia,* showing buds with corolla lobes slightly turned and mature flower with spreading corolla lobes. Primary corona lobes touch dome-like (d) over gynostegium with openings (op) between corona bases. Secondary corona pockets (sc) are present in corolla lobe sinuses. (*Joubert, L. 26*)



Fig. 3.6 Diagrammatic longitudinal section of a *Cryptolepis* flower.



Fig. 3.7 Internal structure of the flower of *C. obtusa*. (a) Lower and upper corolla tubes with corona lobes in the upper corolla tube. (b) Compound style head with translators in grooves and adhesive discs positioned directly above nectar pockets. Scale bars: (a) = 1 mm, (b) = 500  $\mu$ m. ((a, b) *Venter, H.J.T. 8783*)



Fig. 3.8 Light micrographs of *C. oblongifolia* bud. (a) Dextrorsely contorted corolla lobes. (b) Upper corolla tube, formed by post genital fusion of corolla lobes, showing corona lobes and anthers around style head. a: anther; cl: corona lobe; s: style-head. Scale bars: (a, b) =  $200 \mu m.$  ((a, b) *Joubert, L. 26*)



Fig. 3.9 (a) SEM micrograph of a *C. capensis* flower, showing glabrous lower corolla tube below stamen. (b) SEM micrograph of *C. obtusa* flower, showing nectary shelf and cluster of trichomes on lower corolla tube, below stamen insertion. a: anther; f: filament; t: trichomes; n: nectary pocket. Scale bars: (a) =  $500 \mu m$ , (b) =  $100 \mu m$ . ((a) *Venter, H.J.T. 8783*, (b) *Bingham, M.G. 1442*)

# CHAPTER 4 POLLEN AND TRANSLATORS

#### 4.1 Introduction

Palynology has been shown to be of great value in taxonomic and phylogenetic studies in all plant families (Walker and Doyle, 1975). In the Apocynaceae palynological data is of use in differentiating between subfamilies and gives some indication as to phylogenetic relationships of the subfamilies, as well as relationships of genera and species within the subfamilies. In their palynological survey of 408 species representing 114 genera of the Asclepiadoideae (then Asclepiadaceae) Schill and Jäkel (1978) found that palynology mostly supported the classification of Schumann (1897) and that pollen and translator characteristics were useful in differentiating higher taxa. Studies by Galil and Zeroni (1969), El-Gazzar and Hamza (1973), Nilsson (1986, 1990), Endress *et al.* (1990), Kunze (1993), Nilsson *et al.* (1993), Civeyrel (1994), Verhoeven and Venter (2001) and Verhoeven *et al.* (2003) have supported the findings of Schill and Jäkel (1978).

Studies by Arekal and Ramakrishna (1980), Schick (1982), Verhoeven *et al.* (1989), Venter *et al.* (1990a), Kunze (1993), Verhoeven and Venter (1988, 1993, 1994a, 1994b, 1997, 1998) and Nilsson *et al.* (1993) have added greatly to our current knowledge of Periplocoideae pollen. It has been shown by these studies that, although some variation in taxonomic importance does occur regarding the pollen of the subfamily, palynological characteristics show a high level of homogeneity and are generally of little value in distinguishing genera and species (Verhoeven and Venter, 1993). Palynological characteristics listed by Walker and Doyle (1975), which have been shown to be of value in the Apocynaceae, include the pollen-unit, pollen apertures and pollen wall architecture. To this must be added the taxonomic and systematic value of the pollen carrier (translator).
Pollen of the Periplocoideae occurs in tetrads or free pollinia, which are released onto spoon-like translators at anthesis (Verhoeven and Venter, 1998). The spoon-like translators of the Periplocoideae are formed by secretions which are moulded by grooves in the style-head, which alternate with the anthers (Figs. 3.7 a, b). Translators consist of three parts, namely the spoon, stalk and adhesive disc (following the terminology used by Verhoeven and Venter, 1997). The spoon is orientated toward the style-head apex and receives the pollen tetrads or pollinia shed from the two adjoining thecae of neighbouring anthers. The stalk is usually easily distinguished from the spoon, although the transition may be very gradual in some taxa, making the two parts indistinguishable (Verhoeven and Venter, 1997). The stalk connects the spoon to the adhesive disc which is located at the outer rim of the style-head. The adhesive disc is orientated over the entrance to the nectar hollow and attaches the translator to the proboscis of insects feeding on the nectar (Nilsson et al., 1993). Translator shape and structure have taxonomic and systematic value at generic and species level in the Periplocoideae (Verhoeven and Venter, 1997).

The pollen tetrads of the Periplocoideae are usually rhomboidal or decussate, but tetragonal, linear, T-shaped and tetrahedral arrangements have also been observed (Verhoeven and Venter, 2001). *Petopentia* Bullock is the only genus that can be identified accurately using tetrad arrangement since it uniquely has linear and T-shaped tetrads (Verhoeven *et al.*, 1989). Other Periplocoideae genera nearly all have decussate, rhomboidal and tetragonal tetrads and most species also include all of these tetrad types, limiting the taxonomic value of this characteristic (Verhoeven and Venter, 1993, 1994a).

Cohesion of tetrads may occur through connection of the tectum of adjoining grains (simple cohesion) or by connecting wall bridges (crosswall cohesion) (Knox and McConchie, 1986). Studies on the tetrads of *Petopentia*, *Tacazzea* Decne. and *Raphionacme* have shown the cohesion mechanism in Periplocoideae to consist of connecting wall bridges formed by the intine and granular layer (Verhoeven and Venter, 1993,1998; Verhoeven *et al.*, 1989).

33

Only *Raphionacme* (Verhoeven and Venter, 1994a, 1994b) and *Schlechterella* K.Schum. (Venter and Verhoeven, 1998) with 8–16 pores per grain, and *Kappia* Venter, A.P.Dold & R.L.Verh. (Venter *et al.*, 2006a) and *Baseonema* Schltr. & Randle (Taoana, 2001) with 4–8 pores exceed the 4–6 pores per grain found in *Cryptolepis* and the rest of the Periplocoideae. The pores are opposite each other at the junction of adjacent pollen grains, and range from circular to semi-circular (Verhoeven and Venter, 1994a).

Pollen wall architecture is very similar in all Periplocoideae genera that have been studied. The exine is typically smooth and may be divided into a tectum and an underlying granular layer. In *Camptocarpus* Decne. [=*Harpanema* Decne.] the exine is differentiated into three strata. These are the tectum, underlain by a thin granular layer, which is subtended by a foot layer (Verhoeven and Venter, 1994a). In the Periplocoideae the walls separating the grains in a tetrad have the same structure as the outer wall, except in the genera *Camptocarpus* and *Finlaysonia* Wall. where the tectum is absent (Verhoeven and Venter, 1994a).

Although tetrad size is very similar for many genera and overlaps to a great extent, it may be of taxonomic value in distinguishing certain genera and species in the Periplocoideae, as shown by measurements presented by Nilsson *et al.* (1993). Verhoeven and Venter (1994b) found the rhomboidal tetrad size of the monotypic *Ischnolepis* Jum. & H.Perrier to be of taxonomic value in distinguishing this genus from other genera in the subfamily, while Verhoeven *et al.* (1989) found tetrad size of value in distinguishing *Tacazzea* from *Petopentia*, as well as differentiating between different *Tacazzea* species. Tetrad size was also of taxonomic value at species level in *Stomatostemma* N.E.Br. (Verhoeven and Venter, 1993) and *Periploca* (Verhoeven and Venter, 1994b).

In the present study the internal and external pollen structure, arrangement of pollen and translator structure of the six southern African *Cryptolepis* species was studied. The aim of the study was not only to add to the already extensive

34

knowledge of periplocoid pollen and translators but also to identify any pollen or translator characteristics that may be of taxonomic value in distinguishing the genus *Cryptolepis* or species within the genus.

## 4.2 Results

## 4.2.1 Translator

The translators of the species *C. capensis, C. cryptolepioides, C. delagoensis, C. obtusa* and *C. oblongifolia* are virtually indistinguishable. They are all elongateelliptic with an obtuse apex. The spoon gradually narrows towards the base, where it is attached to the adhesive disc, making the spoon and short stalk nearly indistinguishable. The margins of the spoon are curled inward, becoming increasingly curled towards the base, giving the short stalk a u-shaped appearance. The stalk is attached at the upper third to quarter of the adhesive disc. The adhesive disc is semi-elliptic and small, being less than a third of the size of the spoon (Figs. 4.1 a, b, d, e, f).

The translators of *C. decidua* (Fig. 4.1 c) are easily distinguished from those of the other southern African species. The spoon is deltoid with an obtuse apex. The stalk is much easier to distinguish than in the other *Cryptolepis* species. The margin of the lower half of the spoon is curled inward, the curl extending into the stalk, giving it an open u-shaped appearance. The stalk is attached at the upper third of the adhesive disc and a groove runs from the point of attachment to the upper edge of the disc. The upper edge of the adhesive disc is broad and linear. The adhesive disc is more than half the size of the spoon and may be as large as the spoon itself.

Translator size is given in Table 4.1. Translator sizes of the different species overlap to a great extent. On average *C. obtusa* has the shortest translators with a mean length of  $311.9-336 \mu m$ . *C. delagoensis, C. cryptolepioides* and *C. oblongifolia* have slightly longer translators with mean lengths varying from 350.8 to 446.2  $\mu m$ . *C. capensis* has relatively large translators with a mean length of

506–567.8  $\mu$ m. The translators of *C. decidua* are easily distinguished from the other species since their mean length of 569.7–573.7  $\mu$ m but especially the width of 172.3–179  $\mu$ m by far exceed that of any of the other five species.

Table 4.1 Translator sizes of six southern Afri	ican Cryptolepis species
---	--------------------------

Species	Specimen	Translator size (μm)
C. capensis	L.Joubert 31	506 ±3 (503–509) x 94 ±5 (89–99)
	J.M.Wood 11589	567.8 ±21.8 (546.7–594.2) x 91 ±15.6 (68.6–104.7)
C. cryptolepioides	H.J.T.Venter 9075	361 ±16.1 (334.9–377.7) x 72.9 ±10 (56.8–81.4)
	H.H.Burrows 1338	384 ±5.7 (380–388) x 77.5 ±3.5 (75–79.9)
C. decidua	R.L.Verhoeven 165	569.7 ±41.2 (530–649.3) x 179 ±23.1 (141.9–214.8)
	D. van Vuuren 590	573.7 ±18.3 (550.5–602.4) x 172.3 ±19.3 (149.9–196.4)
C. delagoensis	H.J.T.Venter 9335	395.8 ±22.6 (361–436) x 63.7 ±5.1 (57.1–71.1)
	P. Bruyns 9365	350.8 ±13.7 (333–365.8) x 65 ±4.8 (58.4–69.6)
C. oblongifolia	A.E. van Wyk 113	388.5 ±18.1 (368.7–411) x 81.4 ±7.8 (72.6–93.6)
	L. Joubert 26	446.2 ±19.7 (425–464) x 72.1 ±8.1 (63.8–80)
C. obtusa	M.G.Bingham 1442	311.9 ±22.9 (274.3–340.8) x 73.1 ±6.9 (66.3–86.3)
	N.C.Chase 8288	336 ±12 (328.7–353.7) x 73.9 ±5.9 (65.7–78.3)













Fig. 4.1 SEM micrograph of translators of (a) *C. capensis*. (b) *C. cryptolepioides*. (c) *C. decidua*. (d) *C. delagoensis*. (e) *C. oblongifolia*. (f) *C. obtusa*. Scale bars: (a, b, c, e, f) = 100  $\mu$ m, (d) 50 =  $\mu$ m. ((a) *Joubert, L.* 31, (b) *Venter, H.J.T.* 9075, (c) *Verhoeven, R.L.* 165, (d) *Venter, H.J.T.* 9335, (e) *Van Wyk, A.E.* 113, (f) *Bingham, M.G.* 1442 — collected in Zimbabwe)

#### 4.2.2 Pollen

In the six *Cryptolepis* species studied, the pollen grains are present as tetrads, with the grains arranged decussately or rhomboidally. In *C. capensis* (Figs. 4.3 a, b, c) and *C. decidua* (Figs. 4.5 a, b, c) only decussate tetrads are present. In *C. cryptolepioides* (Figs. 4.4 a, b, c), *C. delagoensis* (Figs. 4.6 a, b, c), *C. oblongifolia* (Figs. 4.7 a, b, c) and *C. obtusa* (Figs. 4.8 a, b, c) decussate and rhomboidal tetrads occur, though the latter are rare.

Individual pollen grains of all species are tetraporate with pores arranged opposite each other at the junction of adjacent pollen grains. The pores are circular to semi-circular with irregular margins and are often covered by a thin layer of exine. In *C. capensis* small particles may be observed clogging the pores of several pollen grains (Figs. 4.3 a, b). The exine is generally smooth, but slight perforations, not penetrating the exine, may be observed in some grains of all species (Figs. 4.3 a, b).

In all the species the exine consists of an outer distal stratum (tectum) subtended by a granular stratum consisting of granules of unequal size (Fig. 4.2 a). The intine is poorly differentiated and only clearly visible in the pore area (Figs. 4.2 c, d). The inner walls separating the individual grains of the tetrad have the same structure as the external wall, consisting of tectum, granular stratum and intine. The walls are, however, not continuous, but interrupted by wall bridges consisting of intine and a granular stratum (Fig. 4.2 b).

Tetrad sizes for the species are shown in Table 4.2. The size of individual tetrads varies considerably within each species and species show much similarity in mean tetrad sizes. The mean decussate tetrad size for all species ranges from 36 to 45.5  $\mu$ m in length and 25.8 to 38.2  $\mu$ m in width (Table 4.2). On average the ratio of tetrad length to width is fairly constant for all species, ranging from 1.4 to 1.7, thus giving the tetrads an ellipsoid shape. The only exception to this is *C. decidua* which shows an average length

38

to width ratio of 1.0 to 1.1, the tetrads being more globose than those of the other species.

Species	Specimen	Tetrad size (µm)	Mean ℓ:w
C. capensis	R.G. Strey 8352	41.6 ±3.2 (37.2–46.5) x 28.8 ±2.3 (24.2–31.6)	1.5
	Hilliard and Burtt 7575	45.5 ±0.7 (44.6–46.5) x 29.1 ±1.6 (26.9–31.6)	1.6
C. cryptolepioides	H.J.T.Venter 9182	37.8 ±6.1 (27.9–46.5) x 26.3 ±1.8 (24.2–29.8)	1.5
	H.J.T.Venter 9075	40.6 ±5.1 (33.5–49.3) x 26.7 ±3.4 (22.3–36.3)	1.5
	Codd and Dyer 9139	42.4 ±3.1 (38.1–47.4) x 25.8 ±1.6 (23.3–27.9)	1.7
C. decidua	R.L.Verhoeven 165	38.7 ±1.6 (37.2–41.9) x 34.3 ±1.9 (29.8–37.2)	1.1
	G.J. Beukes 22	36 ±0.9 (34.4–37.2) x 35.3 ±1.1 (33.5–37.2)	1.0
	D. van Vuuren 590	38.7 ±1 (36.3–40) x 38.2 ±1 (36.3–39)	1.0
C. delagoensis	H.J.T.Venter 9335	39.8 ±4.1 (31.6–47.4) x 26.3 ±2.2 (23.3–30.7)	1.5
C. oblongifolia	L.Joubert 26	41.2 ±2.4 (38.2–46.5) x 28.1 ±1.3 (26–31.6)	1.5
	A.D.J. Meeuse 9494	42.4 ±1.8 (40–45.6) x 27.4 ±2 (26–31.6)	1.6
	R.H. Compton 28476	42.8 ±2.6 (38.1–46.5) x 26 ±1.8 (22.3–27.9)	1.7
	C.A. Smith 1293	42.8 ±2.9 (39–48.4) x 27 ±2.4 (24.2–30.7)	1.6
C. obtusa	M.G.Bingham 1442	38.6 ±3.3 (32.6–44.6) x 28.3 ±2.3 (24.2–32.6)	1.4

 Table 4.2 Pollen tetrad sizes of southern African Cryptolepis species



Fig. 4.2 Pollen wall architecture of *Cryptolepis.* (a) Outer pollen wall of *C. oblongifolia* tetrad showing outer tectum, granular layer and intine. (b) Inner pollen wall of *C. oblongifolia* tetrad showing tectum, granular layer, intine and wall bridges. (c) Pores in the outer pollen wall of *C. decidua*, covered by intine. (d) Pore in the outer pollen wall of *C. oblongifolia*, covered by intine and granular layer, i: intine, po: pore, t: tectum, wb: wall bridge. Scale bars: (a) = 0.5  $\mu$ m, (b) = 1  $\mu$ m, (c, d) = 2  $\mu$ m. ((a, b, d) *Joubert, L. 26*, (c) *Verhoeven, R.L.165*))



Fig. 4.3 Pollen tetrads of *C. capensis.* (a, b) SEM micrograph of decussately arranged tetrad. Pollen grains tetraporate with small perforations in exine. (c) Light micrograph of decussately arranged pollen tetrad. pe: perforations; pa: particles in pores. Scale bars: (a, b) = 10  $\mu$ m; (c) = 100  $\mu$ m. ((a, b, c) *Strey, R.G. 8352*)









Fig. 4.4 Pollen tetrads of *C. cryptolepioides.* (a, b) SEM micrograph of decussately arranged tetrad. (c) Light micrograph of decussately arranged tetrad. Scale bars: (a, b) = 10  $\mu$ m, (c) = 100  $\mu$ m. ((a, b) *Venter, H.J.T. 9075*, (c) *Codd, L.E. and Dyer, R.A. 9139*)



Fig. 4.5 Pollen tetrads of *C. decidua*. (a, b) SEM micrograph of deccusately arranged tetrad. (c) Light micrograph of decussately arranged tetrad. Scale bars: (a, b) = 10  $\mu$ m, (c) = 100  $\mu$ m. ((a, b, c) *Beukes, G.J. 22*)

(c)

100 µm





(C)

Fig. 4.6 Pollen tetrads of *C. delagoensis*. (a, b) SEM micrograph of decussately arranged tetrad. (c) Light micrograph of decussately arranged tetrads. Scale bars: (a, b) = 5  $\mu$ m, (c) = 100  $\mu$ m. ((a, b, c) *Venter, H.J.T.* 9335)



(a)





(C)

Fig. 4.7 Pollen tetrads of *C. oblongifolia*. (a, b) SEM micrograph of decussately arranged tetrad. (c) Light micrograph of decussately arranged tetrad. Scale bars: (a, b) = 5  $\mu$ m, (c) 100 =  $\mu$ m. ((a, b) *Joubert, L. 26*, (c) *Smith, C.A. 1293*)





(a)

(b)



(C)

Fig. 4.8 Pollen tetrads of *C. obtusa*. (a, b) SEM micrograph of decussately arranged tetrad. (c) Light micrograph of decussately arranged tetrad. Scale bars: (a, b) = 5  $\mu$ m, (c) = 100  $\mu$ m. ((a, b, c) *Phillips, E. 2236*)

#### 4.3 Discussion

Though translator shape and size may vary considerably and have taxonomic value in distinguishing genera and species in the Periplocoideae, the basic structure of all the translators of the subfamily is the same. Schick (1982) analysed the chemical nature of the translator of *Periploca* and found that the spoon, stalk and adhesive disc all consisted of a solid part of cutin derivates, carbohydrates and terpenes. Safwat (1962) found that the spoon was formed by epithelial cells of the style-head which first secreted a foamy substance that stained with fast green, followed by a solid substance that stained with safranin. In contrast, epithelial cells formed the adhesive disc by first secreting a solid substance, followed by a foamy substance (Safwat, 1962). The foamy substance corresponds to the adhesive material showing cell-like structures, and the solid substance corresponds to the solid layer without cell-like structures described in *Raphionacme* by Verhoeven and Venter (1997). Since Periplocoid translators are mostly similar in structure and development, the translators of *Cryptolepis* were expected to show a structure similar to that of *Periploca* and *Raphionacme*.

Onthogenetic studies on Periplocoid translators have shown that the scutellum, or solid part of the adhesive disc, developed first and that the stalk became attached to the disc before the adhesive substance was added to the lower side of the scutellum or the stalk elongated to connect the adhesive disc to the spoon (Kunze, 1993). The upper part of the adhesive disc and the base of the stalk are regarded as the central element of the Periplocoid translator, being homologous with the corpusculum of the Asclepiadoideae and Secamonoideae (Kunze, 1993). The homology of these two structures is supported by their secretion in the same region of the style-head and the cross-section of the inrolled stalk of the Periplocoid translator and cross-sections of the corpusculum of the Secamonoideae and Asclepiadoideae exhibiting the same shape (Endress, 2001).

Arekal and Ramakrishna (1980) studied the translators of representatives of various Periplocoideae genera. They reported that the translators of *C. buchananii* were

47

boat-shaped, with a thin stipe (stalk) that was not easily distinguishable from the spoon. The translators of *C. yemenensis* Venter & R.L.Verh. were found to be narrowly elliptic with the stalk and spoon nearly indistinguishable and length varying from 338–396  $\mu$ m (Venter and Verhoeven, 1999). Translators of *C. nugaalensis* Venter & Thulin were narrowly elliptic, without a clearly distinguishable stalk and length varying from 367–419  $\mu$ m, while translators of *C. somaliensis* Venter & Thulin were also narrowly elliptic, whithout a clearly distinguishable stalk and length varying from 411–491  $\mu$ m (Venter *et al.*, 2006b). *C. africana* (Bullock) Venter & R.L. Verh. was also found to have narrowly elliptic translators, ranging from 490–607  $\mu$ m (Venter and Verhoeven, 2007).

Comparing the results of the present study with the above mentioned descriptions suggests that translator shape is very constant in the genus. Although Verhoeven and Venter (1997) found translator shape to be of taxonomic value in distinguishing species in *Raphionacme*, this does not seem to be the case in *Cryptolepis* where there is virtually no distinction possible between the species. The great homogeneity in translator shape in *Cryptolepis* would make this a good characteristic for identifying the genus. The question now arises whether *C. decidua*, with its translator shape differing so markedly from that of the other five *Cryptolepis* species, embodies a variation within the genus that is poorly represented in the southern African species, or belongs to a different genus altogether.

In terms of translator size *C. decidua* and *C. capensis* are easily distinguishable from the other species. Where the mean translator sizes of the other species range from  $311.9-446.2 \times 63.7-81.4 \mu m$  the translators of *C. decidua* have a much larger mean size of  $569.7-573.7 \times 172.3-179 \mu m$ , while those of *C. capensis* measure  $506-567.8 \times 91-94 \mu m$ . Although results from the present study suggest that translator size is relatively constant for the genus, with only *C. decidua* and *C. capensis* having translator sizes differing appreciably from the other species, comparison with the results from the already mentioned publications suggests that translator size may be of value in distinguishing *Cryptolepis* species.

In the Apocynaceae the pollen-unit forms one of the most important distinguishing characteristics of the subfamilies. The pollen unit does, however, not only differentiate between the subfamilies of the Apocynaceae, but shows the close relationship between the subfamilies and supports their classification as a single family. The Apocynoideae, with five exceptions, are characterized by having singlegrained pollen (Verhoeven and Venter, 1993, 1994a; Van der Ham et al., 2001). In contrast with other Apocynoideae genera, the genera Apocynum L. [=Poacynum Baill., =Trachomitum Woodson], Callichilia Stapf., Condylocarpum Desf. [=Rhipidia Markgr.], Melodinus J.R.Forst. & G.Forst. and Tabernaemontana L. [=Pagiantha Markgr.] have pollen arranged in tetrads, which suggests a close relationship with the Periplocoideae (Van der Ham et al., 2001). The Apocynoideae are also differentiated from the Periplocoideae, Secamonoideae and Asclepiadoideae by the absence of translators in the former, while the latter three subfamilies all have translators. The style-head of the Apocynoideae secretes an adhesive substance which causes pollen grains to stick to the pollinator's proboscis (Nilsson et al., 1993). The adhesive substance on the dorsal surface of the Peripocoideae translator is regarded as a more specialized form of the adhesive pollination mechanism of the Apocynoideae, further supporting the close relationship between the two subfamilies (Nilsson et al., 1993). Two genera in the Apocynoideae, namely Apocynum [=Trachomitum] and *Forsteronia* G.Mey. have simple, band-like translators that are homologous to those of the Periplocoideae and can be regarded as a connection between the two subfamilies (Verhoeven and Venter, 1998).

In the Asclepiadoideae single pollen grains are agglutinated into two pollinia per anther, while in Secamonoideae pollen tetrads are agglutinated to form four pollinia per anther. In both these subfamilies the pollinia are attached to translators and remain in the anther thecae until removed by the pollinator (Verhoeven and Venter, 1998, 2001). In these two subfamilies the translator consists of a clasping mechanism, the corpusculum (Civeyrel, 1994). In the Secamonoideae the pollinia are attached to the corpusculum via a dorsal process, while pollinia are attached to the corpusculum by two caudicles in the Asclepiadoideae (Wanntorp, 2007).

49

Several previous studies on periplocoid pollen have included one or several *Cryptolepis* species. The tetrads of all *Cryptolepis* species previously belonging to *Curroria*, including *C. decidua*, were described as rhomboidal, tetrahedral or decussate, the most common being decussate and tetrahedral, except in *C. volubilis* (Balf.f.) Schwartz where rhomboidal tetrads were most common (Verhoeven and Venter, 1993). Nilsson *et al.* (1993) described the tetrads of *C. oblongifolia* and *C. buchananii* as being mostly rhomboidal. In *C. somaliensis* and *C. nugaalensis* pollen tetrads were found to be decussate whereas in *C. yemenensis* and *C. africana* tetrads are usually decussate, with rhomboidal tetrads rarely occurring (Venter and Verhoeven, 1999, 2007; Venter *et al.*, 2006b).

The results of the current study were not supportive of the findings of these authors, as no tetrahedral tetrads were observed for any of the species that were included in this study and in that the most common tetrad type in *C. oblongifolia* was not rhomboidal, but decussate. This discrepancy may be due to the great variation that occurs within species and even within individuals and because the sampling size was too small to allow observation of the full spectrum of tetrad shapes. It is, however, clear from these results that decussate tetrads occur in all six southern African *Cryptolepis* species, with rhomboidal tetrads rarely occurring, and that the different types may occur in varying numbers in different species and in different individuals of the same species. Pollen tetrad shape therefore has no taxonomic value in distinguishing *Cryptolepis* as a genus within the Periplocoideae or in distinguishing between any of the southern African *Cryptolepis* species. The pore arrangement and number were also found to be very similar for all the species and very similar to most other genera in the Periplocoideae. Pollen pores are consequently of no taxonomic value in the *Cryptolepis* species examined.

The pollen wall architecture of *Cryptolepis* is very similar to other Periplocoideae genera that have been studied. The outer tetrad wall exine of *Cryptolepis* consists of a solid tectum subtended by a granular stratum. The inner walls separating the individual grains of the tetrad are thinner than and not as regular as the outer wall. They consist of tectum, granular stratum and intine.

Pollen size varies much within each species and most species included in the present study show similar pollen sizes. Comparison with other *Cryptolepis* species supports this observation. In *C. yemenensis* tetrad size varies from  $36.4-44.9 \times 22.2-29.5 \mu$ m, in *C. africana* tetrad sizes range from  $46.5-57.6 \times 29.7-35.3 \mu$ m, *C. nugaalensis* has tetrads of  $37.2-49.3 \times 24.2-28.8 \mu$ m while *C. somaliensis* tetrads ranged from  $40.9-46.5 \times 25.1-31.6 \mu$ m (Venter and Verhoeven, 1999, 2007; Venter *et al.*, 2006b). Tetrad size, therefore, has no taxonomic value in distinguising between *Cryptolepis* species. The tetrad length to width ratio, however, proved to be very constant for the southern African species. Only *C. decidua* had a tetrad length to width ratio that was markedly different from the other five species. Considering that this is the only species to have a very distinct translator it may be postulated that pollen dimensions are related to translator shape. Pollen tetrad length to width ratio, together with translator characteristics, may be taxonomically useful characteristics for identification of the genus *Cryptolepis*.

# CHAPTER 5 LEAF ANATOMY AND MICROMORPHOLOGY OF LEAF EPIDERMAL SURFACES

## 5.1 Introduction

Leaf epidermal characteristics form an important part of the plant's micromorphology. Epidermal characteristics are under strong gene control and are influenced very little by environmental factors (Barthlott, 1981). For this reason it is a reliable characteristic to use in taxonomic studies. Different epidermal characteristics are of value at different taxonomic levels. Barthlott (1981) regards cuticular striation, epicuticular wax and cell shape as mainly useful at lower taxonomic levels, while secondary wall thickenings are used in determining relationships at higher taxonomic levels.

The purpose of this study was to identify leaf epidermal characteristics that could be useful in distinguishing between species and characterizing the genus *Cryptolepis*. These include primary sculpture of epidermal cells, namely cell shape, secondary sculpture which refers to the relief of the cell wall and tertiary structure, which refers to epicuticular secretions (Barthlott, 1981). To this must be added stomatal characteristics which have been shown to have systematic value in several families (Wilkinson, 1979).

Primary sculpture of epidermal cells is a combination of several characteristics. These include the outline of the cells, anticlinal wall patterns, relief of the cell boundary and curvature of the periclinal wall (Barthlott, 1981). Secondary sculpture can be caused by striation, filigree folding, reticulate folding, ridges and wrinkles. Striation alone is also a combination of various characteristics which include length, orientation, pattern and distribution of striations (Wilkinson, 1979). Tertiary sculpture includes a great variety of structures, for instance epicuticular secretions such as waxes, some of which are family or genus specific and are therefore of great taxonomic and systematic value (Barthlott, 1981). Stomatal characteristics include

52

the distribution and arrangement of stomata, shape and arrangement of subsidiary cells, shape of the guard cells and stomatal ledge, and stomatal size (Wilkinson, 1979).

Kotze (1988) found that, though limited, leaf anatomy had taxonomic value in the subfamily Periplocoideae. Leaf anatomy features that have been shown to be of taxonomic value in the subfamily include arrangement of mesophyll cells in dorsiventral and isobilateral leaves.

# 5.2 Results

# Cryptolepis capensis

The leaves of *C. capensis* are dorsiventral with a single, weakly developed layer of palisade parenchyma on the adaxial side (Figs. 5.1.1. a, b). The palisade parenchyma is not continuous above the main vein. The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein. The cells of the upper epidermis are larger than those of the lower epidermis while both epidermal surfaces are covered by a thick cuticle. The outer walls of the epidermal cells are thicker than the anticlinal and inner walls (Fig. 5.1.1 b).

In surface view the adaxial epidermal cells are more or less isodiametric and tetrato hexagonal. The periclinal walls are flat while the anticlinal wall boundaries are straight to slightly curved. The cuticle may be slightly or heavily striated with straight, parallel running striations. Striations are usually restricted to individual cells, but occasionally cross anticlinal wall boundaries (Fig. 5.1.2 a).

The abaxial epidermis consists of more or less isodiametric cells characterized by convex periclinal walls. Anticlinal walls are curved or have loose to tight u-shaped curves with shallow amplitude and are slightly sunken. The cuticle has sparsely arranged straight, parallel striations. These are obscured by a dense, even layer of wax platelets that are arranged randomly, usually perpendicular to the epidermal surface. Wax platelets are absent from the epidermal cells covering veins (Fig. 5.1.2 b).

The leaves are hypostomatic, though stomata may occur along the main vein on the upper leaf surface. Striations on subsidiary cells are parallel or perpendicular to the stomatal opening. The cuticle extends over the guard cells to form a stomatal ledge. Guard cells are covered by the broad stomatal ledge. Stomata are level with surrounding epidermal cells and randomly orientated (Fig. 5.1.2 b).



(b)

Fig. 5.1.1 *C. capensis.* Cross section of portions of leaf showing (a) bicollateral midvein, collenchyma on both sides of the vein and discontinuous palisade parenchyma. (b) Mesophyll showing weakly developed palisade parenchyma and spongy parenchyma. col: collenchyma; p: phloem; pp: palisade parenchyma; sp: spongy parenchyma; x: xylem. Scale bars: (a) = 200  $\mu$ m, (b) = 100  $\mu$ m. ((a, b) *Joubert, L. 31*)



(b)

Fig. 5.1.2 *C. capensis.* (a) Adaxial epidermis showing heavily striated cuticle. (b) Abaxial epidermis showing dense covering of wax platelets. gs: guard cell; sl: stomatal ledge; v: vein; w: wax platelets. Scale bars: (a,b) = 10  $\mu$ m. ((a, b) *Wood, J.M. 11589*)

## Cryptolepis cryptolepioides

The leaves of *C. cryptolepioides* are dorsiventral, with a single, well developed layer of palisade parenchyma below the upper epidermis (Fig. 5.2.1 b). The palisade parenchyma is not continuous above the main vein. The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein (Fig. 5.2.1 a). The cells of the upper epidermis are larger than those of the lower epidermis while both epidermal surfaces are covered by a thick cuticle. The outer walls of the epidermal cells are thicker than the anticlinal and inner walls (Fig. 5.2.1 b).

In surface view the adaxial epidermis consists of more or less isodiametric cells with convex periclinal walls. The irregular anticlinal walls are characterized by loose V-shaped curves with deep amplitude, wide U-shaped curves with shallow amplitude or slight shallow curves. The anticlinal wall boundaries are slightly sunken. The cuticle is smooth to slightly striate. Striations are straight, running parallel and crossing anticlinal wall boundaries (Fig. 5.2.2 a).

The abaxial epidermis consists of isodiametric cells with convex periclinal walls. Anticlinal walls of the lower epidermis show tight, frequent, U-shaped curves of shallow amplitude or slight curves. The cuticle forms a dense network of undulate striations continuous over several cells. The striations reveal no clear pattern (Fig. 5.2.2 b).

The leaves are hypostomatic, though stomata may occur along the main vein on the upper leaf surface. Stomata are paracytic with striations on subsidiary cells running parallel or perpendicular to the stomatal opening. The guard cells are elongate-elliptic and are covered by a narrow stomatal ledge. Stomata are randomly arranged and slightly sunken or level with the surrounding epidermal cells (Figs. 5.2.1 b; 5.2.2 b).







(b)

Fig. 5.2.1 *C. cryptolepioides.* Cross section of portions of leaf showing (a) bicollateral midvein, collenchyma on both sides of the vein and discontinuous palisade parenchyma. (b) Mesophyll showing well developed palisade parenchyma and spongy parenchyma. col: collenchyma; gc: guard cell; p: phloem; pp: palisade parenchyma; sp: spongy parenchyma; x: xylem. Scale bars: (a) = 200  $\mu$ m, (b) = 100  $\mu$ m. ((a, b) *Joubert, L. 27*)



(a)



Fig. 5.2.2 *C. cryptolepioides.* (a) Adaxial epidermis showing sparsely striated cuticle. (b) Abaxial epidermis showing dense, undulate cuticular striations. gc: guard cells; sl: stomatal ledge. Scale bars: (a b) = 10  $\mu$ m. ((a, b) *Burrows, H.H. 1338* – collected in Zimbabwe)

## Cryptolepis decidua

The leaves of *C. decidua* are isobilateral, with three layers of palisade parenchyma cells subtending both epidermal layers (Fig. 5.3.1 a) and spongy parenchyma restricted to the central part of the leaf (Fig. 5.3.1 b). At the main vein the palisade parenchyma is not continuous. The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein. The cells of both the upper and lower epidermal layers are very similar in size, while individual cell size in each layer may vary considerably. The outer walls of the epidermal cells are thicker than the anticlinal and inner walls (Figs. 5.3.1 a, b).

In surface view the adaxial epidermis consists of more or less isodiametric, tetra- to hexagonal cells with flat to convex periclinal walls. Anticlinal walls are straight to slightly curved and anticlinal wall boundaries are level with the periclinal walls. The cuticle is smooth to slightly striate. When present, striations are straight, parallel and restricted to individual cells (Fig. 5.3.2 a). The upper epidermis is unevenly covered by wax platelets. The platelets are mainly concentrated on the anticlinal wall boundaries and around stomata (Fig. 5.3.2 a).

The abaxial epidermal cells are isodiametric and tetra- to hexagonal with flat to convex periclinal walls. The anticlinal walls are straight or slightly curved and the anticlinal wall boundaries are sunken. The cuticle is smooth to slightly striate. Striations are straight, parallel and restricted to individual cells. The lower epidermis is evenly covered by a thin layer of wax platelets (Fig. 5.3.2 b).

The leaves are amphistomatic (Figs. 5.3.2 a, b). The stomata of the upper and lower leaf surfaces are similar in appearance and structure. Striations on the subsidiary cells are perpendicular to the stomatal pore. Guard cells are broadly elliptic with a narrow, elliptic stomatal ledge (Figs. 5.3.2 a, b). Stomata on both surfaces are sunken and randomly orientated (Figs. 5.3.1 b; 5.3.2 a, b).



Fig. 5.3.1 *C. decidua.* Cross section of portions of leaf showing (a) bicollateral midvein, collenchyma on the adaxial and abaxial sides of the vein and discontinuous palisade parenchyma. (b) Mesophyll showing well developed palisade parenchyma and spongy parenchyma. col: collenchyma; gc: guard cell, p: phloem, pp: palisade parenchyma, sp: spongy parenchyma, x: xylem. Scale bars: (a) = 200  $\mu$ m, (b) = 100  $\mu$ m. ((a, b) *Verhoeven, R.L. 165*)



(b)

Fig. 5.3.2 *C. decidua.* (a) Adaxial epidermis showing wax platelets and stomata. (b) Abaxial epidermis showing wax platelets and stomata. gc: guard cell; sl: stomatal ledge; w: wax platelets. Scale bars: (a, b) = 10  $\mu$ m. ((a, b) *Beukes, G.J. 22*)

# Cryptolepis delagoensis

The leaves of *C. delagoensis* are dorsiventral with one to two, poorly developed layers of palisade parenchyma below the upper epidermis and spongy parenchyma above the lower epidermis (Figs. 5.4.1 a, b). The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein (Fig. 5.4.1 a). Cells of the upper and lower epidermis differ greatly in shape and are covered by a thick cuticule. Upper epidermal cells are brick-like whereas lower epidermal cells are papillate (Fig. 5.4.1 b).

The thick cuticle makes the cells of the upper epidermis indistinguishable in SEM micrographs. Periclinal walls are convex (Fig. 5.4.1 b). The cuticule is striated with straight, parallel striations. Striations are either restricted to individual cells or may cross intercellular boundaries (Figs. 5.4.2 a, b).

The lower epidermal surface is densely covered by papillae, while cell shape and anticlinal cell walls are not visible (Figs. 5.4.1 b; 5.4.3 a). The periclinal wall of each epidermal cell protrudes to form a single papilla. The cuticle is heavily striated. Striations are wavy, randomly orientated and mainly occur on the papillae (Fig. 5.4.3 a).

The leaves are hypostomatic. Striations on the subsidiary cells generally run perpendicular to the stomatal pore (Fig. 5.4.3 a). The guard cells are elliptic with a narrow stomatal ledge (Fig. 5.4.3 b). The stomata are at the same level (Fig. 5.4.3 b) as other epidermal cells and randomly orientated.





(b)

Fig. 5.4.1 *C. delagoensis.* Cross section of portions of leaf showing (a) bicollateral midvein, collenchyma present on the adaxial and abaxial side of the vein and discontinuous palisade parenchyma. (b) Mesophyll showing weakly developed palisade parenchyma and spongy parenchyma. gc: guard cells; pa: papillae; pp: palisade parenchyma; sp: spongy parenchyma. Scale bars: (a) = 200  $\mu$ m, (b) = 100  $\mu$ m. ((a, b) *Venter, H.J.T. 9335*)



(b)

Fig. 5.4.2 *C. delagoensis.* (a) Adaxial epidermis showing randomly orientated striations, restricted to individual cells or continuous over several cells. (b) Adaxial epidermis showing parallel striations, continuous over several cells. Scale bars: (a) =  $20 \ \mu m$ , (b) =  $10 \ \mu m$ . ((a, b) *Venter, H.J.T. 9335*)



(b)

Fig. 5.4.3 *C. delagoensis.* (a) Abaxial epidermis showing papillae densely covered by cuticular striations. (b) Abaxial epidermis showing stoma with cuticular striations covering subsidiary cells and a narrow stomatal ledge over the guard cells. gc: guard cells; pa: papillae; sl: stomatal ledge. Scale bars: (a, b) = 10  $\mu$ m. ((a, b) *Venter*, *H.J.T.* 9335)

## Cryptolepis oblongifolia

The leaves of *C. oblongifolia* are isobilateral, with one to two layers of palisade parenchyma on both sides of the leaf (Fig. 5.5.1 b). The palisade parenchyma is discontinuous above and below the main vein. The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein (Fig. 5.5.1 a). The upper epidermal cells are much larger than those of the lower epidermis. Upper epidermal cells show a high degree of consistency in size, while the size of lower epidermal cells may vary considerably. The outer walls of the epidermal cells are thicker than the anticlinal and inner walls (Fig. 5.5.1 b).

In surface view the adaxial epidermis consists of more or less isodiametric, tetra- to hexagonal cells with flat periclinal walls. Anticlinal walls are straight or slightly curved and anticlinal wall boundaries are occasionally slightly sunken. The cuticle is strongly striated with the striations randomly orientated. The striations are restricted to individual cells (Fig. 5.5.2 b) or radiate across anticlinal wall boundaries (Fig. 5.5.2 a). Striations may be straight or branched (Figs. 5.5.2 a, b).

Epidermal cells of the abaxial surface are indistinguishable (Fig. 5.5.2 c). The periclinal walls are straight to slightly convex (Fig. 5.5.1 b). The cuticle on the abaxial leaf surface is heavily striated. The striations are randomly orientated, undulate and continuous over anticlinal wall boundaries which are level with the surrounding epidermal cells (Fig. 5.5.2 c).

The leaves are hypostomatic. Striations on the subsidiary cells cannot be distinguished from the striations over the rest of the leaf surface and striations may run parallel or perpendicular to the stomatal pore (Fig. 5.5.2 c). The guard cells are elongate-elliptic with a narrow stomatal ledge (Fig. 5.5.2 c). The stomata are slightly sunken (Fig. 5.5.1 b) and randomly orientated (Fig. 5.5.2 c).



(a)



(b)

Fig. 5.5.1 *C. oblongifolia.* Cross section of leaf portions showing (a) bicollateral midvein, collenchyma present on both sides of vein and discontinuous palisade parenchyma. (b) Mesophyll showing palisade parenchyma and spongy parenchyma. col: collenchyma; gc: guard cell; p: phloem; pp: palisade parenchyma; sp: spongy parenchyma; x: xylem. Scale bars: (a, b) = 200  $\mu$ m. ((a, b) *Joubert, L. 26*)


(C)

Fig. 5.5.2 *C. oblongifolia.* (a) Adaxial epidermis showing randomly orientated striations, continuous over several cells. (b) Adaxial epidermis showing parallel striations, restricted to individual cells. (c) Abaxial epidermis showing dense, undulating striations and stomata. gc: guard cells; sl: stomatal ledge. Scale bars: (a, b, c) = 10  $\mu$ m. ((a) *Du Preez, P.J. 183,* (b, c) *Botha, D.J. 2348*)

#### Cryptolepis obtusa

The leaves of *C. obtusa* are dorsiventral, with one to two, well developed layers of palisade parenchyma below the adaxial epidermis and spongy parenchyma above the lower epidermis (Fig. 5.6.1 b). The palisade parenchyma is not continuous above the main vein. The bicollateral main vein is embedded in parenchyma with collenchyma present beneath the epidermis on both sides of the vein. Cells of the upper epidermis are much larger than those of the lower epidermis (Figs. 5.6.1 a, b) and both epidermal surfaces are covered by a thick cuticle (Figs. 5.6.2 a, b, c). The outer walls of the epidermal cells are thicker than the anticlinal and inner walls (Figs. 5.6.1 a, b).

The surface view shows that the adaxial epidermal cells are more or less isodiametric and tetra- to hexagonal with convex (Fig. 5.6.2 a) or concave periclinal walls (Fig. 5.6.2 b). The anticlinal walls are straight while the wall boundaries may be either raised or sunken. The cuticle is densely striated with straight, parallel striations continuous over anticlinal wall boundaries (Figs. 5.6.2 a, b).

In surface view the abaxial epidermal cells are more or less isodiametric and tetrato hexagonal with convex periclinal walls. Anticlinal walls are straight or slightly curved and the wall boundaries are slightly sunken. The cuticle is strongly striated. Striations are undulate and arranged as a lattice which is continuous over anticlinal wall boundaries (Fig. 5.6.2 c).

The leaves are hypostomatic. The stomata are paracytic. Striations on the subsidiary cells maintain the lattice pattern present on other epidermal cells (Fig. 5.6.2 c). The guard cells are elliptic with a narrow stomatal ledge (Figs. 5.6.1 b; 5.6.2 c). The stomata are slightly sunken or level with other epidermal cells and arranged randomly.



(b)

Fig. 5.6.1 *C. obtusa.* Cross section of leaf portions showing (a) bicollateral midvein, collenchyma on both sides of the vein and discontinuous palisade parenchyma. (b) Mesophyll showing palisade parenchyma and spongy parenchyma. col: collenchyma; gc: guard cell; p: phloem; palisade parenchyma; sp: spongy parenchyma; x: xylem. Scale bars: (a) = 200  $\mu$ m, (b) = 100  $\mu$ m. ((a, b) *Joubert, L. 29*)



Fig. 5.6.2 *C. obtusa.* (a) Adaxial epidermis showing convex periclinal walls. (b) Adaxial epidermis showing concave periclinal walls. (c) Abaxial epidermis showing reticulate striations and stomata. gc: guard cells; sl: stomatal ledge. Scale bars: (a, b, c) = 10  $\mu$ m. ((a, b, c) *Bingham, M.G. 1442* – Collected in Zimbabwe)

#### 5.3 Discussion

The southern African representatives of *Cryptolepis* are characterized by more or less isodiametric epidermal cells that are tetra- to hexagonal. The cuticle develops slight to dense striations on the abaxial and adaxial epidermal surfaces. The vascular bundle is bicollateral in all the species.

The species may be divided into two groups on the basis of tertiary sculpture. The first group exhibits tertiary sculpture in the form of wax platelets on either or both the adaxial and abaxial epidermal surfaces. The second group shows no tertiary sculpture. Species belonging to the first group, namely *C. capensis* and *C. decidua* are also the only species to have sparse, straight, parallel striations on the lower epidermal surface as opposed to dense, undulate striations on the lower epidermis of the species without tertiary sculpture. This supports the statement by Barthlott (1981) that secondary and tertiary sculpturing exclude each other so that microsculpturing of the cell surface can only be caused by one structural group.

*C. capensis* is distinguished from *C. decidua* by the presence of wax platelets on the abaxial epidermis and a broad stomatal ledge. *C. decidua* has wax platelets on both the adaxial and abaxial epidermal surfaces, whilst the stomatal ledge is narrow. Leaf anatomy is also useful to separate these two species: in *C. capensis* the leaves are dorsiventral as opposed to isobilateral leaves in *C. decidua*. *C. decidua* is also characterized by amphistomatic leaves as opposed to the hypostomatic leaves of the other five species.

Finding amphistomatic leaves in a species that occurs in desert and semi-desert habitats as opposed to hypostomatic leaves in species growing in moist savanna and forests certainly contradicts the view that restricting stomata to the abaxial surface would decrease water loss through transpiration. *C. decidua* does, however, show several adaptations to its dry, hot habitat. The stomata are sunken and wax platelets on both epidermal surfaces may reflect sunlight, thereby preventing overheating and reducing water loss (Barthlott, 1981).

73

It is unlikely that the wax platelets on the abaxial surface of *C. capensis* serve the same function as those of *C. decidua* since *C. capensis* occurs in moist forests. The wax platelets may repel water, reducing surface wettability. Reduced wettability has been shown to reduce the risk of infection in a habitat that is usually moist (Barthlott, 1981).

Leaves of those species that have no wax platelets, namely *C. cryptolepioides, C. delagoensis, C. oblongifolia* and *C. obtusa* are harder to distinguish. In this group *C. delagoensis* is the only species that is easily distinguished due to the papillate lower epidermal cells and dorsiventral leaves. *C. cryptolepioides* may be identified by its U- to V-shaped anticlinal cell margins, smooth or slightly striated upper epidermis and dorsiventral leaves. *C. oblongifolia* has a strongly striated upper epidermis and is the only species with randomly orientated striations on the upper epidermis. *C. oblongifolia* is also the only species in this group with isobilateral leaves. *C. obtusa* is very similar to *C. oblongifolia* but the striations on the upper epidermis are parallel while the striations on the lower epidermis form a characteristic lattice. The leaves of *C. obtusa* are dorsiventral.

The results of this study show that a combination of leaf anatomy and leaf surface characteristics is very useful for distinguishing the southern African *Cryptolepis* species. It is expected that these characteristics may prove to be of taxonomic value in the rest of the genus as well.

# CHAPTER 6 MICROMORPHOLOGY OF SEED COAT SURFACES

#### 6.1 Introduction

Seeds are the reproductive units of flowering plants and function in the dispersal and survival of the species under varying environmental conditions. A great diversity of seed structures have evolved as a result of the different environmental pressures to which seeds are exposed and this diversity often proves to be of taxonomic value (Boesewinkel and Bouman, 1984). Seed surface characteristics may be a useful tool for resolving taxonomic questions; however these characteristics alone have never proven to be sufficient taxonomic evidence and can only be used in combination with other characteristics (Brisson and Peterson, 1976).

Seed coat characteristics are stable during long periods of storage and, provided that seeds at the same developmental stage are used, the characteristics are very reliable in taxonomic studies (Brisson and Peterson, 1976). The taxonomic value of seed coat characteristics is further increased by the relative ease with which these characteristics can be studied. Seeds are easily studied using SEM procedures since the mature seeds are dry and no complicated preparation of the material for SEM work is required. The SEM enables researchers to make detailed observations and study characteristics that would be impossible to observe using the light microscope (Boesewinkel and Bouman, 1984).

Seed coat descriptions follow the terminology of Barthlott (1981) and Boesewinkel and Bouman (1984). Four main characteristics may be distinguished, namely: cellular arrangement, shape of cells (primary sculpture), fine relief of the cell wall (secondary sculpture) and epicuticular secretions (tertiary sculpture) (Barthlott, 1981; Boesewinkel and Bouman, 1984). Cellular arrangement is rarely taxonomically useful, but may occasionally be of value at species or genus level. Cellular arrangement may be observed where different types of cells are interspersed to form a supercellular pattern (Barthlott, 1981). Primary sculpture is one of the most important characteristics of the seed coat surface and includes characteristics such as outline of the cells, anticlinal wall shape, relief of the cell boundary and curvature of the periclinal wall (Barthlott, 1981; Boesewinkel and Bouman, 1984). Secondary sculpture includes striate, reticulate, smooth or micropapillate surfaces and may be caused by cuticular sculpture, secondary wall thickening or subcuticular or cuticular inclusions (Boesewinkel and Bouman, 1984). Striations may be described in terms of a variety of characteristics which include length, orientation, pattern and distribution of striations (Wilkinson, 1979). Tertiary sculpture in the form of epicuticular secretion rarely occurs in seeds and is of little taxonomic importance (Boesewinkel and Bouman, 1984).

Very little research has been undertaken on the seed coat surface of the Periplocoideae and where research has been done the results remain unpublished as in the case of Claasen (1994) and Taoana (2001). Recent taxonomic publications containing data on seed characteristics include papers published by Venter and Verhoeven (1993, 1994a, 1999) and Venter *et al.* (1990c). In the present study the micromorphological characteristics of the southern African *Cryptolepis* species were examined in order to determine their taxonomic value.

## 6.2 Results

Seeds of the southern African *Cryptolepis* species are all flattened with a ridge running along the centre of the lower seed surface, from the micropylar end to the chalazal end of the seed. The seeds of all the species have a characteristic coma of hair at the micropylar end (Fig. 6.2.1 a). The hairs are hollow, with a smooth outer surface (Fig. 6.2.1 b). Seed surface characteristics are described in detail for each species.

## Cryptolepis capensis

The upper seed coat surface shows undulating, longitudinal ridges (Figs. 6.1.1 a, b). Cells of the upper epidermis are isodiametric and tetra- to hexagonal. Periclinal walls

are concave. Anticlinal walls are straight to slightly curved (Figs. 6.1.2 a, c). The cuticle is smooth to slightly granular (Figs. 6.1.2 b, d). Cells from the margin and centre of the seed are similar in appearance (Figs. 6.1.2 a, c).

On the lower surface of the seed, the margins are curled inward giving the seed a closed U-shaped appearance (Fig. 6.1.3). The curled areas represent the upper side of the seed and show the longitudinal ridges described for the upper seed coat surface. The lower epidermal surface is smooth, without warts or ridges. Epidermal cells near the seed margin are isodiametric and tetra- to hexagonal. Periclinal walls are concave. Anticlinal walls are straight to slightly curved and the cuticle smooth to slightly striate (Figs. 6.1.4 a, b, c, d). When present, striations are sparse, parallel and restricted to individual cells (Figs. 6.1.4 a, b). The cells in the middle of the lower surface, near the central ridge, have a slightly granular appearance. Granules are evenly distributed over the entire cell surface and the periclinal walls are concave (Figs. 6.1.4 c, d).





Fig. 6.1.1 *C. capensis.* (a, b) Upper seed surface with longitudinal ridges. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m. ((a, b) *Wood, J.M. 11589*)



(C)

(d)

Fig. 6.1.2 *C. capensis.* (a, b) Upper seed surface cells near seed margin with concave periclinal walls and granular cuticle. (c, d) Cells in centre of upper seed surface with concave periclinal walls and granular cuticle. Scale bars: (a) = 100  $\mu$ m, (b, c, d) = 10  $\mu$ m. ((a, b, c, d) *Wood, J.M. 11589*)



Fig. 6.1.3 *C. capensis.* Lower seed surface with curled margins and central ridge. cr: central ridge. Scale bar = 1 mm. ((a) *Wood, J.M.* 11589)



(C)

(d)

Fig. 6.1.4 *C. capensis.* (a, b) Lower seed surface cells near seed margin, with concave periclinal walls and slightly striated cuticle. (c, d) Lower seed surface cells near central ridge, with concave periclinal walls and granular cuticle. Scale bars: (a, b, d) =  $10 \mu m$ , (c) =  $100 \mu m$ . ((a, b, c, d) *Wood, J.M. 11589*)

## Cryptolepis cryptolepioides

The upper seed coat surface is rough, with cells clustered into tightly packed warts that cover the entire surface (Fig. 6.2.1 a). The warts vary in shape and size and show no clear pattern of organization (Figs. 6.2.2 a, b). The cells forming the warts are isodiametric and tetra- to hexagonal. The periclinal walls are flat to slightly convex. Anticlinal walls are straight. The cuticle is sparsely striated with broad striae following the anticlinal walls or rarely crossing the cell surface (Figs. 6.2.2 c, d). Fine, parallel striations may cross cell boundaries (Fig. 6.2.2 d).

On the lower surface, the seed margin is slightly raised (Fig. 6.2.3 a). The surface between the raised margin and the central ridge is warty, but warts are not as tightly packed as on the upper surface and are often arranged in ridges. The ridges are arranged irregularly or perpendicular to the seed margin (Fig. 6.2.3 a). Cells of the warts are contorted and cell shape is not distinguishable (Figs. 6.2.3 b, c). The cuticle of the epidermal cells near the margin shows parallel striations, while the cuticle of cells near the central ridge is granular or covered by parallel striations. The cells are isodiametric and tetra- to hexagonal (Figs. 6.2.4 a, c, d). Periclinal walls are concave to slightly convex. Anticlinal walls are straight. The cuticle is finely striated and granular. Striations are densely arranged, parallel and continuous over cell boundaries (Fig. 6.2.4 b).





Fig. 6.2.1 *C. cryptolepioides.* (a) Upper seed surface showing warts and coma of hair at micropylar end. (b) Smooth, hollow hairs of coma. Scale bars: (a) = 1 mm, (b) =  $20 \mu m.$  ((a, b) *Venter, H.J.T. 9197*)



(C)

(d)

Fig. 6.2.2 *C. cryptolepioides.* (a, b) Warts on upper seed surface. (c) Boundary between two warts and cells of upper seed surface, showing striations along anticlinal wall boundaries. (d) Cells of the upper seed surface showing broad striations over cell surfaces and fine striations crossing cellular boundaries. Scale bars: (a, b) = 100  $\mu$ m, (c, d) = 10  $\mu$ m. ((a, b, c, d) *Venter*, *H.J.T.* 9197)



Fig. 6.2.3 *C. cryptolepioides.* (a) Lower seed surface showing central ridge and raised seed margin. (b) Seed margin and ridges of deformed cells (area A). (c) Deformed cells of ridge. cr: central ridge. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m, (c) = 10  $\mu$ m. ((a, b, c) *Venter, H.J.T. 9197*)



Fig. 6.2.4 *C. cryptolepioides.* (a, b) Cells near margin on lower seed surface, showing parallel striations. (c, d) Cells near central ridge on lower seed surface, showing parallel striations and granular cuticle. Scale bars: (a, b, c, d) = 10  $\mu$ m. ((a, b, c, d) *Venter, H.J.T. 9197*)

## Cryptolepis decidua

The upper seed surface is covered by evenly distributed protuberances that are formed by raised epidermal cells (Figs. 6.3.1 a, b). Epidermal cells forming these protuberances show no clearly distinguishable shape (Fig. 6.3.1 c). Epidermal cells between the protuberances are more or less isodiametric and tetra- to hexagonal. Periclinal walls are convex. Anticlinal walls are straight to curved. The cells are covered by a heavily striated cuticle. Striations are densely packed, parallel and straight, often continuous over several cells (Figs. 6.3.2 a, b).

On the lower surface, the seed margin is slightly raised. Narrow ridges are formed by compressed epidermal cells along the seed margin (Figs. 6.3.3 a, b). Like the cells forming the protuberances on the upper seed surface, the cells forming the ridges show no clear shape (Figs. 6.3.3 b, c). Cells between the ridges and surrounding the central ridge are more or less isodiametric and tetra- to hexagonal. Periclinal walls are convex, or partially concave. Anticlinal walls are straight to slightly curved. The cuticle is densely striated with straight, parallel striations that cross cellular boundaries (Figs. 6.3.4 a, b). Cells occurring between the ridges on the upper and lower surface are similar in appearance (Figs. 6.3.2 b; 6.3.4 b).



(b)

(C)

Fig. 6.3.1 *C. decidua.* (a) Upper seed surface showing protuberances. (b) Upper seed surface, showing protuberances of deformed cells. (c) Deformed cells forming protuberance. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m, (c) = 20  $\mu$ m. ((a, b, c) *Verhoeven, R.L. 202*)



Fig. 6.3.2 *C. decidua.* (a, b) Cells of upper seed coat surface, between protuberances, showing parallel cuticular striations. Scale bars: (a, b) = 10  $\mu$ m. ((a, b) *Verhoeven, R.L. 202*)



(b)

(C)

Fig. 6.3.3 *C. decidua.* (a) Lower seed surface showing central ridge and raised seed margin. (b) Area A enlarged, showing ridges of deformed cells along seed margin. (c) Deformed cells of ridge. cr: central ridge. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m, (c) = 20  $\mu$ m. ((a, b, c) *Verhoeven, R.L. 202*)



(a)

(b)

Fig. 6.3.4 *C. decidua.* (a) Cells between ridges on the lower seed surface near the seed margin, showing parallel striations. (b) Cells on the lower seed surface near the central ridge, showing parallel striations. Scale bars: (a, b) = 10  $\mu$ m. ((a, b) *Verhoeven, R.L. 202*)

## Cryptolepis delagoensis

The upper seed surface of *C. delagoensis* is smooth (Fig. 6.4.1 a). The epidermal cells are isodiametric, tetra- to hexagonal and tightly packed (Figs. 6.4.1 b, c). Periclinal walls are convex. Anticlinal walls are straight. The cuticle is densely striated. Striations are slightly undulate. Near the seed margin striations are randomly arranged (Figs. 6.4.2 a, b), while cells near the centre of the seed surface have parallel to randomly arranged striations, which are continuous over cell boundaries (Figs. 6.4.2 c, d).

The lower seed surface is smooth with a narrow central ridge (Fig. 6.4.3 a). The margins of the seed are slightly raised (Figs. 6.4.3 a, b). Cells near the seed margin are elongate and tetra- to hexagonal. Periclinal walls are flat, while anticlinal walls are straight (Figs. 6.4.4 a, b). Cells near the central ridge are isodiametric or slightly elongate and penta- to hexagonal. Periclinal walls are flat to convex. Anticlinal walls are straight to slightly curved (Figs. 6.4.4 c, d). The periclinal walls of all cells on the lower seed surface are covered by dense, randomly arranged, striations surrounding smooth centres. The striations are often continuous over cellular boundaries (Fig. 6.4.4 c).



(b)

(C)

Fig. 6.4.1 *C. delagoensis.* (a) Upper seed surface. (b) Area A, upper seed surface near seed margin. (c) Area B, central area of upper seed surface. Scale bars: (a) = 1 mm, (b, c) = 100  $\mu$ m. ((a, b, c) *Fourie, E. 1641*)



Fig. 6.4.2 *C. delagoensis.* (a, b) Upper seed coat surface cells near seed margin, showing randomly orientated striations. (c, d) Cells at centre of upper seed surface, showing parallel to randomly orientated striations. Scale bars: (a, b, c, d) = 10  $\mu$ m. ((a, b, c, d) *Fourie, E. 1641*)



Fig. 6.4.3 *C. delagoensis.* (a) Lower seed surface, showing smooth seed coat and central ridge. (b) Lower seed coat surface near seed margin (area A). cr: central ridge. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m. ((a, b) *Fourie, E. 1641*)



Fig. 6.4.4 *C. delagoensis.* (a, b) Lower seed coat cells near seed margin, showing randomly orientated striations. (c, d) Cells near central ridge on lower seed surface, showing randomly orientated striations. Scale bars: (a, b, c, d) =  $10 \ \mu m.$  ((a, b, c, d) *Fourie, E. 1641*)

## Cryptolepis oblongifolia

The upper seed surface shows ridges running down the middle of the seed. Towards the margins the ridges radiate outward (Fig. 6.5.1 a). The ridges consist of raised epidermal cells that are often deformed and show no cell shape (Figs. 6.5.1 b, c). In between the ridges epidermal cells are isodiametric and tetra- to hexagonal. Periclinal walls are convex. Anticlinal walls are straight. The cuticle is densely striated. Striations are parallel to randomly orientated, straight or slightly undulate and continuous over cell boundaries (Figs. 6.5.2 a, b).

The lower seed surface is smooth, with a narrow central ridge and raised outer margin (Fig. 6.5.3 a). Cells on the raised margin are morphologically similar to those near the central ridge (Figs. 6.5.3 b, c). The cells are isodiametric to elongate and tetra- to hexagonal. Periclinal walls are flat to concave. Anticlinal walls are straight. The cell surfaces are covered by a densely striated cuticle. Striations are randomly orientated, straight to slightly undulate and continuous over cell boundaries (Figs. 6.5.3 b, c).



Fig. 6.5.1 *C. oblongifolia.* (a) Upper seed surface, showing radiating ridges. (b) Upper seed surface (area A) showing ridges near seed margin. (c) Ridge of raised cells, some of which are deformed. Scale bars: (a) = 1 mm, (b) = 100  $\mu$ m, (c) = 10  $\mu$ m. ((a, b, c, d) *Venter, H.J.T. 8805*)



Fig. 6.5.2 *C. oblongifolia.* (a) Upper seed surface cells near seed margin, showing parallel to randomly orientated striations. (b) Cells in the middle of upper seed surface, showing parallel striations. Scale bars: (a, b) =  $10 \mu m$ . ((a, b) *Venter, H.J.T. 8805*)



(b) (c) (c) Fig. 6.5.3 *C. oblongifolia.* (a) Lower seed surface, showing raised seed margin and central ridge. (b) Cells near central ridge, showing randomly orientated striations. (c) Cells on raised seed margin, showing parallel to randomly orientated striations. cr: central ridge. Scale bars: (a) = 1 mm, (b, c) = 10  $\mu$ m. ((a, b, c) *Venter, H.J.T. 8805*)

#### Cryptolepis obtusa

The upper seed surface is covered by evenly distributed protuberances that are formed by raised epidermal cells (Figs. 6.6.1 a, b). Epidermal cells forming these protuberances are deformed (Fig. 6.6.1 c). Epidermal cells between the protuberances are isodiametric and tetra- to hexagonal. Periclinal walls are convex, occasionally concave. Anticlinal walls are straight to curved. The cells are covered by a granular to weakly striated cuticle (Figs. 6.6.2 a, b).

The lower seed surface has a narrow, wavy central ridge and a raised outer margin (Figs. 6.6.3 a, b). Cells on the raised margin are isodiametric and tetra- to hexagonal. Periclinal walls are convex, while anticlinal walls are straight (Figs. 6.6.4 a, b). Cells near the central ridge are isodiametric and tetra- to hexagonal. The periclinal walls are concave and the anticlinal walls are straight to slightly curved (Fig. 6.6.4 c). All cells on the lower seed surface are evenly covered by a granular cuticle (Figs. 6.6.4 a, b, c).



Fig. 6.6.1 *C. obtusa.* (a) Upper seed surface, showing evenly distributed protuberances. (b) Upper seed surface, with evenly distributed protuberances. (c) Upper seed surface, showing protuberances of deformed cells. Scale bars: (a) = 1 mm, (b, c) =  $100 \mu \text{m}$ . ((a, b, c) *Haffern, J.K. 52*)



Fig. 6.6.2 *C. obtusa.* (a, b) Cells near the centre of the upper seed surface, showing granular to weakly striated cuticle. Scale bars: (a, b) = 10  $\mu$ m. ((a, b) *Haffern, J.K. 52*)



(b)

(C)

Fig. 6.6.3 *C. obtusa.* (a) Lower seed surface, showing central ridge and raised seed margin. (b) Central ridge and raised seed margin. (c) Ridges of deformed cells near seed margin on lower seed surface. cr: central ridge. Scale bars: (a) = 1 mm, (b, c) = 100  $\mu$ m. ((a, b, c) *Haffern, J.K. 52*)




Fig. 6.6.4 *C. obtusa.* (a, b) Lower seed coat surface cells on raised seed margin, showing granular to weakly striated cuticle. (c) Cells near central ridge, showing concave periclinal walls and granular cuticle. Scale bars: (a, b, c) = 10  $\mu$ m. ((a, b, c) *Haffern, J.K. 52*)

#### 6.3 Discussion

The seed morphology of the Periplocoideae has been poorly studied. In most studies of periplocoid seeds the results have shown that the seeds are dorsiventrally flattened with a coma of hairs at the micropylar end (Venter and Verhoeven, 1993, 1999; Venter *et al.*,1990c). The hairs of *Stomatostemma* and *Petopentia* are hollow, with a smooth surface and show little variation (Venter *et al.*, 1990c).

The presence or absence of protuberances on seed coat surfaces has been used several times as a supporting characteristic for distinguishing Periplocoideae genera. According to Venter *et al.* (1990b and c) the genera *Petopentia* and *Tacazzea* were characterized by smooth seed surfaces, whereas *Cryptolepis decidua* (then *Curroria decidua* subsp. *decidua*) and *Cryptolepis migiurtina* Chiov. (then *Curroria migiurtina* (Chiov.) Bullock) were characterized by the presence of protuberances on their seed surfaces. The absence of protuberances on the seed surface of *Buckollia volubilis* (Schltr.) Venter & R.L.Verh. was also used as part of the motivation for its removal from the genus *Curroria,* in which all other species had seed surfaces covered by protuberances (Venter and Verhoeven, 1994a). These studies suggest that seed coat surface characteristics may be taxonomically useful in distinguishing genera within the subfamily Periplocoideae. Published results of seed coat studies of *Cryptolepis* species suggest that this genus could be characterized by the presence of protuberances on the seed surfaces. Network, 1999, Venter *et al.*, 1990c).

Cellular arrangement of the seed coat is a taxonomically useful characteristic in the case of the *Cryptolepis* species of southern Africa. Several species can be differentiated using cellular arrangement: *C. decidua* and *C. obtusa* are characterized by evenly distributed protuberances on the upper seed surface. These protuberances are formed by raised epidermal cells and show no clear cell shape. *C. oblongifolia* shows similar cellular arrangement in the middle of the seed on the upper seed surface, while the lower seed surface is smooth. In this case the deformed cells are grouped in ridges that run along the long axis of the seed. *C. cryptolepioides* is easily distinguished from the other species of the region, being the

only species with cells grouped into rough warts. *C. capensis* shows cells arranged in ridges along the upper seed surface while the lower surface is smooth. The ridges are not formed by deformed cells as is the case in *C. oblongifolia*, but are the result of undulations in the seed coat. *C. delagoensis* has no clear cellular arrangement and is rather characterized by its smooth seed surface.

Where species show similar cellular arrangement they are differentiated by primary and secondary sculpture. Though *C. decidua*, *C. oblongifolia* and *C. obtusa* have similar cellular arrangement they have distinct primary and secondary sculpture. *C. decidua* is characterized by cells on the upper and lower seed surfaces with convex periclinal walls and a heavily striated cuticle. *C. oblongifolia* is characterized by epidermal cells on the upper seed surface with convex periclinal walls while the cells on the lower surface, near the central ridge have concave periclinal walls. The cells are covered by a heavily striated cuticle. In the case of *C. obtusa* the periclinal walls of the upper seed surface are convex while the periclinal walls of the cells in the centre of the lower seed surface are concave. The cells are covered by a granular cuticle.

*C. capensis* is characterized by concave periclinal walls on all the seed surfaces and a smooth to slightly granular cuticle covering the epidermal cells. In contrast, the cells of *C. delagoensis* have convex periclinal walls on all seed surfaces and the cells are covered by a heavily striated cuticle.

The seeds of the six southern African species are adapted to anemochoric dispersal. The primary adaptation to anemochoric dispersal is the coma of hairs that occur at the tip of the seed. As in other Apocynaceae genera the coma of hair in *Cryptolepis* is of micropylar origin (Boesewinkel and Bouman, 1984). Claassen (1994) found that the hairs of Cryptolepis seeds were hollow and that hair characteristics were constant for all species in the genus. The current investigation supports these findings.

Sylla and Albers (1989) suggested that the raised seed margin in the Asclepiadoideae (then Asclepiadaceae) was an adaptation to aid anemochoric dispersal. In some Asclepiadoideae genera and in *Finlaysoni obovata* Wall. (Periplocoideae) the seed margin even enlarges to from wings (Venter, pers. com.) or a ring of hair may grow from the margin as in *Raphionacme namibiana* Venter & R.L.Verh. (Periplocoideae) (Venter and Verhoeven, 1986). The raised seed margins of the *Cryptolepis* species, though not as highly developed as in the case of the above mentioned taxa, could therefore be regarded as an aid to wind dispersal.

Surface roughness through heavy surface sculpturing would cause turbulence in laminar air flow and it has been suggested that this increases thermodynamic exchange and leads to cooling of sculptured structures such as seeds that do not have stomata for cooling gas exchange (Barthlott, 1981). In the case of wind dispersed seeds, increased turbulence around the seed could possibly further aid dispersal. Surface sculpturing, such as the protuberances in *C. decidua* and *C. obtusa*, ridges in *C. oblongifolia* and rough warts in *C. cryptolepioides*, possibly aid dispersal by increasing turbulence around the seeds.

It is clear from the results that the *Cryptolepis* species included in this study show a variety of adaptations to anemochoric dispersal and these adaptations have significant taxonomic value at species level. The great variety of seed coat characteristics found in the genus, however, reduces the value of seed characteristics in distinguishing the genus from other genera in the subfamily.

# CHAPTER 7 TAXONOMIC TREATMENT

## 7.1 GENERIC DESCRIPTION OF CRYPTOLEPIS IN SOUTHERN AFRICA

*Cryptolepis* R.Br. On the Asclepiadeae, a natural order of plants separated from the Apocynaceae of Jussieu. p. 58 (1810), preprint of Memoirs of the Wernerian Natural History Society: 1: 12–78 (1811).

Blume: 146 (1850); Benth.: 740 (1876); Baill.: 300 (1891); K.Schum.: 219 (1897); N.E.Br.: 242 (1902), 526–527 (1907); Schltr.: 26 (1905b); H.Huber: 113:2 (1967), 28–29 (1973); Bullock: 279 (1956); P.I.Forst.: 274 (1990).

Type species: C. buchananii Roem. & Schult.

*Curroria* Planch. ex Benth.: 457 (1849), 741 (1876); Walp.: 69 (1852); Baill.: 302 (1891); K.Schum.: 218 (1897); H.Huber: 113:3 (1967); Bullock: 360 (1954).
Type species: *C. decidua* Planch. ex Benth.

**=** *Ectadiopsis* Benth.: 741 (1876); Baill.: 302 (1891); K.Schum.: 219 (1897); Bullock: 267 (1956).

Type species: E. oblongifolia (Meisn.) B.D.Jacks. (Ectadium oblongifolium Meisn.).

## DESCRIPTION

Slender climbers, occasionally small suffrutices or branching shrubs. *Roots* nontuberous. *Stems* woody, densely branching or twining, with white latex, smooth to verrucose; older stems pale brown to dark greyish- or reddish-brown, glabrous to slightly muricate; young stems green to purplish- or bright reddish-brown, glabrous, minutely puberulent or muricate; interpetiolar ridges with dentate colleters. *Leaves* opposite, decussate or rarely fascicled, petiolate to sub-sessile; petiole slightly to deeply grooved; blade simple, elliptic, oblong-elliptic, ovate, obovate, oblongobovate or orbiculate, herbaceous or coriaceous, rarely slightly succulent, mostly glabrous, occasionally slightly hirsute along main vein, rarely slightly puberulent on upper surface and papillate on lower surface, dark -, pale -, yellowish - or bright green above, pale green beneath, purple spots occasionally present along main vein and margin; venation of primary midrib with secondary arching or looping veins and tertiary reticulate veins; apex acuminate, cuspidate, apiculate, acute, rotund, obtuse, obcordate, rarely retuse or mucronate, normal to recurved or up-turned; base obtuse, cuneate or truncate; margin entire, occasionally revolute. Inflorescences terminal and/or axillary, cymose or flowers rarely solitary, pseudo-panicle of 2-6 monochasia or 2-10 dichasia, each peduncle terminating in 1-3 monochasia, lax to compact, few to many flowered, glabrous to muricate. Bracts opposite, acicular, glabrous to fimbriate. Flowers bisexual, actinomorphic, pentamerous. Buds ovoid, oblong-ovoid or narrowly elliptic, apices acute, apiculate, caudate or obtuse, corolla lobes slightly turned, half-turn or full-turn helically twisted. Sepals free, ovate, broadly ovate or oblong-ovate, apices rotund to acute, glabrous, hirsute or fimbriate, paired colleters at inner bases ovate or rarely trichome-like. Corolla white, creamcoloured, pale yellow, greenish, rarely pale mauve or violet; tube campanulate, outside glabrous, inside glabrous to villous below stamen insertion, lobes longer than tube, ovate, linear-ovate, oblong, linear-oblong, apices acute, rotund or obtuse, reflexed or spreading, glabrous. Corona single or double; lower corona of 5 lobes with spongy coronal feet inserted on corolla tube above stamens; lobes awl-shaped, deltoid, oblong, clavate or filiform, free, concealed to slightly exserted, fleshy; upper corona sometimes present, arising from corolla lobe sinuses, pocket-like, glabrous. Stamens inserted at lower third, quarter or fifth of corolla tube; anthers sub-sessile, hastate to triangular, glabrous to villous on outer surface, free, inner bases fused to lower margin of style-head, connivent over apex of style-head. Pollen in tetrads, grains 3–4-porate. Interstaminal nectaries pocket-like at base of upper corolla tube. Ovaries two, semi-inferior, sub-globose, glabrous, compound style terete, glabrous, style-head pentangular-deltoid, glabrous, translators from upper surface, elliptic, rarely deltoid, with sticky disc at distal end. Gynostegium included in corolla tube. Follicles paired, erect or pendulous, divaricate, horizontal or reflected, cylindricallyovoid to narrowly-ovoid, apices blunt, acute or attenuate, bases cuneate to obtuse, finely ribbed. Seeds oblong-obovate, obliquely obovate, oblong, broadly or narrowly elliptic, brown to dark reddish-brown, smooth to warty, with dorsal rib; coma of hairs at micropylar end, white to yellowish-white.

## **DIAGNOSTIC CHARACTERISTICS**

Corolla lobes helically twisted in bud and longer than corolla tube. Corona lobes inserted in upper half of corolla tube and usually included in corolla tube, free from stamens, typically clavate, deltoid, awl-shaped or oblong and fleshy, filiform in *C. decidua*. Stamens inserted below lower third of corolla tube. Gynostegium included in corolla tube. Translators elliptic, in *C. decidua* deltoid.

## DISTRIBUTION AND ECOLOGY

*Cryptolepis* is widely distributed throughout the northern parts of southern Africa, with the largest concentration of species in the north-east of the region, in the South African provinces of Limpopo, Mpumalanga and KwaZulu-Natal. The genus occurs in a great variety of habitats, ranging from desert and semi-desert in the north-western parts of the region to savannah, riverine -, afromontane - and coastal vegetation, and sand forest in the east. *Cryptolepis* is never a dominant component of the vegetation where it occurs. The genus is associated with a great variety of geological formations and soil conditions; the geology ranges from sandstone, granite, quartzite, dolerite, chert, basalt, dolomite, shale to limestone; associated soil types include alluvial loam, sand or silt along rivers and lakes, rocky sand or loam on plains, mountain slopes, along ridges or in ravines. Flowering generally occurs from late spring to late autumn, with a peak in mid-summer. In desert and semi-desert regions flowering seems to be associated with rainfall and may occur from early spring to late autumn.

## 7.2 KEY TO THE SOUTHERN AFRICAN CRYPTOLEPIS SPECIES

1a Leaves slightly succulent; flowers solitary, corona lobes filiform, protruding from the corolla mouth.

### C. decidua

- 1b Leaves herbaceous or coriaceous; inflorescence a cyme; corona lobes clavate, deltoid or awl-shaped, included in the corolla tube.
  - 2a Leaves herbaceous; inflorescence lax to sub-compact; corolla 7–16 mm long; fruit pendulous.
    - Leaf apex acuminate to cuspidate or mucronate, tertiary veins weakly percurrent, areole development incomplete; corolla 10–
       16 mm long, corona single; follicles narrowly divaricate.

## C. capensis

3b Leaf apex obtuse to emarginate, tertiary venation random reticulate, areole development imperfect; corolla 7–10 mm long, corona double; follicles reflected.

## C. obtusa

- 2b Leaves coriaceous; inflorescence compact; corolla up to 6 mm long; fruit erect.
  - 4a Secondary venation indistinct, tertiary and higher order venation not visible; corona single; follicles widely divaricate at 170–180°.

## C. delagoensis

- 4b Secondary and tertiary venation prominent, areoles well developed, veinlets branching; corona double; follicles divericate at 30–135°.
  - 5a Leaves broadly elliptic, broadly obovate or orbiculate, apices rotund, rarely emarginate, apiculate, acuminate or cuspidate, composite intersecondary veins present, tertiary veins less pronounced than secondary veins; follicles widely divaricate at 110–135°, apices apiculate

## C. cryptolepioides

5b Leaves elliptic to narrowly elliptic, apices acute, acuminate, apiculate or occasionally mucronate, intersecondary veins absent, secondary and tertiary venation indistinguishable from each other; follicles divaricate at 30–90°, apices blunt.

## C. oblongifolia

#### 7.3 DESCRIPTION OF SPECIES

*Cryptolepis capensis* Schltr. in Verhandlungen Botanischer Verein der Provinz Brandenburg, 35: 47 (1893); 315 (1896); N.E.Br.: 527–528 (1907); J.M.Wood: 84 (1907).

Type: South Africa, Natal [KwaZulu-Natal Province], Inanda, *J. M. Wood* 1583 (BOL!, holotype; K!, MO!, NH!, isotypes).

A deciduous climber. Stems woody, slender, twining, up to 7 m long, up to 3.5 mm diameter; light brown, verrucose, glabrous; interpetiolar ridges villous, with dentate colleters. Leaves opposite, axils villous, petiolate; petiole green, glabrous, grooved, with bright purple spots occasionally present along groove edge, 8–13(–20) mm long; blade elliptic, rarely obovate, 50–60(–113) x 20–30(–50) mm, herbaceous, smooth, glabrous, dark green above, pale green beneath, bright purple spots occasionally present along main vein; apex acuminate, cuspidate or mucronate, rarely obtuse or retuse, not recurved; base obtuse; venation eucamptodromous to brochidodromous, 4-7 secondary veins on each side of main vein, tertiary veins weakly percurrent, areole development incomplete, veinlets absent. Inflorescences cymose, lax, few flowered, panicle of 2-5 monochasiums, rarely 1-2 dichasiums, each dichasium terminating in 1-3 monochasiums, glabrous; primary peduncle (22-)30-50(-85) mm long, secondary peduncles (15-)20-35(-90) mm long; pedicels (5-)10-20(-25) mm long; bracts opposite, sparsely placed, acicular, 1.5 mm long, glabrous. Buds oblong, apiculate, full-turn helically twisted. Sepals ovate, 3 x 1 mm, acute, glabrous, with paired colleters at inner bases. Corolla white to greenish-white or pale yellow, rarely pale purple or mauve, 10–16(–20) mm long; tube campanulate, (2–)4–5 mm long, glabrous; lobes reflexed, linear-ovate, 5–11 x 3 mm, apices acute. Corona single, inserted at upper third of corolla tube, concealed, lobes deltoid to awl-shaped, fleshy, 0.8-1.0 mm long, glabrous, apices fitting tightly dome-like over gynostegium, with apertures between bases. Stamens inserted at lower third of corolla tube; anthers hastate, attenuate, villous outside, ± 1 mm long. Ovaries 0.5-1.0 mm long; style ± 1 mm long, style-head acutely bifid, ± 0.5 x 0.5 mm. Follicles pendulous, narrowly divaricate at 20–50°, cylindrically ovoid, falcate, 121–204 x 3–4 mm, apices attenuate, bases cuneate, finely ribbed, light brown, slightly nodose. *Seeds* oblong-obovate,  $4-9 \ge 1.5-2.0$  mm, dark brown, finely ribbed to slightly warty; coma white,  $\pm 20$  mm long. (Figs. 6.1.1 a; 6.1.3; 7.1.1).

## **Diagnostic characters**

*C. capensis* is a climber. The leaf blade is usually elliptic with an acuminate to cuspidate apex. Leaves are large,  $50-60 \times 20-30$  mm and herbaceous. Flowers are grouped in lax, few-flowered cymes and carried on long pedicels, 10-20 mm long. The corolla is 10-16 mm long, with reflexed corolla lobes. Follicles are pendulous, narrowly divaricate at  $20-50^{\circ}$ , cylindrically ovoid, falcate,  $121-204 \times 3-4$  mm, slightly nodose.

## **Distribution and habitat**

*C. capensis* has the most southerly range of all *Cryptolepis* species. It is distributed along the eastern side of South Africa, occurring mainly in the KwaZulu-Natal Province, with isolated populations in the provinces of Limpopo, Mpumalanga and the Eastern Cape, at altitudes from 50–1000 m (Fig. 7.1.2). This species is found in afromontane and coastal forest where it is most common along the forest margin and in clearings. Associated species include *Cola natalensis* Oliv., *Drypetes arguta* (Müll.Arg.) Hutch., *Protorhus longifolia* (Bernh.) Engl., *Rinorea angustifolia* (Thouars) Baill., *Rhus acocksii* Moffett, *Rothmannia capensis* Thunb., *Syzygium gerrardii* (Harv. ex Hook.f.) Burtt Davy and *Xymalos monospora* (Harv.) Baill. Flowering occurs from October to April, with a peak from November to February.

### Notes

Leaves, stems and roots are used to prepare an antihelminthic remedy.

## Vernacular name

Tsonga: nyokane.

## **Voucher specimens**

- 2330 (Tzaneen): Letaba, Duiwelskloof (- CA), Scheepers, J.C. 1187 (PRE).

- 2731 (Louwsburg): Ngome Forest (- CD), Venter, H.J.T. 8999 (BLFU).

- **2831** (Nkandla): Zululand, Eshowe, opposite Town Hall (- CD), *Lawn, J.G. 111* (NH).

- **2930** (Pietermaritzburg): Camperdown, Drummond old road (- DA), *Strey, R.G.* 7310 (NH, NU).

— **3130** (Port Edward): Port Edward, along Izingolweni road, Clearwater Trails, along Fish Eagle Trail (– AA), *Joubert, L. 31* (BLFU).

— **3228** (Butterworth): Elliotdale district, The Haven (– BB), *Gordon-Gray, J.L. 1311* (NU).



Fig. 7.1.1 *Cryptolepis capensis.* (a) Plant habit, (b) fruit, (c) part of inflorescence, (d) external view of a mature flower, (e) bud opened showing sepals, helically twisted corolla lobes, clavate corona lobes, stamens with narrowly hastate anthers and pistil of semi-inferior apocarpous ovaries, style and style head. Scale bars: (a) = 20 mm, (b) = 10 mm, (c) = 5 mm, (d, e) = 1 mm. ((a) *Venter, H.J.T. 8783*; (b) *Wood, J.M. 11589*; (c, d, e) *Joubert, L. 31*)



Fig. 7.1.2 Known geographical distribution of *Cryptolepis capensis* in southern Africa. [o : Type locality]

*Cryptolepis cryptolepioides* (Schltr.) Bullock in Kew Bulletin 11: 281 (1956); J.M.Wood: 84 (1907). *Ectadiopsis cryptolepioides* Schltr.: 10 (1895).

Type: South Africa, Botsabelo, *Schlechter 4082* (B<sup>+</sup>, holotype; BOL!, lectotype here designated; BMx2!, BR!, Gx2!, GRA!, Kx3!, NBG-SAM!, NH!, PRE!, Z!, isotypes).

= *C. transvaalensis* Schltr.: 315 (1896); N.E.Br.: 528-529 (1907); Eyles: 446 (1916). Type: homotypic with *C. cryptolepioides.* 

A climber or scrambler. Stems woody, slender, densely branched, twining, up to 2 m long, up to 5 mm diameter; older stems dark grey-brown, slightly verrucose, glabrous; young stems dark reddish-brown, smooth or slightly verrucose, glabrous; interpetiolar ridges villous, with dentate colleters. *Leaves* decussate, axils villous, petiolate; petiole bright purplish-red, glabrous, grooved, 4-9(-20) mm long; blade broadly obovate or broadly elliptic to orbiculate, (20-)29-41(-110) x (14-)19-29(-59) mm, coriaceous, rugose, glabrous, dark green above, pale green beneath, bright purple spots occasionally present along abaxial side of main vein; apex rotund, rarely emarginate, apiculate, acuminate or cuspidate, recurved; base obtuse; venation brochidodromous, composite intersecondary veins present, tertiary veins random reticulate, prominent, areoles well developed, veinlets branching. Inflorescences cymose, compact, many flowered, panicle of 5-10 dichasiums, terminating in monochasiums, glabrous; primary peduncle 4-10(-25) mm long, secondary peduncles 2-6(-11) mm long; pedicels 2-3(-12) mm long; bracts opposite, densely packed, acicular, 1.5 mm long, margin fimbriate. Buds ovoid, acute to rotund, half-turn helically twisted. Sepals broadly ovate, ± 1.5 x 1.0 mm, rotund, margins fimbriate, with paired colleters at inner bases. Corolla greenish, deep cream or pale yellow, 4-5 mm long; tube campanulate, 1.5-2.0 mm long, glabrous; lobes spreading, oblong, 2-3 x 1 mm, apices rotund to obtuse. Corona double; lower corona inserted at middle of corolla tube, concealed, lobes clavate, apices conical, fleshy, 0.8–1.0 mm long, glabrous, apices touching dome-like over gynostegium, with apertures between bases; upper corona in corolla lobe sinuses, pocket-like, glabrous. Stamens inserted at lower third to guarter of corolla tube; anthers hastate, attenuate, villous outside, ± 0.5 mm long. Ovaries ± 0.5 mm long;

style  $\pm$  0.3 mm long, style-head acutely bifid,  $\pm$  0.5 x 0.5 mm. *Follicles* erect, widely divaricate at 110–135°, narrowly ovoid, (32–)41–57 x 6–15 mm, apices apiculate, bases obtuse, brown, finely ribbed. *Seeds* obliquely obovate to obovate, 4–9 x 2–4 mm, brown, warty; coma white to yellowish-white, 19–27 mm long. (Figs. 6.2.1 a; 6.2.3 a; 7.2.1).

## **Diagnostic characteristics**

*C. cryptolepioides* is a climber or scrambler. The leaves are usually broadly obovate to broadly elliptic or orbiculate with rotund-apiculate apices. Leaves are medium sized,  $29-41 \times 19-29$  mm and coriaceous. Flowers are grouped into compact, many-flowered cymes and carried on short pedicels, 2–3 mm long. The corolla is 4–5 mm long. Follicles are erect, widely divaricate at 110–135°, narrowly ovoid to ovoid, 41–57 x 6–15 mm, apices apiculate to attenuate.

## **Distribution and habitat**

In South Africa this species is distributed throughout the Limpopo Province, the eastern parts of North West Province, Gauteng Province, and the northern parts of Mpumalanga Province, at altitudes from 750 to 1500 m (Fig. 7.2.2). Its' distribution range also extends into Zimbabwe and Mozambique. *C. cryptolepioides* occurs in bushveld, scrub and ravine forest, on mountain slopes, cliffs and plateaus. This species is associated with sandy soil on granite or sandstone outcrops, where it is most common in moist areas such as ravines, along riverbeds and around dams. Associated species include *Celtis africana* Burm.f., *Cryptolepis oblongifolia, Cussonia spicata* Thunb., *Diospyros lycioides* Desf., *Ekebergia capensis* Sparrm., *Englerophytum magalismontanum* (Sond.) T.D.Penn., *Faurea saligna* Harv., *Ficus ingens* (Miq.) Miq., *Melinis repens* (Willd.) Zizka, *Nuxia floribunda* Benth., *Protea caffra* Meisn., *Rhus dentata* Thunb. and *Rhus leptodictya* Diels. Flowering occurs in summer and early autumn, from November to April, with a peak from December to February.

## **Voucher specimens**

- **2230** (Messina): Zoutpansberg, Makonde Mission Station, 24 km north-east of Sibasa (– DC), *Codd, L.E. 6854* (SRGH).

— **2427** (Thabazimbi): Waterberg district, Kranzberg area (– BC), *Germishuizen, G. 253* (PRE).

- 2429 (Zebediela): 51 km north of Potgietersrus (- AA), Venter, H.J.T. 9197 (BLFU).

— **2430** (Pilgrim's Rest): Second look out point along road from Bourke's Luck to Aventura Resort, near Drie Rondawels (– DB), *Joubert, L.* 27 (BLFU).

- 2528 (Pretoria): Wonderboom (- CA), Thode, J. 2653 (NBG).

- 2531 (Komatipoort): Komatipoort (- BD), Rogers, F.A. s.n. (SRGH).

× а b С d

Fig. 7.2.1 *Cryptolepis cryptolepioides*. (a) Plant habit, (b) fruit, (c) inflorescence, (d) flower opened showing corolla, clavate corona lobes, stamens with hastate anthers, hairy sepals and pistil of semi-inferior apocarpous ovaries, style and style-head. Scale bars: (a, b) = 10 mm, (c, d) = 1 mm. ((a) *Chase, N.C. 7261*; (b) *West, D. 2162*; (c) photograph by *Hyde, M.*; (d) *Joubert, L. 33*)



Fig. 7.2.2 Known geographical distribution of *Cryptolepis cryptolepioides* in southern Africa. [o : Type locality; ↑ : Indicating northward distribution]

*Cryptolepis decidua* (Planch. ex Benth.) N.E.Br. in Dyer, Flora of Tropical Africa 4: 243 (1902). *Curroria decidua* Planch. ex Benth.: 457–458 (1849).; Walp.: 69 (1852); Engl.: 244 (1889); 148 (1895); K.Schum.: 218–219 (1897); H.Huber:113:3 (1967). Type: Lower Guinea, Angola, *Curror* s.n. (K!, holotype).

#### = Curroria decidua subsp. decidua Bullock: 361 (1954).

A suffrutescent dwarf-shrub. Stems woody, erect, branching, 0.5–1.0 m high, up to 5 mm diameter; older stems grey to pale brown, smooth, glabrous; young stems dark reddish-brown, smooth, glabrous; interpetiolar ridges villous, with dentate colleters, inconspicuous on younger branches, absent on older branches, branchlets often contracted. Leaves opposite or fascicled, axils villous, sub-sessile to petiolate; petiole green, glabrous, slightly grooved, 0.5-2.0 mm long; blade oblong, occasionally oblong-elliptic or oblong-obovate, 9-45 x 1-6 mm, slightly succulent, smooth, glabrous, light green above and beneath, occasionally with purple spots on both surfaces; apex obtuse to acute, occasionally emarginate, mucronulate to mucronate, villous, not recurved; base cuneate, occasionally obtuse; secondary and tertiary venation not visible. Flowers single on contracted branchlets; pedicels 5-10(-18.5) mm long; bracts absent or 1-2 per pedicel, opposite or spirally arranged, acicular, 0.5–1.0 mm long, fimbriate with long silky trichomes. Buds oblong-ovoid, acute, slightly turned to half-turn helically twisted. Sepals oblong-ovate, 0.5-2.0(-2.5) x 0.5–1.0 mm, acute, margin fimbriate with long silky trichomes, trichomes at inner bases. Corolla violet, 8.5-11.5 mm long; tube shortly campanulate, (2.0-)2.5-3.0 mm long, glabrous; lobes spreading, linear-oblong, 6.0-8.5 x 1 mm, apices obtuse. Corona single, inserted at lower third of corolla tube, slightly exserted, lobes filiform, simple, occasionally bifid, 2-3 mm long. Stamens inserted at lower quarter to fifth of corolla tube; anthers triangular, acute, glabrous, 0.7-1.0 mm long. Ovaries 0.3–0.8 mm long; style ± 0.3 mm long, style-head obtuse to acutely bifid, 0.7–1.0 x 0.6–1.0 mm. Follicles erect, widely divaricate to horizontal at 110°–180°, narrowly ovoid, (25–)48–65 x 3–10 mm, apices attenuate, bases cuneate, light brown, finely ribbed. Seeds oblong to broadly elliptic, 3–6 x 1–2 mm, light to dark brown, slightly warty; coma white to yellowish-white, 11–20 mm long. (Figs. 6.3.1 a, 6.3.3 a, 7.3.1).

## **Diagnostic characteristics**

*C. decidua* is a dwarf-shrub. The leaves are usually oblong with obtuse to acute apices, small to medium sized,  $9-45 \times 1-6$  mm, and slightly succulent. The flowers are solitary on contracted lateral branchlets, with pedicels 5-10 mm long. The corolla is violet and 8.5-11.5 mm long. The corona is filiform and slightly exserted. Follicles are erect, widely divaricate to horizontal, at  $110-180^{\circ}$ , narrowly ovoid,  $48-65 \times 3-10$  mm, apices attenuate.

## **Distribution and habitat**

*C. decidua* is restricted to the dry regions along the western part of southern Africa, at altitudes from 550 to 1500 m. It is widespread throughout the desert and semidesert regions of Namibia, as well as the northern parts of the Orange River Nama Karoo (Mucina *et al.*, 2005) in the Northern Cape Province, South Africa (Fig. 7.3.2). *C. decidua* is also known from Angola. This species grows on rocky hillsides, on plains and along dry ravines in sandy soil and is associated with red nama sandstone, granite, quartzite, dolerite, basalt, dolomite, shale and limestone outcrops. Associated species include *Colophospermum mopane* (Kirk ex Benth.) J.Léonard and *Commiphora* spp. Flowering occurs from August to May and is probably determined by rainfall.

### Notes

Roots are used as a medicine for treating stomach ailments while the arial parts are also used as animal feed.

### Vernacular names

Khoisan: Girihais, giri-haib; Afrikaans: jakkalsbos; German: schakalbush.

## **Voucher specimens**

— **2016** (Otjiwarongo): Outjo, Twyfelfontein farm (– AA), *Van Vuuren, D. 590* (PRE, SRGH, WIND).

— **2418** (Stampriet): Stampriet, 10 km east of Mariental on Stampriet road, Narris Farm (– CA), *Venter, H.J.T. 9061* (BLFU).

- 2618 (Keetmanshoop): 75 km south of Keetmanshoop (- DC), Verhoeven, R.L. 165 (BLFU).

- 2718 (Grünau): Grünau, 88 km north of Grünau (- AB), Venter, H.J.T. 9007 (BLFU).

- 2818 (Warmbad): Warmbad, Homs River (- DA), Beukes, G.J. 024 (BLFU).



Fig. 7.3.1. *Cryptolepis decidua*. (a) Plant habit with paired follicles, (b) stem with leaves and flowers, (c) flower opened showing corolla, filiform corona lobes, stamens with triangular anthers, sepals and pistil of semi-inferior apocarpous ovaries, style and style-head. Scale bars: (a, b) = 10 mm, (c) = 1 mm. ((a) *Beukes, G.J. 24*, (b) *Beukes, G.J. 22*, (c) *Beukes, G.J. 32*)



Fig. 7.3.2 Known geographical distribution of *Cryptolepis decidua* in southern Africa. [Type locality outside southern Africa, not indicated;
↑ : Indicating northward distribution]

*Cryptolepis delagoensis* Schltr. in Engl., Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 38: 26 (1905b); N.E.Br.: 528 (1907). Type: Zulu-Natal [Mosambique], Lourenco-Marques [Maputo], *Schlechter* s.n. (0/12/1897) (B†, holotype); South Africa, KwaZulu-Natal, Tembe Game Reserve, Ngobozana Trail, *Venter, H.J.T.* 9335 (BFLU!, neotype here designated; PRE! isoneotype).

A climber or climbing shrub. Stems woody, slender, twining, up to 4 m long, up to 3.5 mm diameter; older stems greyish-brown, slightly verrucose, glabrous; young stems purplish-brown, smooth, inconspicuously puberulent; interpetiolar ridges glabrous, rarely slightly scabrous, with dentate colleters. Leaves decussate, axils glabrous, rarely slightly scabrous, petiolate; petiole green to purple, glabrous, grooved, 1–3 mm long; blade elliptic to broadly elliptic, ovate, rarely obovate,  $11-20(-23) \times 4-7(-$ 12) mm, coriaceous, smooth, upper surface microscopically puberulent, lower surface microscopically papillate, yellowish-green above, pale green beneath; apex obtuse-apiculate, cuspidate, acute or acuminate, occasionally curved upward; base obtuse. rarely truncate or cuneate; margin revolute; venation weakly brochidodromous, secondary veins indistinct, 4–8 on either side of main vein, higher order venation indistinguishable. Inflorescences cymose, compact, few-flowered, panicle of 2-6 monochasiums, rarely a dichasium with each branch terminating in 2-3 monochasiums, glabrous; primary peduncle 1-3(-10) mm long, secondary peduncles 1-2 mm long; pedicels 1-3 mm long; bracts opposite, densely packed, acicular, 0.5-1.0 mm long, glabrous to fimbriate. Buds ovoid, acute to apiculate, fullturn helically twisted. Sepals broadly ovate, ± 1.0 x 0.5 mm, acute, glabrous, occasionally fimbriate, with paired colleters at inner bases. Corolla white to creamcoloured, 3-6 mm long; tube campanulate, 1.5-2.0 mm long, glabrous; lobes spreading, linear-oblong, 1.5–3.5 x 0.7 mm, apices obtuse. Corona single; inserted at upper third of corolla tube, concealed, lobes oblong to clavate, apices emarginate to acute, fleshy, 0.3-0.5 mm long, glabrous, apices touching dome-like over gynostegium, with apertures between bases. Stamens inserted at lower third of corolla tube; anthers hastate, apices acicular, villous outside, 0.7-0.9 mm long. Ovaries ± 0.5–0.7 mm long; style 0.2–0.3 mm long, style-head acute, 0.5–0.6 x 0.5–

0.6 mm. *Follicles* erect, widely divaricate at  $170-180^{\circ}$ , narrowly ovoid,  $29-49 \times 4.5-6.0$  mm, apices acute, recurved, bases cuneate, dark brown, finely ribbed. *Seeds* narrowly elliptic, 8–11 x 2.5 mm, dark reddish-brown, smooth; coma white, 13–17 mm long. (Figs. 6.4.1 a, 6.4.3 a, 7.4.1).

#### **Diagnostic characteristics**

*C. delagoensis* is a climber or climbing shrub. The leaves are usually elliptic to broadly elliptic or ovate with obtuse-apiculate, cuspidate, acute or acuminate apices. The leaves are small,  $11-20 \times 4-7$  mm, and coriaceous, with revolute margins. Flowers are grouped in compact, few-flowered cymes and carried on short pedicels, 1–3 mm long. The corolla is 3–6 mm long. Follicles are erect, widely divaricate at 170–180°, narrowly ovoid, 29–49 x 4.5–6.0 mm, apices acute, recurved.

## **Distribution and habitat**

This species has a restricted distribution in South Africa with only six known locations, at altitudes from 50–900 m. It occurs in the northern parts of KwaZulu-Natal Province and the eastern parts of the Mpumalanga Province, along the Swaziland border (Fig. 7.4.2). The distribution range extends into Mozambique. *C. delagoensis* grows in sand forest and bushveld vegetation, and is associated with sandy soil overlying sandstone outcrops or ravine slopes. Associated species include *Cladostemon kirkii* (Oliv.) Pax & Gilg., *Strophanthus gerrardii* Stapf, *Strychnos madagascariensis* Poir. and *Terminalia sericea* Burch. ex DC. Flowering occurs during summer, from December to February.

### **Voucher specimens**

 2531 (Komatipoort): Near Swaziland border at Havelock, Ida Doyer Reserve on Schoonoord farm (– CC), *Fourie, E. 1641* (PRE).

- 2630 (Carolina): Amsterdam, 9 km south of town (- DA), Bruyns, P. 9365 (BOL).
- 2731 (Louwsburg): Vryheid district, road to Bhivarte (Paris) Dam (- CA), *Bruyns, P.* 9357 (BOL).
- 2732 (Ubombo): Tembe Elephant Park (- AB), Ward, C.J. 1928 (NH, PRE).



Fig. 7.4.1. *Cryptolepis delagoensis.* (a, c) Plant habit, (b) fruit, (d) flower opened showing corolla, clavate corona lobes, stamens with hastate anthers, sepals and pistil of semi-inferior apocarpous ovaries, style and style-head. Scale bars: (a, b, c) = 10 mm, (d) = 1 mm. ((a) *Bruyns, P. 9365;* (b) *Fourie, E. 1641;* (c) *Goyder, D.J. 5034* – collected in Mozambique; (d) *Bruyns, P. 9357*)



Fig. 7.4.2 Known geographical distribution of *Cryptolepis delagoensis* in southern Africa. [o : Neotype locality; holotype locality outside southern Africa, not indicated; ↑ : Indicating northward distribution]

*Cryptolepis oblongifolia* (Meisn.) Schltr. in Journal of Botany 34: 315 (1896); N.E.Br.: 249–250 (1902), 529 (1907); Eyles: 446 (1916); Robyns: 86 (1947); Brenan: 64 (1949); F.W.Andrews: 406 (1952); H.Huber: 113:2 (1967); Bullock: 269 (1956); Compton: 444 (1975). *Ectadium oblongifolium* Meisn. in Hook.: 542 (by error 442) (1843); Walp.: 481 (1847); Bullock: 268 (1956).

Type: [South Africa, KwaZulu-Natal], Port Natal [Durban], Umgani [Umgeni], *Krauss 132* (K-herb. Bentham!, lectotype here designated; K-herb. Hooker!, BM!, MO!, isotypes).

*Ectadiopsis acutifolia* (Sond.) Benth.: 741 (1876); K.Schum.: 219 (1897);
 Bullock: 269 (1956). Secamone acutifolia Sond.: 76–77 (1850); Walp.: 48 (1852);
 Schltr.: 10 (1895); J.M.Wood: 84 (1907); Bullock: 268 (1956).

Type: South Africa, Magaliesberg, *Zeyher 118*2 (S!, lectotype here designated; G!, K!, P!, isotypes); Port Natal [Durban], *Guienzius 431* (S!, syntype).

**=** *Ectadiopsis oblongifolia* (Meisn.) B.D.Jacks.: 822 (1893); Schltr.: 14 (1894), 10 (1895); K.Schum.: 219 (1897); Bullock: 268 (1956).

Only synonyms relating to southern Africa are listed.

A suffrutescent dwarf-shrub or rarely a climber. *Stems* woody, slender, sub-erect, occasionally twining, up to 1 m high, up to 10 mm diameter; older stems dark reddish-brown, smooth to slightly verrucose, glabrous; younger stems bright orange-red, smooth, glabrous to muricate; interpetiolar ridges villous, with dentate colleters. *Leaves* decussate, axils villous, petiolate; petiole green, glabrous or hirsute, grooved, 1-3(-6) mm long; blade elliptic to narrowly elliptic, occasionally ovate or obovate,  $(3-)15-60(-131) \times (1-)6-27$  mm, coriaceous, smooth, glabrous or slightly hirsute along main vein, bright green above, pale green beneath; apex acute, acuminate, apiculate or occasionally mucronate, not recurved, base obtuse, margin revolute; venation brochidodromous to reticulodromous, secondary and tertiary venation prominent, indistinguishable from one another, intersecondary veins absent, areoles well developed, veinlets branched. *Inflorescences* cymose, compact,

many-flowered, panicle of 3-7 dichasiums, each dichasium terminating in 1-3 monochasiums, muricate; primary peduncle 2-10(-30) mm long, secondary peduncles 2-4 mm long; pedicels 1-10(-29) mm long; bracts opposite, densely packed, acicular, ±1.5 mm long, margin fimbriate. Buds ovoid, apiculate, half-turn helically twisted. Sepals ovate to broadly ovate, 1–2 x 0.8–1.5 mm, rotund to acute, hirsute, margin fimbriate, with paired colleters at inner bases. Corolla yellow, 4-6 mm long; tube campanulate, 1.5–2.0 mm long, outside glabrous, inside slightly villous below stamen insertion; lobes spreading, ovate to linear-ovate, 2.5-4.0 x 1 mm, apices rotund. Corona double; lower corona inserted at middle of corolla tube, concealed, lobes clavate, apices obtuse, fleshy, ± 0.3-0.8 mm long, glabrous, apices touching dome-like over gynostegium, with apertures between bases; upper corona in corolla lobe sinuses, pocket-like, glabrous. Stamens inserted at lower quarter of corolla tube; anthers hastate, attenuate, glabrous, ± 0.5 mm long. Ovaries ± 0.5 mm long; style ± 0.5 mm long, style-head acute, ± 0.8 x 0.8 mm. Follicles erect, divaricate at  $\pm$  30–90°, narrowly ovoid, (37–)50–125(–173) x 3–15 mm, apices blunt, bases cuneate, finely ribbed, brown. Seeds oblong-obovate, (4–)6–10 x 1–3(– 4) mm, slightly warty; coma white, 16–46 mm long. (Figs. 6.5.1 a, 6.5.3 a, 7.5.1).

### **Diagnostic characteristics**

In southern Africa *C. oblongifolia* occurs as a dwarf-shrub. The leaves are usually elliptic to narrowly elliptic with acute, acuminate, apiculate or mucronate apices. Leaf size varies greatly,  $15-60 \times 6-27$ mm, and leaves are coriaceous with revolute margins. Flowers are grouped in compact, many-flowered cymes and carried on 1-10 mm long pedicels. The corolla is 4-6 mm long. Follicles are erect, divaricate at  $30-90^{\circ}$ , narrowly ovoid,  $50-125 \times 3-15$  mm, apices blunt.

### **Distribution and Ecology**

This species is common, with the widest distribution of all *Cryptolepis* species in southern Africa, and has been collected from central and north-eastern Namibia, northern and southern Botswana, Swaziland and South Africa (Fig. 7.5.2). In South Africa it is common in the eastern parts of the North-West Province and throughout the provinces of Limpopo, Gauteng, Mpumalanga and KwaZulu-Natal. Altitude

ranges from 90 to 2000 m. This species is widely distributed throughout sub-Sahara Africa. *C. oblongifolia* occurs in shallow loam or sandy soil on rocky mountain slopes, on ridges and in ravines, and is associated with a wide range of geological formations, including granite, quartzite, dolerite, chert, sandstone and shale. The vegetation consists of grassland and savannah, where it is associated with *Eriosema* spp., *Hyparrhenia hirta* (L.) Stapf, *Lippia javanica* (Burm.f.) Spreng., *Protea caffra, Raphionacme procumbens* Schltr., *Rhus dentata* Thunb., *Salvia* spp., *Schizoglossum* sp. and *Vernonia oligochephala* (DC.) Sch.Bip. ex Walp. Flowering occurs from October to June, with a peak from November to January.

## Vernacular names

Kuangali: Kahuisamasini. Zulu: emoHalahaleni.

## Note

Bullock (1956) cited the author incorrectly when referring to *Ectadiopsis oblongifolia* (Meisn.) Schltr. and this mistake was subsequently repeated by Gilli (1973). Authors cited by Bullock (1956), namely Schlechter (1894 and 1895) and Schumann (1895), both correctly referred to *E. oblongifolia* (Meisn.) Benth.

## **Voucher specimens**

— **2428** (Nylstroom): Between Nylstroom and Naboomspruit, 30.2 km north of Nylstroom, along highway (– CB), *Venter, H.J.T. 9196* (BLFU).

— **2430** (Pelgrimsrust): Blydepoort Nature Reserve (– DB), *Botha, D.J. 2348* (BLFU); First look out point towards Mariepskop, along road from Bourke's Luck to Aventura Resort (– DB), *Joubert, L. 26* (BLFU).

- 2528 (Pretoria): Pretoria Hills (- CA), Leendertz, R. 145 (BLFU, GRA, K).

- 2626 (Klerksdorp): Klerksdorp district, Faan Meintjies Nature Reserve (- DC), *Venter, H.J.T. 8802* (BLFU).

- 2627 (Potchefstroom): Vredefort district, Mispah (- CD), *Du Preez, P.J.* 299 (BLFU).



Fig. 7.5.1 *Cryptolepis oblongifolia*. (a) Plant habit, (b) inflorescence and external view of flowers, (c) fruit, (d) flower opened showing corolla, upper corona of corolla sinus pockets, lower corona of clavate lobes, stamens with hastate anthers, hairy sepals and pistil of semi-inferior apocarpous ovaries, style and style-head. Scale bars: (a, c) = 10 mm, (b, d) = 1 mm. ((a) *Botha, D.J. 2348*; (b, d) *Joubert, L. 26;* (c) *Venter, H.J.T. 8805*)



Fig. 7.5.2 Known geographical distribution of *Cryptolepis oblongifolia* in southern Africa. [o: Type locality; ↑ : Indicating northward distribution]

*Cryptolepis obtusa* N.E.Br. in Kew Bulletin 1895: 110 (1895); 246 (1902); 528 (1907); K.Schum.: 424 (1895); 219 (1897); Brenan: 64 (1949); Bullock: 281 (1956). Type: Mosambique, between Tete and sea coast, *Kirk s.n.* (0/3/1860) (K!, lectotype declared by Bullock 1955); [Malawi], valley of Shire River, *Meller s.n.* (K!, syntype); [Mosambique], Luabo River, *Kirk 38* (K!, syntype); [Mosambique], Shupanga, *Kirk s.n.* (10/12/1883) (K!, syntype); Mosambique, Delagoa Bay [Maputo], *Forbes s.n.* (K!, syntype); Mosambique, Delagoa Bay [Maputo], Speke s.n. (K!, syntype).

#### = *C. obtusa* K.Schum.: 320 (1895).

Type: East Africa, *Stuhlmann 78*27 (B<sup>+</sup>). Synonymy according to description, also see N.E.Br. 246 (1902) and Bullock 281 (1956).

A suffrutescent twining or rambling climber. Stems woody, slender, up to 4 m long, up to 4 mm diameter; older stems light brown, slightly verrucose, glabrous to slightly muricate; younger stems green to slightly purplish-green, smooth, glabrous, rarely slightly muricate; interpetiolar ridges villous, with dentate colleters. *Leaves* opposite, axils villous, petiolate; petiole green, glabrous, grooved, (1-)4-10 mm long; blade oblong to oblong-obovate, rarely elongate-elliptic or oblong-ovate, 28-73(-95) x (7-)13-32(-38) mm, herbaceous, smooth, glabrous, bright green above, pale green beneath, bright purple spots occasionally present along abaxial side of main vein; apex obtuse to emarginate, rarely obcordate, mucronate, not recurved; base obtuse, occasionally truncate or cuneate: venation eucamptodromous, rarely brochidodromous, 6-12 secondary veins on either side of main vein, tertiary venation random reticulate, areole development imperfect, veinlets branching. Inflorescences cymose, sub-compact, many-flowered, panicle of 2-7 dichasiums, each dichasium terminating in 2–3 monochasiums, glabrous; primary peduncle 4–15 mm long, secondary peduncles (2.5-)5-6(-10) mm long; pedicels 2(-4) mm long; bracts opposite, sparsely placed, acicular, 1.0–1.5 mm long, glabrous. Buds broadly ellipsoid, apex caudate, full-turn helically twisted. Sepals broadly ovate, 1.5-2 x 1 mm, acute, glabrous, rarely fimbriate, with paired colleters at inner bases. Corolla yellowish-white, greenish-yellow or yellow, 7–10 mm long; tube shortly campanulate, (1.0–)1.5–2.0 mm long, outside glabrous, inside villous below stamens; lobes spreading, oblong-ovate, 5–8 x 1.0–1.5 mm, apices acute. *Corona* double; lower corona inserted at middle of corolla tube, concealed, lobes clavate or awl-shaped, apices obtuse or acute, fleshy, 0.5–1.0 mm long, glabrous, apices touching dome-like over gynostegium, with apertures between bases; upper corona in corolla lobe sinuses, pocket-like, glabrous. *Stamens* inserted at lower third of corolla tube; anthers hastate, acuminate, glabrous, 0.5–0.9 mm long. *Ovaries* ± 1 mm long; style ± 0.5 mm long, style-head acute to obtuse, ± 0.5 x 0.7 mm. *Follicles* pendulous, reflected at 180–225°, cylindrically ovoid, (49–)74–125(–148) x 3–8(–11) mm, apices attenuate, bases cuneate, finely ribbed, dark brown. *Seeds* oblong to oblong-obovate, 4–6(–9) x 1–2(–3) mm, dark reddish-brown, slightly warty; coma white, (16–)25–35(-41) mm. (Figs. 6.6.1 a; 6.6.3 a; 7.6.1).

## **Diagnostic characteristics**

*C. obtusa* is a climber. The leaf blades are oblong to oblong-obovate with obtuse to emarginated apices. The leaves are large,  $28-73 \times 13-32$  mm, and herbaceous. Flowers are grouped in sub-compact, many-flowered cymes, with short pedicels, 2 mm long. The corolla is 7–10 mm long. Follicles are pendulous, reflected at 180–225°, cylindrically ovoid, 74–125 x 3–8 mm, apices attenuate.

## **Distribution and habitat**

*C. obtusa* occurs along the north-eastern border of South Africa, in the north of the Limpopo Province, the east of Mpumalanga Province and the north-east of KwaZulu-Natal Province as well as the eastern parts of Swaziland (Fig. 7.6.2). The species is also found in Mozambique, Tanzania, Malawi, Zimbabwe, Zambia and Kenya. Altitude ranges from about 100 to 700 m. It is common in savanna, forest margins and reedbeds along rivers and lakes. The habitats include red alluvial loam, sand or silt. Associated species include *Acacia brevispica* Harms subsp. *dregeana* (Benth.) Brenan, *Acacia xanthophloea* Benth., *Capparis sepiaria* L., *Dichrostachys cinerea* (L.) Wight and Arn., *Ficus sycomorus* L., *Grewia* spp., *Lippia javanica* (Burm.f.) Spreng., *Panicum maximum* Jacq., *Pavetta lanceolata* Eckl., *Rauvolfia caffra* Sond., *Tabernaemontana elegans* Stapf and *Trichilia emetica* Vahl. Flowering occurs in late autumn, from April to May.

## Notes

Though both Brown and Schumann published the name *C. obtusa* in 1895, the description of Brown is considered to be the prior publication since it appeared in April/May, whereas that of Schumann only appeared in August.

## **Voucher specimens**

- 2531 (Komatipoort): Kruger National Park, 29 km north of Malelane (– AD), *Codd, L.E. 5508* (K, MO, PRE, SRGH); Crocodile Bridge, Elephant Walk Retreat (– BD), *Joubert, L.* 29 (BLFU).

- 2632 (Bela Vista): Ingwavuma district, Ndumu Game Reserve (- CD), *Pooley, E.S.* 489 (NU).

— 2732 (Ubombo): Josini Dam, 1 km east of dam wall (– AD), Venter, H.J.T. 8792 (BLFU); Mkuzi Game Reserve (– CA), *Tinley, K.L.* 619 (K, NH).


Fig. 7.6.1. *Cryptolepis obtusa.* (a, b) Plant habit, (c) fruit, (d) opened flower showing corolla, upper corona of corolla sinus pockets, lower corona of clavate lobes, stamens with hastate anthers, hairy sepals and pistil of semi-inferior apocarpous ovaries, style and style-head. Scale bars: (a, b, c) = 10 mm, (d) = 1 mm. ((a) *Ngoni, J.F. 218*; (b) *Luke, W.R.G. and Luke, P.A. 3755*; (c) *Astle, W.L. 5704*; (d) *Bingham, M.G. 1442* )



Fig. 7.6.2 Known geographical distribution of *Cryptolepis obtusa* in southern Africa. [Type locality outside southern Africa, not indicated;  $\uparrow$ : Indicating northward distribution]

### CHAPTER 8 DISCUSSION AND CONCLUSIONS

#### 8.1 Taxonomically important characteristics for distinguishing the genus

In the Periplocoideae, genera are mainly distinguished using the relative position of the corona, the presence or absence of a distinct corolla tube and the relative length of the corolla tube when compared to the corolla lobes (Venter and Verhoeven, 1994b). According to Liede and Kunze (1993) the corona is one of the most frequently used features for identification of taxa in the Asclepiadoideae and Periplocoideae. Three other genera are very similar to *Cryptolepis* in that they all have distinct corolla tubes, with corolla lobes always longer than the corolla tubes. These genera are *Stomatostemma, Ectadium* E.Mey. and *Maclaudia* Venter & R.L.Verh.

In southern Africa the distribution range of *Stomatostemma* coincides with that of most of the *Cryptolepis* species, being distributed along the north-eastern parts of the sub-region (Venter and Verhoeven, 1993). *Stomatostemma* is characterized by clavate corona lobes arising from the corolla lobe sinuses in the mouth of the corolla tube. Indeed the generic name, *Stomatostemma*, refers to "a mouth with a crown" (Venter and Verhoeven, 1993). Though clavate corona lobes are also a characteristic of *Cryptolepis*, these arise just above the middle of the corolla tube and are usually included in the corolla tube. In *Stomatostemma* interstaminal discs are absent (Venter and Verhoeven, 1994b), whereas in *Cryptolepis* interstaminal discs are present.

*Ectadium* species occur in the arid regions along southern Africa's west coast, in the Namib Desert (Venter *et al.*, 1990a), where *C. decidua* can also be found. Like *C. decidua* the *Ectadium* species consist of shrubs with erect to divaricate or decumbent stems, but *Ectadium* species may be distinguished from *Cryptolepis* by their subulate corona lobes which arise from the corolla lobe sinuses at the corolla mouth (Venter *et al.*, 1990a). The hairy stomatal crypts in the leaves of *Ectadium* 

species also distinguish them from the *Cryptolepis* species of the region, in which this characteristic is absent.

The genus *Maclaudia* is represented by only two collections from Guinea. Like *Stomatostemma, Maclaudia* differs from *Cryptolepis* in that the corona lobes arise from the corolla mouth. *Maclaudia* is also differentiated from *Cryptolepis* and *Stomatostemma* by corniculate corona lobes as opposed to clavate lobes in the latter two genera (Venter and Verhoeven, 1994b).

## 8.2 Taxonomically important characteristics for distinguishing the southern African *Cryptolepis* species

Generally leaf shape and size are characteristic for each of the six southern African *Cryptolepis* species. Leaf characteristics provide the easiest means of identification since they are easily observed and are mostly available throughout the year, whereas flowers and fruit are only available for short periods. The leaves of *C. capensis* are large with sizes varying from 50–60 x 20–30 mm and typically elliptic with acuminate apices. *C. cryptolepioides* is characterized by orbiculate leaves with rotund, mucronate apices, with sizes ranging from 29–41 x 19–29 mm. *C. decidua* typically has oblong leaves, with obtuse, mucronate apices and sizes ranging from 9–45 x 1–6 mm. Leaves of *C. delagoensis* are usually elliptic to broadly elliptic with apices obtuse-apiculate, cuspidate, acute or acuminate. The leaves are small, ranging from 11–20 x 4–6 mm. *C. oblongifolia* typically has elliptic to narrowly elliptic leaves with acute, acuminate or apiculate apices, with leaf size varying from 15–60 x 6–27 mm. In *C. obtusa* leaves are typically oblong with obtuse to emarginated apices. Leaves are large with sizes varying from 28–73 x 13–32 mm.

However, leaf shape and size are very variable in each species and exceptions to the characteristic shape and size are common. Since all this variation must be taken into account, leaf shape and size cannot effectively be used in diagnostic keys, except in combination with several other taxonomically useful characteristics. Characteristics such as leaf venation, whether the leaves are coriaceous, herbaceous or slightly succulent and the presence of revolute margins or recurved apices compliment leaf shape and size well in distinguishing between the six southern African species.

Leaf epidermal surface characteristics and anatomy are taxonomically useful as well. The species may be divided into two groups, namely a group with tertiary sculpture in the form of wax platelets and a group without tertiary sculpture. In the group with tertiary sculpture, consisting of *C. capensis* and *C. decidua*, the species are differentiated using leaf anatomy and stomatal distribution. *C. capensis* is characterized by hypostomatic, dorsiventral leaves, whereas *C. decidua* has amphistomatic, isobilateral leaves. In the group where tertiary sculpture is absent, *C. delagoensis* is easily distinguished from the other species on the basis of primary sculpture, whereas the other species may be distinguished using a combination of secondary sculpture and anatomy. The results show that a combination of leaf epidermal characteristics and leaf anatomy is effective for distinguishing all the *Cryptolepis* species in southern Africa.

Growth form is also useful for identifying species, though this characteristic may also be variable. *C. capensis* and *C. obtusa* are true, slender climbers. *C. cryptolepioides* and *C. delagoensis* may be climbers or stragglers. The growth form of *C. oblongifolia* varies considerably over its distribution range, but in southern Africa it occurs only as a shrub with a tendency to climb onto any larger plant or other object in its vicinity. *C. decidua* is a shrub and never displays a tendency to climb.

Floral characteristics are generally of little taxonomic value since they vary little in the different species. However, floral size and inflorescence characteristics are taxonomically useful. In five of the species flower size and compactness of the inflorescence seem to be interrelated. *C. decidua* is easily distinguishable from the other species in that its flowers are solitary. *C. capensis* has the largest flowers, ranging from 10–20 mm, and lax inflorescences. *C. obtusa* has smaller flowers, ranging in size from 7–10 mm long, and sub-compact inflorescences. *C.* 

*cryptolepioides, C. delagoensis* and *C. oblongifolia* all have small flowers, around 3– 6 mm long, and compact inflorescences.

The presence of a secondary corona in *C. cryptolepioides, C. oblongifolia* and *C. obtusa*, and the absence thereof in *C. capensis, C. decidua* and *C. delagoensis* is a useful distinction between the two groups. The secondary corona may, however, be difficult to observe and the variation in size reduces its taxonomic value. The presence of trichomes on the anthers and inner corolla tube also has taxonomic value. *C. capensis, C. cryptolepioides* and *C. delagoensis* have slightly villous anthers, whereas *C. decidua, C. oblongifolia* and *C. obtusa* have glabrous anthers. The insides of the corolla tubes of *C. oblongifolia* and *C. obtusa* are slightly villous below the stamens, in contrast to the glabrous condition in all the other species. These characteristics may prove to have taxonomic value in sub-generic classification.

Pollen and translator characteristics proved to have little taxonomic value for distintuishing between the *Cryptolepis* species of southern Africa, the only species differing from the others being *C. decidua* with its, for the genus, unique translator.

Fruit characteristics proved to be taxonomically useful for distinguishing most of the southern African species. The combination of follicle orientation (i.e. pendulous or erect), angle between paired follicles, follicle size and shape is unique for each species and can be effectively used to identify all species in the region. Seed coat characteristics also proved to have taxonomic significance. Results from seed coat surface studies have shown that a combination of cellular arrangement and primary and secondary sculpture can be effectively applied to distinguish all *Cryptolepis* species in the region. These fruit and seed coat characteristics are, however, very variable in the Periplocoideae and cannot be used to delimit the genus *Cryptolepis*.

#### 8.3 Taxonomical position of C. decidua

*C. decidua* is very distinct from the other *Cryptolepis* species of the region. Characteristics that are remarkably homogenous in the other five *Cryptolepis* species, and may even be considered to be genus characteristics, differ completely in *C. decidua*. The difference in growth form has already been mentioned. *C. decidua* completely lacks the tendency to climb that is present in all other species in the region. This characteristic is probably due to strong environmental pressure against a climbing habit in the arid regions inhabited by *C. decidua* or may be due to a fundamental genetic difference from the other species. *C. decidua* is the only species with amphistomatic leaves, while the other five species all have hypostomatic leaves.

Another important difference between *C. decidua* and the other species is the absence of an inflorescence in *C. decidua*, while the other species all have complex inflorescences. Where floral characteristics are normally very constant in the *Cryptolepis* species of southern Africa, *C. decidua* is unique in a number of important instances. Firstly, the corona of all the other five *Cryptolepis* species consists of fleshy, clavate, oblong, deltoid or awl-shaped lobes which are short, never protruding from the corolla mouth. In contrast, the corona of *C. decidua* consists of filiform lobes that often protrude from the corolla mouth. The filiform corona lobes also do not touch to from a nearly closed dome over the gynostegium as is the case for all the other species. As a result the flowers of *C. decidua* are not as strongly directional to pollinators as those of the other five *Cryptolepis* species. This reduced control over pollinator movement and, possibly, reduced pollination efficiency further supports the possibility of *C. decidua* being less highly evolved than the other *Cryptolepis* species.

Secondly, all the *Cryptolepis* species included in this study have prominent, paired, dentate colleters at the inner bases of the sepals. However, in *C. decidua* the dentate colleters are replaced by trichomes. Thirdly, the translators of all the species except in *C. decidua* are virtually indistinguishable in terms of shape. The translators

of *C. decidua* differ markedly in shape and size from those of the other species. This difference in translator size and shape is not related to floral size since *C. capensis* has larger flowers than *C. decidua*, while the flowers of *C. decidua* and *C. obtusa* are very similar in size, yet the translators of *C. capensis* and *C. obtusa* are virtually indistinguishable and those of *C. decidua* are much larger. The pollen tetrads of *C. decidua* differ from those of the other species in that they are spherical, in contrast to the elliptic tetrads in the other species. This suggests that translator shape and size, and pollen tetrad dimensions are interrelated.

All of these uniquely distinguishing characteristics suggest that *C. decidua* possibly does not belong to *Cryptolepis*. There has been much speculation about this in the past and *C. decidua* has been moved to and fro between *Cryptolepis* and *Curroria* (currently regarded as a synonym of *Cryptolepis* (Venter and Verhoeven, 1997)) several times. However, the scope of the present study does not allow a final conclusion about this issue. It will be necessary to also study the remaining 24 *Cryptolepis* species to determine whether the characteristics in which *C. decidua* differs from the other species are indeed diagnostic genus characteristics or are simply characteristics that are poorly represented in the southern African *Cryptolepis* species. Conclusive answers will hopefully be obtained through molecular studies.

If *C. decidua* does, however, belong to the genus *Cryptolepis*, it probably became isolated from the other species early in the evolutionary history of the genus. Due to this isolation and different environmental pressure in its completely different habitat, it retained several plesiomorphic floral characteristics that had been lost by more recently diverged species.

#### REFERENCES

Alkire, L.G. 2005. Periodical Title Abbreviations. Gale Research Co., Detroit, p. 1563.

Andrews, F.W. 1952. The flowering plants of the Anglo-Egyptian Sudan, vol. 2. T. Buncle & Co., Arbroath, Scotland, pp 485.

Ansah, C., Khan, A., Gooderham, N.J. 2005. In vitro genotoxicity of the West African anti-malarial herbal *Cryptolepis sanguinolenta* and its major alkaloid cryptolepine. Toxicology 208, 141–147.

Arekal, G.D., Ramakrishna, T.M. 1980. Pollen-carriers of Periplocaceae and their systematic value. Proceedings. Indiana Academy of Science. Plant Sciences 89(6), 429–435.

Baillon, H. 1891. Histoire des plantes. Librairie Hachette & Cie., Paris, pp 293–304.

Barthlott, W. 1981. Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. Nordic Journal of Botany 1(3), 345–355.

Bentham, G. 1849. *Curroria.* In: Hooker, J.D., Bentham, G. (Eds.), Flora Nigritiana. In: Hooker, W.J. (Ed.), Niger Flora. Hippolyte Bailliere, London, pp 453–458.

Bentham, G. 1876. Asclepiadeae. In: Bentham, G., Hooker, J.D. (Eds.), Genera Plantarum, vol. 2. J. Cramer, Weinheim, pp. 728–785.

Blume, C.L. 1850. Museum Botanicum Lugduno-Batavum sive stirpium exoticarum, novarum vel minus cognitarum es vivis aut siccis brevis exposition et descriptio, vol 1. Leiden, pp.146–147.

Boesewinkel, F.D., Bouman, F. 1984. The seed: structure. In: Johri, B.M. (Ed.), Embryology of Angiosperms, Springer-Verlag, Berlin, pp. 567–610.

Brenan, J.P.M. 1949. Checklists of the forest trees and shrubs of the British Empire No 5, Tanganyika, part 2, p. 64.

Brisson, J.D., Peterson, R.L. 1976. A critical review of the use of scanning electron microscopy in the study of the seed coat. Scanning Electron Microscopy 1976 (7), 477–495.

Brown, N.E. 1895. Cryptolepis obtusa. Kew Bulletin 1895, 110.

Brown, N.E. 1902. Asclepiadeae. In: Thiselton-Dyer, W.T. (Ed.), Flora of Tropical Africa, vol. 4(1). Lovell Reeve & Co., London, pp. 242–246.

Brown, N.E. 1907. Asclepiadeae. In: Thiselton-Dyer, W.T. (Ed.), Flora Capensis, vol. 4(1). Lovell Reeve & Co., London, pp. 518-535.

Brown, R. 1810 (1809–1811). On the Asclepiadeae, a natural order of plants separated from the Apocineae of Jussieu. preprint of Memoirs of the Wernerian Natural History Society 1, 12–78 (1811).

Brummitt, R.K., Powell, C.E. 1992. Authors of plant names. Royal Botanic Gardens, Kew, pp 732.

Bullock, A.A. 1954. Notes on African Asclepiadaceae 3. Kew Bulletin 9, 329-372.

Bullock, A.A. 1955. Notes on African Asclepiadaeae 5. Kew Bulletin 10, 579–587.

Bullock, A.A. 1956. Notes on African Asclepiadaceae 6. Kew Bulletin 11, 265-282.

Cimanga, K., Pieters, L., Claeys, M., van den Berghe, D., Vlietinck, A.J. 1991. Biological activities of cryptolepine, an alkaloid from *Cryptolepis sanguinolenta*. Planta Medica 57(2), S98–S99.

Cimanga, K., De Bruyne, T., Lasure, A., Poel, B.V., Pieters, L., Clayes, M., van den Berghe, D., Kambu, K., Tona, L., Vlietnick, B.J. 1996a. In vitro biological activities of alkaloids from *Cryptolepis sanguinolenta*. Planta Medica 62, 22–27.

Cimanga, K., De Bruyne, T., Pieters, L., Clayes, M., Vlietinck, A. 1996b. New alkaloids from *Cryptolepis sanguinolenta*. Tetrahedron Letters 37, 1703–1706.

Cimanga, K., De Bruyne, T., Pieters, L, Vlietinck, A.J. 1997. In vitro and in vivo antiplasmodial activity of cryptolepine and related alkaloids from *Cryptolepis sanguinolenta*. Journal of Natural Products 60, 688–691.

Civeyrel, L. 1994. Variation et evolution des types polliniques du genre *Secamone* (Asclepiadaceae, Secamonoideae). Comptes Rendus. Academie des Sciences. Serie 3. Sciences de la Vie 317, 1159–1165.

Civeyrel, L., Le Thomas, A., Ferguson, K., Chase§, M.W. 1998. Critical reexamination of palynological characters used to delimit Asclepiadaceae in comparison to the molecular phylogeny obtained from plastid *mat*K sequences. Molecular Phylogenetics and Evolution 9(3), 517–527.

Claasen, H.E. 1994. Taksonomiese aspekte van *Cryptolepis*. Unpublished honours report. University of the Free State, Bloemfontein, South Africa, pp 99, unpublished.

Compton, R.H. 1975. The flora of Swaziland, pp 444–446.

Dutta, S.K., Sharma, B.N., Sharma, P.V. 1980. A new nicotinyl glucoside from *Cryptolepis buchanani*. Phytochemistry 19, 1278.

Dyer, R.A. 1975. The genera of southern African flowering plants, vol 1. Department of Agricultural Technical Services, Pretoria, pp 756.

Edwards, D., Leistner, O.A. 1971. A degree reference system for citing biological records in southern Africa. Mitteilungen Botanische Staatssammlung München 10, 501–509.

El-Gazzar, A., Hamza, M.K. 1973. Morphology of the twin pollinia of Asclepiadaceae. Pollen et spores 15 (3–4), 459–470.

Endress, M.E. 2001. Apocynaceae and Asclepiadaceae: united they stand. Haseltonia 8, 2–9.

Endress, M.E., Bruyns, P.V. 2000. A revised classification of the Apocynaceae s.I. Botanical Review 66(1), 1–56.

Endress, M.E., Hesse, M., Nilsson, S., Guggisberg, A., Zhu, J. 1990. The systematic position of *Holarrheninae* (Apocynaceae). Plant Systematics and Evolution 171, 157–185.

Engler, A. 1889. Asclepiadaceae. In: Engler, A. (Ed.), Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 10, 244.

Engler, A. 1895. Asclepiadaceae. In: Engler, A. (Ed.), Botanische Jahrbücher für systematic, Pflanzengeschichte und Pflanzengeographie 19, 128–152.

Erdtman, G. 1960. The acetolysis method. Svensk Botanisk Tidskrift 54(4), 561– 564.

Eyles, F. 1916. A record of plants collected in Southern Rhodesia. Transactions of the Royal Society of South Africa 5, 1–564.

Forster, P.I. 1990. Notes on Asclepiadaceae 2. Austrobaileya 3(2), 273–289.

Galil, J., Zeroni, M. 1969. On the organization of the pollinium in *Asclepias curassavica*. Botanical Gazette 130(1), 1–4.

Germishuizen, G., Meyer, N.L. (Eds.) 2003. Plants of southern Africa: an annotated checklist. Strelitzia 14. National Botanical Institute, Pretoria, pp 1231.

Gilli, A. 1973. Beiträge zur flora von Tanganyika und Kenya 4. Annals of the Natural History Museum 77, 15-57.

Good, R. 1952. An atlas of the Asclepiadaceae. New Phytologist 51, 198–208.

Greuter, W., McNeill, J., Barrie, F.R., Burdet, H.M., Demoulin, V., Filgueiras, T.S., Nicolson, D.H., Silva, P.C., Skog, J.E., Trehane, P., Turland, N.J., Hawksworth, D.L. 2000. International code of botanical nomenclature. Koeltz Scientific Books, Köningstein, p. 474.

Hallier, H. 1905. Provisional scheme of the natural (phylogenetic) system of flowering plants. New Phytologist 4, 151–162.

Hesse, M., Waha, M. 1989. A new look at the acetolysis method. Plant Systematics and Evolution 163, 147–152.

Hickey, L.J. 1979. A revised classification of the architecture of dictyledonous leaves. In: Metcalfe, C.R., Chalk, L. (Eds.), Anatomy of the Dicotyledons. Clarendon Press, Oxford, pp. 25–39.

Holmgren, P.K., Holmgren, N.H., Barnett, L.C. 1990. Index Herbariorum, part 1, 8<sup>th</sup> edition. New York Botanical Gardens, New York, pp. 693.

Hooker, J.D. 1883. The flora of British India, vol. 4. L. Reeve & Co., London pp 780.

Huber, H.F.J. 1967. Periplocaceae. In: Merxmüller, H. (Ed.), Prodromus Südwest Afrika, Botanische Staatssamlung, München, 113, 1–7

Huber, H.F.J. 1973. Periplocaceae and Asclepiadaceae. In: Abeywickrama, B.A. (Ed.), Flora of Ceylon, Vol. 1. University of Ceylon, Sri Lanka, pp. 1–57.

Hutchinson, J. 1973. Families of flowering plants. Clarendon Press, Oxford, pp 968.

Ionta, G., Judd, W.S. 2007. Phylogenetic relationships in Periplocoideae (Apocynaceae s.I.) and insights into the origin of pollinia. Annals of the Missouri Botanical Garden 94, 362–377.

Jackson, B.D. 1893. In Index Kewensis 1(2). Claredon Press, Oxford, p. 1268.

Judd, W.S., Sanders, R.W., Donoghue, M.J. 1994. Angiosperm family pairs: Preliminary phylogenetic analyses. Harvard Papers in Botany 1(5), 1–51.

Jussieu, A. de. 1789. Genera Plantarum. Viduam Herissant, Paris, pp 526.

Klackenberg, J. 1999. Revision of the Malagasy genera *Pentopetia* and *Ischnolepis* (Apocynaceae s.I., Periplocoideae). Candollea 54, 257–339.

Knox, R.B., McConchie, C.A. 1986. Structure and function of compound pollen. In: Blackmore, S. and Ferfuson, I.K. (Eds.), Pollen and Spores, form and function, Academic Press, London, pp 264–282.

Kotze, J.D.S. 1988. Taksonomies-morfologiese studie van *Ectadium, Petopentia* en *Tacazzea* (Periplocaceae). Unpublished M.Sc. dissertation, University of the Free State, Bloemfontein, South Africa.

Kunze, H. 1993. Evolution of the translator in Periplocaceae and Asclepiadaceae. Plant Systematics and Evolution 185, 99–122. Kunze, H. 1996. Morphology of the stamen in the Asclepiadaceae and its systematic relevance. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 118, 547–579.

Kunze, H. 2005. Morphology and evolution of the corolla and corona in the Apocynaceae s.l. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 126(3), 347–383.

Lawrence, G.H.M. 1951. Taxonomy of vascular plants. The MacMillan Company, New York, pp 823.

Leistner, O.A., Morris, J.W. 1976. South African place names. Annals of the Cape Provincial Museum 2, 1–565.

Liede, S., Kunze, H. 1993. A descriptive system for corona analysis in *Asclepiadaceae* and *Periplocaceae*. Plant Systematics and Evolution 185, 275–284.

Linnaeus, C. 1753. Species Plantarum, vol. 1. Holmiae, Stockholm, pp. 560. Meisner, C.F. 1843. Flora of South Africa. In: Hooker, J.D. (Ed.), London Journal of Botany 2, 542 (by error 442).

Metcalfe, C.R. 1979. The leaf: general topography and ontogeny of the tissues. In: Metcalfe, C.R., Chalk, L. (Eds.), Anatomy of the Dicotyledons. Clarendon Press, Oxford, pp. 61–75.

Meisner, C.F. 1843. Flora of South Africa. In: Hooker, J.D. (Ed.), London Journal of Botany 2, 542 (by error 442).

Mucina, L., Rutherford, M.C., Powrie, L.W. (eds.) 2005. Vegetation Map of South Africa, Lesotho and Swaziland, 1:1 000 000 scale sheet maps. South African National Biodiversity Institute, Pretoria.

Nilsson, S. 1986. The significance of pollen morphology in the Apocynaceae. In: Blackmore, S., Ferguson, I.K. (Eds.), Pollen and Spores. Academic Press, London, pp. 359–374.

Nilsson, S. 1990. Taxonomic and evolutionary significance of pollen morphology in the Apocynaceae. Plant Systematics and Evolution (Supplement) 5, 91–102.

Nilsson, S., Endress, M.E., Grafström, E. 1993. On the relationship of the Apocynaceae and Periplocaceae. Grana 1993(2), 3–20.

Omlor, R. 1996. Do *Menabea venenata* and *Secamonopsis madagascariensis* represent missing links between Periplocaceae, Secamonoideae and Marsdenieae (Asclepiadaceae)? Kew Bulletin 51, 695–715.

Paulo, A., Pimentel, M., Viegas, S., Pires, I., Duarte, A., Cabrita, J. 1994. *Cryptolepis sanguinolenta* activity against diarrhoeal bacteria. Journal of Ethnopharmacology 44, 73–78.

Paulo, A., Gomes, E.T., Houghton, P.J. 1995. New alkaloids from *Cryptolepis* sanguinolenta. Journal of Natural Products 58, 1485–1491.

Paulo, A., Gomes, E.T., Duarte, A., Perrett, S., Houghton, P.J. 1997. Chemical and antimicrobial studies on *Cryptolepis obtusa* leaves. Fitoterapia 68, 558–559.

Paulo, A., Gomes, E.T., Steele, J., Warhurst, D.C., Houghton, P.J. 2000a. Antiplasmodial activity of *Cryptolepis sanguinolenta* alkaloids from leaves and roots. Planta Medica 66, 30–34.

Paulo, A., Jimeno, M.L., Gomes, E.T., Houghton, P.J. 2000b. Steroidal alkaloids from *Cryptolepis obtusa*. Phytochemistry 53, 417–422.

156

Paulo, A., Houghton, P.J. 2003. Chemotaxonomic analysis of the genus *Cryptolepis*. Biochemical Systematics and Ecology 31, 155–166.

Potgieter, K., Albert, V.A. 2001. Phylogenetic relationships within Apocynaceae s.I. based on *trn*L intron and *trn*L-F spacer sequences and propagule characters. Annals of the Missouri Botanical Gardens 88, 523–549.

Purushothaman, K.K., Vasanth, S., Connolly, J.D., Rycroft, D.S. 1988. New sarverogenin and isosarverogenin glycosides from *Cryptolepis buchananii* (Asclepiadaceae). Revista Latinoamericana de Quimica 19, 28–31.

Reitsma, T. 1969. Size modifications of recent pollen grains under different treatments. Review of Palaeobotany and Palynology 9, 175–202.

Robyns, W., 1947. Flore des Spermatophytes du Parc National Albert, vol. 2, Bruxelles, pp 627.

Roemer, J.J., Schultes, J.A. 1819. Systema Vegetabilium, vol. 4. J.G. Gottae, Stuttgardt, p. 409.

Safwat, F.M. 1962. The floral morphology of *Secamone* and the evolution of the pollinating apparatus in Asclepiadaceae. Annals of the Missouri Botanical Garden 49, 95–129.

Santapau, S.J., Irani, N.A. 1960. The Asclepiadaceae and Periplocaceae of Bombay. P.C. Manaktala and sons Pty. Ltd., Bombay, pp 116.

Schick, B. 1982. Zur Morphologie, Entwicklung, Feinstruktur und Function des Translators von *Periploca* L. (Asclepiadaceae). In: Rauh, W. (Ed.), Akademie der Wissenschaften und der Literatur. Tropische und subtropische Pflanzenwelt 40, 515–553.

157

Schill, R., Jäkel, U. 1978. Beitrag zur Kenntnis der Asclepiadaceen-pollinarien. Tropische und subtropische Pflanzenwelt 22, 7–22.

Schlechter, F.R.R. 1893. Beiträge zur Kenntnis der Orchidaceen und Asclepiadaceen Südafrikas. Verhandlungen Botanischer Verein der Provinz Brandenburg 35, 47–48.

Schlechter, F.R.R. 1894. Beiträge zur Kenntnis südafrikanischer Asclepiadeen. In: Engler, A. (Ed.), Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 18 (45), 1–37.

Schlechter, F.R.R. 1895. Beiträge zur Kenntnis südafrikanischer Asclepiadeen. In: Engler, A. (Ed.), Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 20 (51), 1–56.

Schlechter, F.R.R. 1896. Revision of extratropical South African Asclepiadaceae. Journal of Botany 34, 311–315.

Schlechter, F.R.R. 1905a. Periplocaceae. In: Schumann, K., Lauterbach, K. (Eds.), Nachträge zur Flora des Deutschen Schutzgebiete in der Südsee. Borntraeger, Leipzig, pp. 351–353.

Schlechter, F.R.R. 1905b. Asclepiadacee Africanae. In: Engler, A. (Ed.), Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 38, 26–56.

Schlechter, F.R.R. 1924. Periplocaceae. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9, 23–40.

Schumann, K. 1895. Asclepiadaceae. In: Engler, A. (Ed.), Pflanzenwelt Ost-Africas, Vol. C: 320–425.

Schumann, K. 1897. Asclepiadaceae. In: Engler, A., Prantl, K. (Eds.), Die natürlichen Pflanzenfamilien, Vol. 4(2). verlag von Wilhelm Engelmann, Leipzig, pp. 109–305.

Sennblad, B., Bremer, B. 1996. The familial and sub-familial relationship of Apocynaceae and Asclepiadaceae evaluated with *rbcL* data. Plant Systematics and Evolution 202, 153–175.

Shah, B.B., Khare, M.P. 1981. *Cryptolepis buchananii* Roem. and Schult., a new source of sarmentogenin. Journal of the Nepal Chemical Society 1, 103–107.

Sonder, O.W., 1850. Beiträge zur Flora von Südafrica. Linnaea 23(1), 1–138.

Stafleu, F.A., Cowan, R.S. 1976. Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types, vol. 1–7. Bohn, Scheltema & Holkema, Utrecht.

Stearn, W.T. 1991. Botanical Latin (ed. 7). Redwood Press Ltd., England, Melksham, pp 1–566.

Swarupanandan, K.J.K., Mangaly, T.K., Sonny, K., Kishorekumar, K., Chand Basha, S. 1996. The subfamilial and tribal classification of the family Asclepiadaceae. Botanical Journal of the Linnean Society 120, 327–369.

Sylla, T., Albers, F. 1989. Samenentwicklung und samenmorphologie krautiger und sukkulenter Asclepiadaceae. Botanische Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie 110(4), 479–492.

Systematics association committee for discriptive biological terminology, 1962. Terminology of simple symmetrical plane shapes. Taxon 11, 145–156 & 245–247. Takhtajan, A. 1997. Diversity and classificaton of flowering plants. Columbia University Press, New York, pp. 643.

Taoana, T.R.N. 2001. Taxonomy of the genera *Baseonema, Batesanthus, Mangenotia, Mondia, Sacleuxia, Sarcorrhiza* and *Zacateza* (Periplocoideae, Apocynaceae). Unpublished M.Sc. thesis, University of the Free State, Bloemfontein, South Africa, pp. 1–153.

Thomas, V. 1991. Structural, functional and phylogenetic aspects of the colleter. Annals of Botany 68, 287–305.

Thomas, V., Dave, Y. 1991. Comparative and phylogenetic significance of the colleters in the family Apocynaceae. Feddes Repertorium 102(1991), 177–182.

Thorne, R.F. 1992. An updated phylogenetic classification of the flowering plants. Aliso 13, 365–389.

Van der Ham, R., Zimmermann, Y., Igersheim, S.A. 2001. Pollen morphology and phylogeny of the Alysieae (Apocynaceae). Grana 40(4–5), 169–191.

Venter, H.J.T., Field, D.V. 1989. A new species of *Stomatostemma* (Periplocaceae) from Mozambique, Africa. Botanical Journal of the Linnean Society 99, 397–400.

Venter, H.J.T., Verhoeven, R.L. 1986. A new species of *Raphionacme* (Periplocoideae) from South West Africa/Namibia. South African Journal of Botany 52(4), 332–334.

Venter, H.J.T., Verhoeven, R.L. 1993. A taxonomic account of *Stomatostemma* (Periplocaceae). South African Journal of Botany 59(1), 50–56.

Venter, H.J.T., Verhoeven, R.L. 1994a. *Buckollia,* a new genus in the Periplocaceae. South African Journal of Botany 60(2), 93–98. Venter, H.J.T., Verhoeven, R.L. 1994b. *Maclaudia felixii*, a new genus and species in the Periplocaceae from Guinea, West Africa. Botanical Journal of the Linnean Society 115, 57–63.

Venter, H.J.T., Verhoeven, R.L. 1997. A tribal classification of the *Periplocoideae* (Apocynaceae). Taxon 46, 705–720.

Venter, H.J.T., Verhoeven, R.L. 1998. A taxonomic revision of *Schlechterella* (Periplocoideae, Apocynaceae). South African Journal of Botany 64, 350–355.

Venter, H.J.T., Verhoeven, R.L. 1999. A new species of *Cryptolepis* (Periplocoideae, Apocynaceae) from Arabia. Botanical Journal of the Linnean Society 131, 417–422.

Venter, H.J.T., Verhoeven, R.L. 2001. Diversity and relationships within the Periplocoideae (Apocynaceae). Annals of the Missouri Botanical Gardens 88, 550–568.

Venter, H.J.T., Verhoeven, R.L. 2007. A re-appraisal of *Cryptolepis sinensis* subsp. *africana* (Apocynaceae: Periplocoideae) and a description of the pollen apparatus. South African Journal of Botany 73, 40–42.

Venter, H.J.T., Kotze, J.D.S., Verhoeven, R.L. 1990a. A taxonomic revision of *Ectadium* (Periplocaceae). South African Journal of Botany 56(1), 113–124.

Venter, H.J.T., Verhoeven, R.L., Kotze, J.D.S. 1990b. A monograph of *Tacazzea* (Periplocaceae). South African Journal of Botany 56(1), 93–112.

Venter, H.J.T., Verhoeven, R.L., Kotze, J.D.S. 1990c. The genus *Petopentia* (Periplocaceae). South African Journal of Botany 56(3), 393–398.

Venter, H.J.T., Dold, A.P., Verhoeven, R.L., Ionta, G. 2006a. *Kappia lobulata* (Apocynaceae, Periplocoideae), a new genus from South Africa. South African Journal of Botany 72, 529–533.

Venter, H.J.T., Thulin, M., Verhoeven, R.L. 2006b. Two new species of *Cryptolepis* (Apocynaceae: Periplocoideae) from Somalia, North-east Africa. South African Journal of Botany 72, 139–143.

Verhoeven, R.L., Venter, H.J.T. 1988. Pollen morphology of *Raphionacme* (Periplocaceae). South African Journal of Botany 54, 123–132.

Verhoeven, R.L., Venter, H.J.T. 1993. Pollen morphology of *Curroria, Mondia, Socotranthus* and *Stomatostemma* (Periplocaceae). Bothalia 23, 105–110.

Verhoeven, R.L., Venter, H.J.T. 1994a. Pollen morphology of the Periplocaceae of Madagascar. Grana 33, 295–308.

Verhoeven, R.L., Venter, H.J.T. 1994b. Pollen morphology of *Periploca* (Periplocoideae). South African Journal of Botany 60(4), 198–202.

Verhoeven, R.L., Venter, H.J.T. 1997. The translator of *Raphionacme* (Periplocaceae). South African Journal of Botany 63(1), 46–54.

Verhoeven, R.L., Venter, H.J.T. 1998. Pollinium structure in Periplocoideae (Apocynaceae). Grana 37, 1–14.

Verhoeven, R.L., Venter, H.J.T. 2001. Pollen morphology of the Periplocoideae, Secamonoideae, and Asclepiadoideae (Apocynaceae). Annals of the Missouri Botanical Gardens 88, 569–582.

162

Verhoeven, R.L., Venter, H.J.T., Kotze, J.D.S. 1989. Pollen morphology of *Petopentia* and *Tacazzea* (Periplocaceae). South African Journal of Botany 55, 207–214.

Verhoeven, R.L., Liede, S., Endress, M.E. 2003. The tribal position of *Fockea* and *Cibirhiza* (Apocynaceae: Aslepiadoideae): evidence from pollinium structure and cpDNA sequence data. Grana 42, 70–81.

Walker, J.W., Doyle, J.A. 1975. The basis of Angiosperm phylogeny: palynology. Annals of the Missouri Botanical Garden 62, 664–723.

Walpers, G.G. 1847. Asclepiadeae. Repertorium Botanices Systematicae, 6, 479–481.

Walpers, G.G. 1852. Annales Botanices Systematicae 3, 48-69.

Walton, C. 1984. Reader's Digest Atlas of southern Africa. The Reader's Digest Association of South Africa (Pty) Ltd. Cape Town, pp 256.

Wanntorp, L. 2007. Pollinaria of *Hoya* (Marsdenieae, Apocynaceae)—shedding light on molecular phylogenetics. Taxon 56(2), 465–478.

Wilkinson, H.P. 1979. The plant surface (mainly leaf). In: Metcalfe, C.R., Chalk, L. (Eds.), Anatomy of the Dicotyledons. Clarendon Press, Oxford, pp. 97–165.

Wood, J.M. 1907. A handbook to the Flora of Natal. Bennett & Davis Printers, Durban, pp 202.

#### SUMMARY

A taxonomic revision of *Cryptolepis* R.Br. (Apocynaceae, Periplocoideae) in southern Africa is presented. This revision comprises investigations into the micromorphology of pollen, translators, leaf anatomy, leaf epidermal surfaces and seed coat surfaces; macro-morphology of the plant parts; nomenclature, geographical distribution and ecological characteristics of the six species indigenous to southern Africa. The investigations resulted in descriptions with appropriate nomenclature and the compilation of an identification key for the six species.

All available type specimens related to *Cryptolepis* in southern Africa were studied. Where holotype specimens could not be located lectotypes were designated from available isotypes or syntypes. Where no isotypes or syntypes could be located, neotypes were declared. In cases where only syntypes had been given by authors of species names, lectotypes were declared.

*Cryptolepis* is widely distributed throughout the northern parts of southern Africa, with the largest concentration of species in the north-east of the region. Some species, such as *C. oblongifolia,* are common, while others have very restricted distribution ranges. *C. delagoensis,* for instance, is known from only six localities in southern Africa. Only *C. decidua* occurs in the desert and semi-desert habitats in the north-west of southern Africa, while the other five species inhabit savannah, sand forest, riverine -, afromontane - and coastal vegetation in the eastern parts of the region.

In southern Africa *Cryptolepis* consists of slender climbers, occasionally small suffrutices or branching shrubs with white latex and interpetiolar ridges with dentate colleters. Leaves are opposite, decussate or rarely fascicled. A combination of leaf anatomy and leaf surface characteristics proved to be taxonomically useful for distinguishing the southern African species. The fruit consists of paired follicles. Seeds of *Cryptolepis* are adapted to anemochoric dispersal through a coma of hair at the micropylar end. All southern African species can be differentiated from each

164

other using cellular arrangement and primary and secondary sculpture of their seed coat surfaces.

Floral characteristics are taxonomically useful for distinguishing *Cryptolepis* from related genera. *Cryptolepis* is characterized by a distinct corolla tube, with corolla lobes always longer than the corolla tube, corona lobes arising just above the middle of the corolla tube, and usually included in the corolla tube, and stamens arising at the lower third of the corolla tube, with interstaminal discs always present. Two, semi-inferior, apocarpous ovaries are present. The styles unite to form a compound style and pentagonal style-head, on which five translators are formed by epithelial cells in grooves alternating with the stamens. The anthers are fused to the style head, forming a gynostegium.

In the five species that occur in the eastern parts of the region flowers are arranged in cymes. Prominent, paired colleters are found at the inner bases of the sepals. The corona lobes may be oblong, clavate, deltoid or awl-shaped. The corona lobes are always included in the corolla tube, where they touch or fit tightly, forming a dome which closes off the lower corolla tube. Pollen characteristics and translator shape are similar for all five species and have little taxonomic value.

*C. decidua* differs from the eastern species in that its flowers are solitary. The colleters at the inner sepal bases are replaced by trichomes. The corona lobes are filiform, do not form a dome over the lower corolla tube and may be exserted from the corolla tube mouth. Pollen tetrad shape and translator shape and size differ markedly from those of the other species. All these unique characteristics in *C. decidua* suggest that this species may not belong in *Cryptolepis*.

**Keywords:** *Cryptolepis* (Apocynaceae, Periplocoideae), southern Africa, taxonomy, micromorphology, palynology.

#### **OPSOMMING**

'n Taksonomiese hersiening van *Cryptolepis* R.Br. (Apocynaceae, Periplocoideae) in suider-Afrika word aangebied. Die ondersoek behels studies van: mikromorfologie van die stuifmeel, stuifmeeldraers, blaar- en saadhuidoppervlakke, anatomie van die blare, makromorfologie van die plantdele, nomenklatuur, geografiese verspreiding en ekologiese eienskappe van die ses inheemse spesies. Bogenoemde ondersoek het tot beskrywings en nomenklatoriese verklarings van die onderskeie spesies gelei, asook tot die opstel van 'n uitkenningsleutel.

Alle beskikbare tipe-eksemplare van die ses spesies is bestudeer. Waar geen holotipes gevind is nie, is geskikte iso- of sintipes tot lektotipes verklaar. Lektotipes is ook verklaar waar slegs sintipes aangewys is. In een geval is 'n neotipe aangewys.

*Cryptolepis* is wyd oor suider-Afrika versprei, met die grootste konsentrasie in the noordooste van die streek. Sommige spesies, soos *C. oblongifolia* kom algemeen voor, terwyl ander beperkte verspreidings toon. *C. delagoensis* is byvoorbeeld in slegs ses plekke gevind. Alleenlik *C. decidua* kom in die woestyn en halfwoestyn in die noordweste van suider-Afrika voor. Die ander vyf spesies word in savanna en sand-, rivieroewer-, berg- en kusplantegroei aangetref.

Vier van die Suider-Afrikaanse *Cryptolepis* spesies is klimplante, twee is struikagtig. Die plante besit almal wit melksap, interpetiolêre riwwe met tandagtige kolleters, teenoorstaande -, kruisgewys-teenoorstaande - of selde saamgehoopte blare. 'n Kombinasie van anatomiese en blaaroppervlak-eienskappe blyk nuttig in die onderskeiding van die suider-Afrikaanse soorte te wees. Die vrug bestaan uit gepaarde kokervrugte. Die saad is deur die besit van saadpluise vir windverspreiding aangepas. Al ses spesies kan op grond van die bou van hulle saadhuidoppervlakke van mekaar onderskei word. Blomkenmerke onderskei *Cryptolepis* van naverwante genera in die subfamilie. *Cryptolepis* word aan die volgende blomeienskapppe uitgeken: 'n duidelike kroonbuis, kroonlobbe wat gewoonlik langer as die kroonbuis is en tot meerdere of mindere mate helies in die knop opgerol is, bykroonlobbe wat net bokant die middel van die kroonbuis ingeplant is en gewoonlik in die kroonbuis ingesluit is, meeldrade wat direk onder die bykroonlobbe naby die basis van die kroonbuis ingeplant is en nektarklierskywe wat afwisselend met die meeldrade by die basis van die kroonbuis voorkom. Die blom word verder onderskei deur twee halfonderstandige vrye vrugbeginsels, vergroeide style wat in 'n vyfhoekige stylkop eindig en waarop stuifmeeldraers afkomstig uit epiteelselle neergelê word. Die helmknoppe is met die stylkoppe vergroei om ginostegiums te vorm.

Die vyf oostelike soorte se blomme is in byskerms gerangskik, opvallende gepaarde kolleters kom by die binneste basisse van die kelkblare voor, die bykroonlobbe is langwerpig, knuppelvormig, driehoekig of elsvormig en is altyd in die kroonbuis ingesluit waar hulle koepelvormig oor die ginostegium buig om die onderste deel van die kroonbuis af te sluit. In al vyf spesies is die kroonbuis om die vrugbeginsels haarloos, en die stuifmeeltetrades en stuifmeeldraers baie eenders in voorkoms en besit min onderskeidingswaarde.

*C. decidua* van die noordwestelike woestynagtige streek verskil van die oostelike spesies ten opsigte van die volgende kenmerke: die blomme is alleenstaande, die kolleters by die kelkblaarbasisse is deur hare verplaas, die bykroonlobbe is draadvormig en by die kroonbuis uitgestoot, en die voorkoms en grootte van die stuifmeeldraers verskil noemenswaardig van die ander vyf spesies. Al hierdie unieke kenmerke mag daarop dui dat *C. decidua* nie in *Cryptolepis* hoort nie.

**Sleutelwoorde:** *Cryptolepis* (Apocynaceae, Periplocoideae), Suider-Afrika, taksonomie, mikromorfologie, palinologie.

#### ACKNOWLEDGEMENTS

My sincere appreciation and gratitude to the following persons and institutions who contributed in some way towards the completion of this thesis.

- My supervisor, Dr. A.M. Venter, who not only gave guidance and valuable taxonomic insight, but also encouraged and inspired me throughout the completion of this thesis. My deep appreciation for all the wonderful opportunities afforded me to gain the best experience and education possible.
- My co-supervisor, Prof. R.L. Verhoeven, for patient training and invaluable advice for all micromorphological and anatomical work. For long hours spent working at the microscope, assistance with literature and proof reading, my sincere thanks.
- Prof. H.J.T. Venter, for never-ending patience and assistance with all taxonomic problems. Also for much trouble taken in arranging travels for field work and herbarium visits.
- The curators of the different herbaria, listed in chapter 3, who allowed me to examine their collections or sent the material on loan.
- The staff of the National Herbarium in Pretoria, in particular Mrs Estelle Potgieter, Mrs Hester Steyn, Mrs Hannelie Snyman and Dr. Bredenkamp, for their friendly and efficient assistance and attention to each enquiry.
- Staff of Kew Herbarium, in particular Dr. David Goyder, and staff of the Kew Herbarium Library for their kind assistance.
- Technical assistance from Prof. Pieter van Wyk and Ms Beanelri Janecke at the Centre for Confocal Microscopy.
- Ms Anet Kotze for the wonderful black and white drawings for the thesis as well as her valuable advice and support.
- Ms Gretchen lonta for photographs of live plants and companionship during fieldwork.
- My parents who first taught me to love nature and inspired me to study its wonders.
- My family, friends and colleagues who encouraged and supported me throughout this endeavour. A special word of thanks to my fellow students who enlivened many days of hard work with good humour and sincere interest.

#### ADDENDUM

# Herbarium specimens of southern African *Cryptolepis* species examined

#### C. capensis

#### South Africa:

— **2330** (Tzaneen): Gazankulu-Giyani district, Giyani (–BC), *Liengme, C.A. 96* (PRE); Letaba, Duiwelskloof (–CA), *Scheepers 1187* (G, K, M, PRE, PRU, Z); Letaba district, S of Farm Silver Leaves, Langbult portion of farm (–CC), *Reid, C 1171* (PRE).

— 2430 (Pilgrim's Rest): Lekgalametse Nature Resort, past Malta-Marinella (–AA),
Stabmans 960 (K); Blydepoort Holiday Resort, Dadishi Trail (–DB), Buitendag, E.
1200 (K, MO, NBG, PRE).

— **2530** (Lydenburg): Lydenburg, Witklip Forestry Station (–DB), *Kluge, J.P.* 334 (PRE); Barberton, Moodies (–DD), *Thorncroft, J.* 607 (NH).

— 2531 (Komatipoort): Barberton (–CC), Janse, A.J.T. 9872 (PRE); Barberton (–CC), Thorncroft, J 9595 (GRA, PRE).

- 2632 (Bela Vista): Ndumo Game Reserve (-CD), Venter, H.J.T. 8983 (BLFU).

— 2730 (Vryheid): Vryheid district, Nhlagatshe Mountain (–DD), Burtt & Hilliard 3356 (NU).

— **2731** (Louwsburg): Zululand, Hluhluwe district, Makowe Hill, near Hluhluwe Forest (–CC), *Wells, J.M. 2149* (SRGH); Vryheid district, Ngome Forest (–CD), *Hilliard & Burtt 5941* (K, NH, NU); Ngome Forest, along footpath to waterfall (–CD), *Venter H.J.T. 8999* (BLFU); Louwsburg, Ngomi Forest, 50 m from crossing over stream under water fall (–CD), *Venter, H.J.T 8783* (BLFU).

- 2732 (Ubombo): Ingwavuma Gorge (-AA), Wells, J.M. 2204 (G, K, M, PRE, Z).

- 2831 (Nkandla): Hlabisa district, Wome (-BB), *Gerstner, J. 2845* (NH); Eshowe, forest opposite town hall (-CD), *Acocks, J.P.H. 12969* (PRE), *Kotze, P.C. 6708* (PRE), *Lawn, J.G. 111* (NH).

- **2832** (Mtubatuba): Zululand, Hlabisa district, Hluhluwe Game Reserve (–AA), *Ward, C.J. 2820* (NH, PRE), *Ward, C.J. 3287* (K, M, NH, NU, PRE, SRGH).

2930 (Pietermaritzburg): Pietermaritzburg, Winterskloof, NW of railway station, overlooking "Worlds View" (–CB), *Smith, C.A.* (PRE); Camperdown, Drummond old road (–DA), *Strey, R.G. 7310* (BR, K, M, NH, NU, PRE), *Wood, J.M. 1583* (BM, BOL, K, MO, NH), *Wood, J.M. 701* (K), *Wood, J.M. 886* (SAM), *McKen 6* (K); Pietermaritzburg, Ismont (–DC), *Strey, R.G. 8352* (K, NH, NU, PRE, SRGH, WAG); Pietermaritzburg, Krantzkloof (–DD), *Haygarth, W.J. 91* (STE); Pinetown district, Everton, Molweni Gorge (–DD), *Hilliard & Burtt 7575* (K, NU).

— **2931** (Stanger): Nonoti River (–AD), *Gerrard 1319* (BM, K); Durban, forest above Umhlanga Rocks Hotel (–CA), *Watmough, R. 445* (K, M, NH, PRE, W); Mount Edgecombe (–CA), *Wood, J.M. 11589* (GRA, J, NH, NU, PRE, Z); Beach Terminus (–CC), *2656* (STE); Durban (–CC), *McKen 21* (K, PRE).

— 3030 (Port Shepstone): Umtamvuna Nature Reserve, river trail (–AA), Abbott, A.
1564 (NH, PRU); Alexandra, Dumisa, Umpambinyoni (–AD), Rudatis, H. 2058 (STE); Port Shepstone, Oribi Gorge, Hills Gate (–CA), Balkwill & Crow 232 (J); Umtamvuna Nature Reserve, Verrassendkloof (–CC), Abbott, A. 1497 (NH, PRU); Umtamvuna Nature Reserve, SE of Rooielsbos (–CC), Abbott, A. 1687 (NH, PRU).

- **3128** (Umtata): Transkei, Elliotdale district, The Haven (–DC), *Gordon-Gray, J.L. 1311* (NU).

- 3129 (Port St. Johns): Port St. Johns (-DA), Hutchings & Plumstead 1559 (NH).

**—3130** (Port Edward): Port Edward, along Izingolweni road, Clearwater Trails, along Fish Eagle Trail (– AA), *Joubert, L. 31* (BLFU).

- 3228 (Butterworth): Kentani (-CB), Pegler, A. 663 (BOL).

## *C. cryptolepioides* South Africa:

 2229 (Waterpoort): Soutpansberg, Wylliespoort, western side of ravine (–DD), Ihlenfeldt, H.D. 2194a (PRE); Waterpoort district, Louis Trichardt, Wylliespoort (– DD), Venter, H.J.T. 9203 (BLFU).

— 2230 (Messina): Soutpansberg, Makonde Mission Station, 24 km NE of Sibasa (–
DC), Codd, L.E. 6854 (K, PRE, SRGH).

2329 (Pietersburg): Matoks (–BC), *Hutchinson & Gillett 4476* (K); Pietersburg district, Blaauwberg, ravine leading to Beacon Steep (–CD), *Codd, L.E. & Dyer 9084* (K, PRE); Blaauwberg, Mohlakeng Plateau (–CD), *Codd, L.E. & Dyer, R.A. 9139* (K, PRE); Pietersburg (–CD), *Fries, Norlindh & Weimarck 2021* (MO, PRE); Pietersburg, Blaauwberg (–CD), *Van der Schijff, H.P. 5350* (PRE, PRU); Pietersburg, University of the North campus (–CD), *Van Vuuren, D.R.J. 1415* (PRE); Houtbosch (–DD), *Rehmann, A. 5880* (BM, K, Z).

— 2427 (Thabazimbi): Waterberg district, Kranzberg area (–BC), Germishuizen, G. 253 (BR, K, MO, PRE); Thabazimbi district, Kransberg (–BC), Venter, F. 1941 (K, PRE, SRGH); Thabazimbi district, near western tip of Kranzberg (–CB), Venter, F. 1941 (SRGH).

2428 (Nylstroom): Waterberg district, Warmbad (–CD), *Bolus, H. 12154* (BOL, K).
2429 (Zebediela): Zebediela, 51 km N of Potgietersrus, at granite dams (–AA), *Venter, H.J.T. 9197* (BLFU); Lydenburg district, Sekukuneland, Magnet Heights Farm "Moraro" (–DD), *Barnard & Mogg 869* (K, PRE).

— 2430 (Pilgrim's Rest): Letaba, citrus farm near Ofcalaco (–AB), *Rennie & Scheepers s.n.* (PRE); Second look out point along road from Bourke's Luck to Aventura Resort, near "Drie Rondawels" (– DA), *Joubert, L. 27* (BLFU); Bourke's Luck, river-bank at potholes (–DB), *Herman 719* (K); Bourke's Luck, opposite Treur River waterfall (– DB), *Joubert, L. 28* (BLFU).

2527 (Rustenburg): Rustenburg district (–CA), Acocks, J.P.H. 18738 (PRE);
Rustenburg Nature Reserve (–CA), Jacobsen, N.H. 902 (PRE); Rustenburg district,
Magaliesberg (–CA), Moss 21331 (J); Rustenburgkloof Resort (–CA), Venter, H.J.T.
9075 (BLFU), Venter, H.J.T. 9182 (BLFU), Venter, H.J.T. 9183 (BLFU), Venter,

*H.J.T.* 9184 (BLFU); Magaliesberg (–CA), *Mogg, A.O.D.* 10312 (SAM); Magaliesberg, near Olifantsnek Dam (–CD), *Venter, F.* 39463 (J); Rustenburg, Magaliesberg, Jackson's garden (–DD), *Obermeyer, A.A.* 4110 (PRE); Brits, Jackson's Garden, 8 km W of Hartebeespoort Dam (–DD), *Acocks, J.P.H.* 12355 (PRE), *Story, R.* 728 (BR, PRE), *Story, R.* 741 (PRE).

2528 (Pretoria): Pretoria, Wonderboom. (-CA), Dyer, R.A. 3134 (PRE), Galpin, E.E. 6978 (PRE), Lauham, F.N. 37654 (SRGH), Meebold, A. 12556 (M), Repton, J.E. 1513 (PRE), Smith, C.A. 1691 (PRE), Strey, R.G. 3168 (PRE), Thode A432 (NH, PRE, STE), Wasserfall & Van Niekerk, s.n. (NBG, PRE); Wonderboom Park (-CA), Bredenkamp 883 (PRU); Pretoria district, Wonderboompoort (-CA), Leendertz, R. 519 (BOL, K, PRE), Rehmann, A. 4506 (Z), Rogers, F.A. 2502 (K, PRE); Pretoria district, Magaliesberg, near Wonderboom Reserve (-CA), Marais, W. 259 (PRE, SRGH); Pretoria, surrounding koppies (-CA), Murray, D.P. 688 (PRE); Pretoria, Wonderboom, on mountain behind Wonderboom (-CA), Smith, C.A. 289 (J, PRE); Pretoria, Klein Wonderboom (-CA), Van Son, G. 38168 (PRE); Pretoria, Wonderboom Nature Reserve, on N-slope of Magaliesberg (-CA), Codd, L.E. 1148 (PRU), Venter, H.J.T. 9181 (BLFU); Pretoria (-CA), Wilson, E.H. 132 (PRE); Pretoria, Baviaanspoort (-CB), Smith, C.A. 641 (PRE).

2529 (Witbank): N of Witbank (–AC), *Mogg, A.O.D.* 35883 (MO); Loskop Dam, Zaagkuil (–AD), *Theron, G.K.* 1490 (PRE, PRU); Witbank district, Middelburg, Doornkop (–CB), *Du Plessis, C.J.* 1333 (PRU); Botsabelo (–CB), *Schlechter, R.* 1236 (SRGH); Witbank district, Botsabelo (–CB), *Schlechter, R.* 4082 (SRGH); Botsabelo (–CB), *Schlechter, R.* 4082 (BM, BOL, G, GRA, K, NH, PRE, SAM, Z); Botsabelo (–CB), *Schlechter, R.* s.n. (SRGH).

- **2530** (Lydenburg): Barberton, Schagen, eastern side of mountain (–BD), *Liebenberg, L.C.C. 2350* (PRE).

- 2531 (Komatipoort): Komatipoort (-BD), Rogers, F.A. 12633 (SRGH).
- 2632 (Bela Vista): Ndumo Game Reserve (-CD), Venter, H.J.T. 8983 (BLFU).

#### *C. decidua* Namibia:

- **1613** (Vila de Aviz): Kao district, W of Epupa Falls (-CD), *Owen-Smith, G.* 197 (WIND).

— 1712 (Posto Velho): Kao district, Baynes Mountains at Quelle Okonbambi (–BB), Giess, W. 8986 (K, M, PRE, WIND); Otjihipa Mountains, (–BC), Vahrmeijer, J. & Du Preez, P. 2573 (PRE).

1713 (Swartbooisdrif): Epupa, (-AA), *Kotze* 97 (M, PRE, WIND); Kaokoveld, 15 km W of Otjiyanyasemo, Swartbooisdrif (-AC), *Giess, W. & Van der Walt, J.J.A.* 12686, (M, PRE, WIND); Kowarib, 22 km from hotsprings opposite Oiri-bridge (-BB), *Lukaschik, M.* 15 (M, WIND); Swartbooisdrif, at memorial stone (-BD), *Merxmüller, H. & Giess, W. 30480* (M, WIND); Kaokoveld, Otjiwero (-CD), *De Winter, B. & Leistner, O.A.* 5389 (K, M, PRE, WIND).

— 1714 (Ruacana Falls): Kunene, Great Falls [Ruacana] (–AC), Barnard, K.H. 556 (SAM); 15 km W of Ruacana Falls, Kunene (–AC), De Winter, B. & Giess, W. 7105 (K, M, PRE, W); Ovamboland, 13 km W of Ruacana Falls (–AC), De Winter, B. & Giess, W. 7105 (PRE, SRGH, WIND).

— 1812 (Sanitatas): Kaokoveld, Orupembe (–BA), Hall, H. 379 (BOL, NBG); Kaokoveld: Orupembe at Anabib (–BA), Story 5740 (BM, K, M, PRE); Sanitatas, Hereroland, Ehambambura (–BD), Smith, G.O. & Malan, J. 310 (WIND); Khumib River (–DA), Müller, M. & Loutit, B. 2303 (WIND); 10 km W of Purros (–DD), Viljoen, P.J. 282 (WIND).

- 1813 (Ohopoho): Kaokoveld (-CD), Theron, G.K. s.n. (PRU).

- 1814 (Otjitundua): Sargdeckelberg, Okongwe (-CC), Seydel, R. 3036 (K, MO).

- **1912** (Hoanib Mouth): Hoanib, 20 km S of Hoanib River, 40 km from sea (–BD), *Cooper, T.G. 20* (WIND).

- 1913 (Sesfontein): Sesfontein, Khowarib (-BD), Rusch, W. s.n. (WIND).

— 2013 (Unjab Mouth):Unjab River mouth, 17 km from Kamanjab Khorixas-Torra
Bay intersection (–BB), *Venter, H.J.T. 9037* (BLFU); 15 km S of Springbokwater (–
BC), *Müller, M. & Loutit, B. 1147* (WIND).

2014 (Welwitschia): Welwitschia, Bloemhof farm (-BC), Müller, M. & Giess, W. 388 (M, PRE, WIND); Welwitschia Rest Camp (-BD), Carr, J.D. 43 (PRE); Welwitschia, (-BD), Galpin & Pearson 7495 (K, PRE, SAM), Pearson, H.H.W. 4414 (BOL, K); Outjo district, Twyfelfontein farm (-CB), Craven, P. 651 (WIND), Schmidt 210 (M, WIND), Van Vuuren, D. 590 (BLFU, PRE, SRGH, WIND); Omaruru, Otjihorongo Reserve at Ugab, SW of Anigab (-CC), Merxmüller, H. 1623 (M); Khorixas, S of Dores, near Goantagab River (-CD), Craven, P. & Craven, D. 439 (WIND); Otjihorongo Reserve, S of Ugab (-DD), Giess, W. 5016 (K, M, PRE, WIND).

- 2015 (Otjihorongo): Othihorongo Reserve (-CC), *Merxmuller, H. 16*23 (PRE, WIND).

- **2016** (Otjiwarongo): Outjo, near Brandberg, Henrysvelde farm (–AA), *De Winter, B. 3140* (BLFU, K, M, NBG, PRE, W).

— 2114 (Uis): Uis district, Brandberg, Numas Valley (–AB), *Craven, P. & Craven, D.* 21 (WIND); Brandberg (–AB), *Nordenstam 2457* (M); Brandberg, Zirabschlucht (–
AB), *Von Wettstein 400* (M).

— **2115** (Karibib): Karibib, Groot Spitskoppe, Usakos (–CC), Van Koenen, E. 596 (WIND); along Usakos road to Ameib, Goabeb farm, 63.1 km N of Usakos (–CD), *Wanntorp, H. & Wanntorp, H.E. 868* (K); Usakos, Ameib farm (–DC), Jensen, M.K. 93 (PRE, WIND), Omaruru district, around Brandberg, at White Lady (–DD), *Giess, W. 9179* (M, WIND); Karibib (–DD), *Dinter, K. 6773* (K, PRE); *Kinges, H. 3226* (PRE); Karibib, Dernburgbruch (–DD), *Seydel, R. 1950* (M); road from Karibib to Usakos, Kranzberg farm, 59.1 km before Usakos (–DD), *Wanntorp, H. & Wanntorp, H.E. 865* (K, WIND).

- 2214 (Swakopmund): Hentiesbaai district (-AB), Kers, L.E. 298 (WIND).

— **2215** (Trekkopje):Karibib district, Nordenburg 76 (–AD), *Griffin, E. 190* (WIND); Karibib, Nudis farm (–BC), *Seydel, R. 316* (K, M, MO, WAG, Z), *Walter, H. & Walter, E. 1194* (WIND).

- 2216 (Otjimbingwe): Otjosondu (-AA), *Seydel, R. 4330/3293* (G, K, M, MO, SRGH, WAG, WIND); Hereroland, along the Kuiseb River (-DC), *Fleck 501* (Z).

- 2314 (Sandwich Harbour): Swakopmund, W of Kuiseb canyon (–DB), *Giess, W.* 9134 (WIND).

— 2315 (Rostock): Namib Desert Park (–AA), *Hofmeyer, J.M. H8* (WIND); Namib Desert Park, Anachanbiab Beacon Hill (–AA), *Ward, J.D. 173* (NU, WIND).

— 2316 (Nauchas): Djab, Gamsberg Pass (–AB), Jensen, M.K. 468 (PRE); Abbabis,
N of Geitsigubib (–CC), Pearson, H.H.W. 9257 (K).

2317 (Rehoboth): Rehoboth, Koos farm (–AC), *Schmudsfeger 4299* (WIND);
Rehoboth district, Buellsport (–AC), *Strey s.n.* (M, NBG, PRE); Rehoboth,
Gravenstein *REH 65* (–BC), *Leippert, H. 4628* (WIND), *Volk, O.H. 11565* (M, WIND).
2319 (Aminuis): 12 km W of Sandverhaar (–CC), *Pearson, H.H.W. 4630* (K).

— **2416** (Maltahöhe): Maltahöhe, farm Tzais (–AA), *Müller, M. & Tilson 896* (M, PRE, WIND); Nomtsas (–BD), *Pearson, H.H.W. 9312* (K, BOL); Malthahöhe, Zaries Mountains (–CD), *Basson, P.A. 209* (PRE).

— 2417 (Mariental): Mariental, Hardap Dam Reserve (–BD), *Goldblatt, P. & Manning, J. 8782* (G); Mariental district, Hardap (–BD), *Watt, D.J. 242* (WIND); Mariental, Karichab farm (–CC), *Van Koenen, E. 68* (WIND); Gibeon, Friedabrun (–DA), *Steyn, D.G. 1913* (PRE, WIND); Gibeon district, Haribes (–DA), *Volk, O.H. 12176* (M); Mariental, Haribes (–DA), *Volk, O.H. s.n.* (WIND); N of Mariental on road to Kalkrand (–DB), *De Winter, B. 3488* (K, PRE); 50 km from Mariental on Maltahöhe road (–DB), *Hardy, D.S. 1951* (K, PRE, WIND); Between Marienthal & Aris (–DB), *Werdemann & Oberdieck 2261* (K, PRE, WAG).

— 2418 (Stampriet): Stampriet, 10 km E of Mariental on Stampriet road, Narris farm
(– CA), Venter, H.J.T. 9061 (BLFU).

— 2516 (Helmeringhausen): Helmeringhausen, Boais BET. 13 (–DD), Müller, M. 41 (PRE, PRU, WIND).

— 2517 (Gibeon): Gibeon, Sandrücken farm (–AA), Van Koenen, E. 60 (WIND);
Bersaba (–DD), Schenk 353 (Z).

- 2615 (Lüderitz): Lüderitz (-CA), Brem 111 (Z).

— 2616 (Aus): Aus (–AB), Logan 327 (GRA, WIND); Bethanien, Chamis South (– BB), Walter, H. & Walter, E. 2179 (PRE, WIND); Kuibus village (–DB), Range, P. 1672 (SAM).

- 2617 (Bethanie): Great Karasberg Mountain, waterfall at ravine (-AD), *Pearson, H.H.W.* 8464 (BOL); Sandverhaar (-CD), *Dinter, K.* 4211 (BM, G, SAM, Z);

Tschaunaup Mission (–DA), *Gerstner, J.* 6353 (NBG, PRE); Seeheim (–DD), *Pearson, H.H.W.* 3729 (K, BOL, PRE).

— 2618 (Keetmanshoop): Keetmanshoop (–CA), Liebenberg, L.C.C. 5202 (PRE), Müller, M. 161 (WIND); 11 km from Keetmanshoop, on road to Seeheim (–CA), Oliver, Muller & Steenkamp 6315 (K); Keetmanshoop, Narubis (–DC), Venter, H.J.T. 9009 (BLFU); 75 km S of Keetmanshoop (–DC), Verhoeven, R.L. s.n. (BLFU).

— 2717 (Chamaites): Inachab (–BA), *Dinter, K. 1046* (Z); Chamaites, Uisig farm, LUS 82 (–CA), *Wendt, W. & Giess, W. 14739* (WIND); 30.5 km from Ai-Ais (– CB), *Henrici, R. 76* (PRE); Fish River Canyon, at look out point (–DA), *Venter, H.J.T. 9351* (BLFU).

2718 (Grünau): Grünau, 75 km S of Keetmanshoop / 88 km N of Grunau (–AB), *Venter, H.J.T. 9007* (BLFU); Klein Karasberg Mountain, Holoog (–AD), *Pearson, H.H.W. 9764* (K, MO, BOL, SAM); Great Karasberg foothills (–BB), *Lynes, H. 1918* (BM); Great Karasberg Mountain (–BC), *Pearson, H.H.W. 5072* (K); Great Karasberg Mountain, Naruda South (–BD), *Pearson, H.H.W. 8325* (BM, BOL, K, SAM); Grünau, 93 km from Grünau, on road to Keetmanshoop (–CA), *Clarke, B. 661* (PRE).

— 2719 (Tränental): Warmfontein, Irangental (–AB), *Lensing, J.E. A161/75* (WIND);
Warmfontein (–AB), *Müller, M. 161* (WIND); Karasburg, Numdis (–AD), *Auret, W.P.* 5576 (PRE).

— 2817 (Vioolsdrif): Between Sjambok River and Ousenkjer (–AD), *Pillaus, N.S.* 6475 (BOL); Nabas (–AD), *Williamson 3678* (MO).

2818 (Warmbad): S of Warmbad (–BC), Pearson, H.H.W. 4024 (BM, BOL, K, SAM, Z); Warmbad, Sandfontein farm (–DA), Beukes, G.J. 022 (BLFU); Warmbad (–DA), Verhoeven, R.L. s.n. (BLFU); Warmbad, Homs River (–DA), Beukes, G.J. 024 (BLFU); Little Bushmanland, Dabenoris (–DC), Pearson, H.H.W. 3007 (BOL, K, SAM), 3018 (K, BOL).

— **2819** (Ariamsvlei): Warmbad, 1 km NW of Orange River along road between Onseepkans and Karasburg (–CB), *Davidse, G. & Loxton, A. 6199* (M, MO, PRE, WAG), *6200* (PRE, WAG).
#### **South Africa:**

- 2817 (Vioolsdrif): Vioolsdrif (-DC), Van der Schijff, H.P. 8194 (PRE, PRU).

2818 (Warmbad): Northern Cape Province, Warmbad (–BC), *Fleck s.n.* (Z);
 Northern Boesmanland, near Goodhouse, S of Orange River (–CC), *Beukes, G.J.* 002 (BLFU); 16 km S of Goodhouse (–DC), *Schlieben 9090* (K).

2820 (Kakamas): Upington, Noab Hills (–AC), Barnard, K.H. 36083 (SAM);
Kakamas, Rooipad (–CB), Leistner, O.A. 3332 (K, PRE, SRGH WIND); southern
Augrabies National Park, along Rooipad (–CB), Werger, M.J.A. 336 (PRE, SRGH);
Kakamas, northern bank of Orange River (–DA), Esterhuysen, E. 23574 (BLFU,
BOL, K, PRE); Kenhardt, 24 km WSW of Alheit (–DC), Acocks, J.P.H. 14268 (PRE);
Kenhardt, 30.5 km E of Kakamas Post Office (–DC), Acocks, J.P.H. 14288 (PRE).
2919 (Pofadder): Groot Pella Mountain (–AA), Van Jaarsveld, E. & Patterson, J.
6715 (NBG).

### C. delagoensis

## South Africa:

— **2531** (Komatipoort): Barberton (–CC), *Thorncroft, G. 825* (NU, NH); Ida Doyer Reserve on farm Schoonoord 380JU, near Swaziland border at Havelock (–CC), *Fourie, E. 1641* (PRE).

- 2630 (Carolina): Amsterdam, 9 km S of town (-DA), Bruyns, P. 9365 (BOL).

— 2731 (Louwsburg): Vryheid district, road to Bhivarte (Paris) Dam (–CA), *Bruyns, P.* 9357 (BOL); Itala Game Reserve, slope above square davel (–CB), *MacDevette* 2220 (NH, PRE-photocopy).

— **2732** (Ubombo): Tembe Elephant Park (–AB), *Ward 1928* (NH, PRE); Tembe Game Reserve, Ngobozana trail (–AB), *Venter, H.J.T. 9335* (BLFU, PRE); False Bay, Bird Sanctuary, near Mr Redmans house (–CD), *Gerstner 4731* (PRE).

# *C. oblongifolia* Botswana:

- 1921 (Aha Hills): S of Aha Hills (-CC), Smith 3438 (K, SRGH).

2425 (Gaborone): 80 km W of Molepolole (–BC), *Morwe, F.O. 113* (PRE, SRGH).
2525 (Mafeking): Pharing, near Kanye (–AB), *Miller, O.B. B/52* (PRE), *B/543* (PRE); 3.2 km SE of Lobsatsi, Bon Acord farm (–BA), *Leach & Noel 114* (K, SRGH), *Tapscott, S. 2549* (KMG), *Woollard, J 957* (SRGH).

## Namibia:

- **1718** (Kuring-Kuru): Omuramba Mpungu, on road to Tsinsabis (–CB), *De Winter, B. 3892,* (K, M, PRE, WIND).

- **1722** (Chirundi): Western Caprivi, near Bwabwata camp (–DC), *Tinley, K.L. 1476* (PRE, W).

- 1819 (Karakuwisa): Grootfontein-North, N of Bumbi (-BB), Merxmüller 1860 (M).

— **1820** (Tarikora): 32 km N of Mamso, along road to Kapupahedi Camp (–AD), *De Winter, B. & Marais 4742* (K, M, PRE, WIND); Tarikora, Kandtara School (–BB), *Müller, M & Giess, W. 486* (W).

— **1821** (Andara): Dikundu, 19.5 km S of Andara (–AB), *Giess, W. 11340* (M, PRE, WIND).

- **1917** (Tsumeb): Amboland, Ombanje (–BC), *Schinz 2043* (Z); Otavi (–CB), *Dinter 5774* (Z).

- **1920** (Tsumkwe): Grootfontein, 48 km N of Gautscha Pan (–DC), *Story, R. 6428* (PRE, WIND).

- 2317 (Rehoboth): Rehoboth, Buellsport (-AC), Strey, R.G. s.n. (PRE).

## South Africa:

- 2229 (Waterpoort): Soutpansberg (-CD), *Junod, H.A. 4159* (PRE); Soutpansberg, Vivo district, Scott's farm, 6 km E of Soutpansberg on mountain slope (-DB), *Scott, L. 211* (PRE); Soutpansberg, Wylliespoort (-DD), *Gillett, J.B. 2891* (BOL).

- 2230 (Messina): Soutpansberg (-AC), Rogers, F.A. 20006 (NH).

- 2327 (Ellisras): Waterberg, 45 km N of Vaalwater (–DD), Van Rooyen, N 1561 (PRU).

— 2328 (Baltimore): Pietersburg, Leipzig-Blaauwberg (–BB), Bremekamp & Schweickerdt 104 (PRE, PRU).

— **2329** (Pietersburg): Blaauwberg (–AA), *Smuts & Pole-Evans 828* (PRE); Louis Trichardt, Happy Rest School (–BA), *Gerstner, J. 6030* (PRE); Soutpansberg, near Louis Trichardt (–BB), *Hutchinson 2032* (BOL, K).

- 2330 (Tzaneen): Letaba (-CA), Scheepers 1051 (BM, K, M, PRE, PRU, SRGH).

- 2425 (Gaborone): Marico, Lekkerlach (-DD), Louw, W.J. 614 (PRE).

— **2427** (Thabazimbi): Krantzberg (–BC), *Dyer, R.A.* & *Verdoorn, I. 4*233 (PRE); Nylstroom, top of Krantzberg (–BC), *Prosser, S.M. 17*26 (PRE, UPE).

2428 (Nylstroom): Nylstroom district, Alma (-AC), Van Wyk, A.E. 49 (BLFU, PRE, PRU); Waterberg (-AD), Rogers, F.A. 21711 (SAM); Nylstroom, Sterk River Dam Nature Reserve (-BC), Jacobsen, N. 2041 (PRE); Nylstroom district, Moorddrift (-BD), Leendertz, R. 7319 (PRE); between Warmbad and Nylstroom (-CB), Smuts & Gillett 3442 (PRE); Nylstroom, between Nylstroom and Naboomspruit, at marker 30.2 km N of Nylstroom along highway (-CB), Venter, H.J.T. 9196 (BLFU); Warmbad (-CD), Gerstner, J. 5287 (BOL, PRE), Leendertz, R. 7598 (PRE); Naboomspruit, Mosdene (-DA), Galpin, E.E. 495 (PRE, W, Z).

2429 (Zebediela): Potgietersrust, Naboomfontein (–AA), Galpin, E.E. 13472
 (BOL, K, PRE, W); Potgietersrust, Riebeeckrest (–AA), McDonald, G. 235 (PRE);
 Immerpan (–AC), Meeuse, A.D.J. 9494 (PRE, SRGH); Zebediela, Mogoto Ravine (–
 AC), Robbertse, P.J. 534 (PRU).

2430 (Pilgrim's Rest): The Downs (–AA), *Rogers, F.A. 18916* (PRE); Shiluvane Mission (–AB), *Junod, H.A. 864* (G, K, Z); Pilgrim's Rest, Orighstad Nature Reserve (–CC), *Jacobsen, N. 1332* (PRE); Blydepoort Nature Reserve (–DB), *Botha, D.J. 2002* (PRU); Pilgrim's rest, Blydepoort Nature Reserve, upper footpath (–DB), *Botha, D.J. 2348* (BLFU); Pilgrim's Rest, Bourke's Luck (–DB), *Davidson, L.E. 2226* (J), *82* (J); Lebowa, Mapulaneng Wilderness area, Welgevonden Forest (–DB), *Venter, F. 10677* (UNIN); Blydepoort, Lowveld lookout point (– DB), *Venter, H.J.T. 9208* (BLFU); First look out point over Mariep's Hill, along road from Bourke's Luck

to Aventura Resort (– DB), *Joubert, L. 26* (BLFU); Orighstad Nature Reserve, E of dam (–DC), *Theron, G.K. 3472* (PRE, PRU); 8 km from Kowynspas, on Acornhoek road (–DD), *Galpin, E.E. 14653* (PRE); Graskop, Kowyns Pass (–DD), *Galpin, E.E. 32211* (BOL, PRE).

- 2431 (Acornhoek): Klaserie (-CA), Killick & Strey, R.G. 2510 (PRE).

- 2525 (Mafeking): Mafeking, Ferndale (-DC), Brueckner, A. 587 (KMG, PRE).

Zwartruggens (– DA), Sutton, J.D. 806 (PRE).

2527 (Rustenburg): Mankwe district, Houwaterdam farm (-AC), Matlhaku, L. 89 (PRE); Magaliesberg, Castle Gorge, Elandskraal, Hekpoort (-AD), Van Wyk, A.E. 113 (PRE, PRU); Rustenburg, Buffelspoort (-BA), Turner, F.A.S. 28 (PRE); Rustenburg (-CA), Leendertz, R. 9589 (PRE), Nakien, O. 23 (K, PRE), Pegler, A. 1019 (BOL, GRA, SAM), Van Dam, J. 16506 (PRE); Rustenburg, Rainhill Farm, 8 km SW of Rustenburg (-CA), Codd 1088 (K, PRE), Moss, M. 21009 (J); Rustenburg Nature Reserve (-CA), Jacobsen, N. 840 (PRE); Rustenburg, Bergheim, ravine in Magaliesberg (-CA), Merxmüller 259 (BM, K, M); Rustenburg, 8 km SW of Rustenburg (-CA), Story, R. 980 (PRE); Rustenburg, Uitkomst (-DC), Coetzee, B.J. 410 (PRE, PRU); Hennops River (-DD), Bremekamp, B.L. 262 (PRU); Pretoria, Hennops River (-DD), Moss, C.E. 8636 (J); Brits, Jackson's garden (-DD), Van Vuuren, D. 377 (PRE).

2528 (Pretoria): Pretoria, Rust de Winter (-AB), Smuts & Gillett 3294 (PRE);
Pretoria, Roodeplaat, near gates of Transvaal Regional Research Station (-BC), Clarke, B. 556 (PRE); Enkeldoorn (-BC), Eyles, F. 2795 (SAM); 32 to 48 km NE of
Pretoria (-BC), Werdermann, E. & Oberdieck 1262 (WAG); Pretoria (-CA), Leeman, A. 20, (PRE), Leendertz, R. 145 (GRA, K), 345 (GRA, K), Marloth, R. 9506 (STE,
PRE); Pretoria, 75 km W of Pretoria (-CA), Bruce, E.A. 114 (PRE); Pretoria Hills (-CA), Leendertz, R. 8455 (PRE), 8456 (BLFU, PRE, U), Verdoorn, I.C. 85 (PRE);
Pretoria, Groenkloof (-CA), Mogg, A.O.D. 9750, 9069 (PRE); Pretoria, Schanskop
Fort (-CA), Pole-Evans, I.B. 180 (PRE); Pretoria, Apies Poort (-CA), Schlieben 7766 (G, K, M); Pretoria district, Hornsnek, 19 km W of Pretoria (-CA), Schlieben 7766 (G, K, M); Pretoria, Ashbury (-CA), Smith, C.A, 1328 (PRE); Pretoria, Louis Botha
Home (-CA), Smith, C.A. 1237 (PRE); Pretoria, reservoir E of Union Buildings (- CA), *Smith, C.A.* 1293 (PRE); Pretoria, Leeuwhoek (–CA), *Swart, L.S. SKF* 481 (PRE); Pretoria National Botanical Gardens (–CB), *Dryfhout, P.* 986, (PRE), Pretoria, Koedoespoort (–CB), *Smith, C.A.* 1530 (PRE); Pretoria, Baviaanspoort (–CB), *Smith, C.A.* 345 (J, PRE); Roodeplaat Dam Reserve (–CB), *Van Rooyen, N.* 2129 (PRU); Pretoria-West, Swartkop (–CC), *Dahlstrand, K.Å.* 3791 (UPE); Pretoria, Monument Hill (–CC), *Hardy* 933 (K, PRE, Z); Pretoria, Waterkloof (–CC), *Hofmeyer, J.M. s.n.* (PRE), *Mogg, A.O.D.* 15727 (PRE); Irene, Doornkloof (–CC), *Hutchinson* 2394 (BM, K); Pretoria, near CSIR (–CC), *Joynt, V.* 3 (PRE); Pretoria, Fonteinedal (–CC), *Moss, C.E.* 10003 (J), *Repton, J.E.* 119 (PRE), *Verdoorn, I.C.* 587 (PRE); Pretoria, hills south of Pretoria (–CC), *Young, R.G.N.* 2583 (J, PRE); Pretoria, Rietvallei 221 (–CD), *Acocks* 11269 (K, PRE); Pretoria, Premier Mine (–DA), *Phillips, E.P.* 3123 (GRA, PRE, SAM); Premier Mine (–DA), *Rogers, F.A.* 18962 (J); Magaliesberg (–DC), *Burke* 322 (K, PRE, SAM); Pretoria, Garsfontein hills (–DC), *Liebenberg, L.C.* 8640 (K, MO, PRE, SRGH).

2529 (Witbank): Groblersdal (–AB), Acocks 20917 (K, PRE); Loskop Dam, NE of dam (–AD), Theron, G.K. 1302 (PRE, PRU); Loskop Dam, E of Scheepersloop (– AD), Theron, G.K. 810 (PRE, PRU); Middelburg, Broodboomspruit (–CB), Du Plessis, C.J. 246 (PRE, PRU); Botsabelo (–CB), Schlechter 4096 (BM, BOL, G, GRA, K, SAM, Z), Thode, J. 2652 (STE); Middelburg, Buffelsvlei (–CD), Rudatis, H.H. 70 (STE); Klein Olifants River (–CD), Schlechter 3804, (K, M, PRE, SRGH, Z).

2530 (Lydenburg): Sabie, Langverwag (–BB), Louw, W.J. 2333 (STE);
Lydenburg, Wonderkloof Nature Reserve (–BC), Elan-Puttick, D. 125 (PRE), 315 (PRE); Nelspruit (–BD), Breyer, H.G. 17079 (PRE), Noel 1735 (GRA); Nelspruit, Lowveld Botanical Gardens (–BD), Buitendag, E. 298 (PRE, NBG); Lydenburg, Witklip (–BD), Kluge, J.P. 355 (PRE, PRU); Nelspruit, 5 km S of town (–BD), Leach 11347 (BM, K, M, PRE, SRGH, Z); Nelspruit, Schagen (–BD), Liebenberg, L.C. 2955 (PRE); Waterval Boven (–CB), Rogers, F.A. 14285 (NH); Nelspruit-Barberton road, Hilltop Pass (–CB), Viljoen, G. 37 (PRE).

- 2531 (Komatipoort): Kruger National Park, Numbi (– AA), Van der Schijff, H.P. 1626 (PRE); Kaapmuiden (– CB), *Mogg, A.O.D. s.n.* (PRE); Barberton, Saddleback

Mountain (– CC), *Galpin, E.E.* 833 (BOL, PRE); Barberton (– CC), *Rogers, F.A.* 18357 (J, K), *Thorncroft, G.* 2024 (PRE).

— 2626 (Klerksdrop): Klerksdorp, Faan Meintjies Nature Reserve (– DC), Venter, H.J.T. 8802 (BLFU), Venter, H.J.T. 9187 (BLFU).

2627 (Potchefstroom): Potchefstroom, Blyvooruitzicht (–AD), Phillips, J. 1268 (PRE); Krugersdorp, Jack Scott Nature Reserve (–BA), Wells 2237 (K, PRE, SRGH); Witpoortjie Falls (–BB), Dahlstrand, K.Å. 3790 (UPE); 3 km NE of Krugersdorp, Honingklip 72 (–BB), Mogg, A.O.D. 18158 (J); Krugersdorp Municipal Reserve (–BB), Mogg, A.O.D. 20347 (J); Witpoortjie Ravine (–BB), Moss, C.E. 10001 (BM, J), Rogers, F.A. 19308 (G); Krugersdorp (–BB), Phillips, J. 1098 (PRE); Witpoortjie Falls, 32 km W of Johannesburg (– BB), Prosser, S.M. 1318 (J, K, NBG, PRE); Losberg, Elandsfontein (–BC), Theron, J.J. 922 (PRU); Johannesburg, Klipriviersberg (–BD), Mogg, A.O.D. 17661 (J); Krugersdorp, Skeerpoort (–BD), Phillips, J. 1211 (PRE); Potchefstroom, Boskop (–CA), Louw, W.J. 462 (PRE); Potchefstroom, Laerberg (Losberg, Elandsfontein) (–CA), Theron, J.J. 844 (PRE); Potchefstroom, Sandfontein (–CA), Venter, H.J.T. 8805 (BLFU); Vredefort, Mispah (–CD), Du Preez, P.J. 299 (BLFU); Vredefort, Esperanza (–CD), Du Preez, P.J. s.n. (BLFU); Vereeniging, Houtkop 3, Langerand Hills (–DB), Mogg, A.O.D. 21034 (J).

2628 (Johannesburg): Johannesburg, Orange Grove (–AA), *Conrath, P. 1061* (K);
Johannesburg (–AA), *Gilfillan, D.F. 132* (PRE); Johannesburg, Jeppestown Ridge (–
AA), *Gilfillan, D.F. 6144* (K); Johannesburg, Park View (–AA), *Moss, C.E. 10002* (J);
Heidelberg Ravine (–AD), *Mogg, A.O.D. 20484* (BOL, J); Heidelberg (–AD), *Murray, D.P. 687* (PRE), *Thode, J. 1327* (K, NH, PRE); 54 km SE of Johannesburg,
Houtpoort 309 (–CB), *Mogg, A.O.D. 18483* (J).

— 2731 (Louwsburg): Itala Nature Reserve, Craiga Dam farm, Mabamvu Ridge (– CA), *McDonald, G. 390,* (K, PRE); Ngome (–CD), *Gerstner, J. 5173* (K, PRE, SRGH); Zululand, Umlalazi (–DD), *Lawn, J.G. 2281* (NH).

- 2832 (Mtubatuba): Mtubatuba (-AA), *Bourquin, O. 655* (PRE); Hlabisa district, Hluhluwe Game Reserve (-AA), *Hitchins & Ward 11* (NH, PRE), *Ward, C.J. 2934,* (PRE, NH).

— **2930** (Pietermaritzburg): 28 km from Wartburg on Noodsberg Road (–BC), *Edwards 2998* (K, M, PRE); Camperdown, Shongweni Dam (–DA), *Morris, J.W.* 770

(PRE); Umgeni River (–DA), *Krauss s.n.* (G, in herb. Boissier), *Schinz s.n.* (Z);
Inanda (–DB), *Wood, J.M. 446* (BM, BOL, G, K, SAM); Westville (–DD), *Coleman, T.A. 210* (NH); Pinetown (–DD), *Coleman, T.A. 390* (NH); Northdene (–DD), *Evans, M.S. 593* (NH); Krantzkloof (–DD), *Haygarth, W.J. 23852* (PRE); *Rogers, F.A. 30191* (Z); Pinetown, first view site Forest Hills (–DD), *Johnson, S.M. 1371* (NH, PRE);
Pinetown, Forest Hills (–DD), *Redshaw, C. 2* (PRE, NH); Hill Crest (–DD), *Thode, J. 2654* (STE); New Germany (–DD), *Thode, J. 2655* (STE), *Wood, J.M. 12568* (PRE);
Sydenham (–DD), *Wood, J.M. 12482* (PRE); near Northdene (– DD), *Wood, J.M. 4984* (Z).

2931 (Stanger): Natal, Umdloti River, Oakfort (–CA), *Rehmann 8466* (Z); Natal Bay [Durban] (–CC), *Krauss 661* (M); Durban (–CC), *Wood, J.M. 9084* (NH); Durban, Sydenham (–CC), *Wood, J.M. 12428* (NH).

— 3030 (Port Shepstone): Alexandra district, St. Dumisa (–AD), *Rudatis, H.H.* 272 (BM, G, PRE, STE, WAG, Z), *Rudatis, H.H.* 641 (BM, G, K, PRE, STE); Oribi Gorge (–CA), *Davidson, L.E.* 2522 (J).

#### Swaziland:

— 2531 (Komatipoort): Mbabane, Komati Pass (–BD), Compton, R.H. 31035 (K, NBG, PRE).

2631 (Mbabane): Mbabane (-AC), Bolus, H. 12155 (BM, BOL); 16 km SE of Mbabane (-AC), Codd, L.E. 4753 (PRE), Compton, R.H. 22451 (NBG), Rogers, F.A. 11658 (GRA, J, PRE); Mbabane district, Little Usutu River (-AC), Compton, R.H. 28476 (K, NBG, PRE, SRGH); Mbabane, Evelyn Boring Bridge (-AC), Compton, R.H. 30373 (NBG); Blue Jay Ranch, 3.6 km SE of western entrance to Umbuluzi Gorge, Lebombo Mountains (-AC), Culverwell, J. 748 (K, MO, PRE); Mbabane, Malagwane Hill (-AC), Dlamini, B. s.n. (NBG); Mbabane, Mpalaleni (- AC), Karsten, M. s.n. (PRE, NBG); Hhohho district (-AC), Kemp 657 (WAG, MO); Usutu Government Farm (-CA), Muller, D.B. 5/191 (PRE); Black Imbuluzi Valley (- CD), Compton, R.H. 31874 (PRE, NBG).

## C. obtusa

## South Africa:

- **2228** (Maasstroom): Soutpansberg, Mpefu Location, at hotspring (–DA), *Smuts, J.C. 2044* (K, PRE).

- 2229 (Waterpoort): Soutpansberg, foot of mountain (-CD), Schweickerdt & Verdoorn 591 (K, PRE, W).

- **2230** (Messina): Soutpansberg, Makonde Mission, 24 km NE of Sibasa (-DC), *Codd, L.E. 6812* (PRE).

- 2431 (Acornhoek): Kruger National Park, Skukuza, at guesthouse (–DC), Van der Schijff, H.P. 459 (PRE).

2531 (Komatipoort): Kruger National Park, Pretoriuskop, Seekoeigat (–AB), Van der Schijff, H.P. 2445 (PRE); Kruger National Park, 29 km N of Malelane (–AD), Codd, L.E. 5508 (K, MO, PRE, SRGH); Kruger National Park, Lower Sabie road (– BB), Van der Schijff, H.P. 2720 (PRE); Komatipoort (–BD), Rogers 472 (GRA), Rogers 900 (K); Crocodile Bridge, Elephant Walk Retreat (– BD), Joubert, L. 29 (BLFU).

— 2632 (Bela Vista): Ingwavuma district, Ndumu Game Reserve, Usutu Forest (– CD), *Pooley, E.S. 489* (NU); S of Ndumu Nature Reserve, at bridge over Ingwavuma River (–CD), *Venter, H.J.T. 8985* (BLFU).

— 2732 (Ubombo): Pongola River Pont between Otobotini and Maputa (–AB), Vahrmeijer & Tölken 973 (K); Makanespont Bridge (–AB), Venter, H.J.T. 8986 (BLFU); Joubert, L. (BLFU); Lebombo Mountains, Pongolapoort, Jozini (–AC), Repton, J.E. 6036 (PRE); Josini Dam, 1 km E of wall, on bank of Pongola River (– AC), Venter, H.J.T. 8792 (BLFU); Zululand, Ubombo district, Mkuzi Game Reserve (–CA), Tinley 619 (K, NH).

- **2831** (Nkandla): Zululand, Hlabisa district, Bushveld Reserve Bird Sanctuary (– BB), *Gerstner, F.C. 4731* (PRE).

## Swaziland:

- 2632 (Bela Vista): Blue Jay Ranch (-AA), Culverwell 895 (K, PRE).