Leaf structure in southern African species of *Salsola* L. (Chenopodiaceae)

by

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"The mystical is not how the world is, but what it is."

Ludwig Wittgenstein

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***Salsola zeyheri*: habit**

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Photos: AW Klopper

CHAPTER 1

INTRODUCTION

1.1 GENERAL NOTES ON *SALSOLA* L.

The Chenopodiaceae or goosefoot family consists of about 100 genera and 1 500 species. It has a cosmopolitan distribution and is especially abundant in desert and semi-desert regions. Many species are halophytes or weeds of waste places and cultivated fields. Members of this family, which include herbs, shrubs and small trees, often have succulent leaves and stems (Echardt 1964; Cronquist 1981) and typically shows Crassulacean Acid Metabolism or C4-photosynthesis. Clustered crystals or crystal sand of calcium oxalate are commonly present in parenchymatous tissues. Pollen of the Chenopodiaceae dates back to the Maestrichtian and thus provides the oldest known fossils in subclass Caryophyllidae (Cronquist 1981).

Salsola L., with 150 species of arid or semi-arid and sometimes saline regions, is one of the largest genera within the family (Cronquist 1981). A fair proportion of the species is more or less cosmopolitan (Dyer 1975; Mabberley 1987). The genus is classified into subfamily Salsoloideae, which is distinguished from subfamily Chenopodioideae by the presence of a spirally coiled embryo and the usual absence of perisperm (Lawrence 1970; Cronquist 1981). *Salsola* itself is divided into seven sections, of which only one, section *Caroxylon* (Thunb.) Fenzl, is native to southern Africa (Botschantzev 1969a, 1969b). This section is characterised by shrubs and semi-shrubs, with a few annuals; plants covered with simple, smooth, rough or serrated hairs; leaves having a small nodule at the base; dense, small and smooth anther appendages; and horizontal seeds. Only shrub species of this section occur in southern Africa (Botschantzev 1969a, 1969b).

Leaves of *Salsola* are alternate, small and sessile. They are often succulent, covered with hairs and are usually densely packed, thus covering the branches (Solereder 1908; Dyer 1975; Hobson & Jessop 1975). The genus displays Kranz anatomy, which corresponds to the C4-type photosynthesis and specific habitat preference of *Salsola* (Solereder 1908; Metcalfe & Chalk 1979). However, its leaf anatomy shows a peculiar bundle sheath and therefore differs from the typical Kranz syndrome (Carolin *et al.* 1975; Carraro *et al.* 1993; Patrignani *et al.* 1993). Oxalic acid and salts of calcium, potassium or other minerals are commonly dissolved in the aqueous mesophyll cells of *Salsola* species (Solereder 1908; Watt & Breyer-Brandwijk

1962). Members of the genus are also rich in sodium sulphate (Watt & Breyer-Brandwijk 1962).

As with many other taxa of the African arid regions (Werger 1978), the geographical range of *Salsola* is divided into two isolated regions: the smaller is located in southern Africa and Madagascar, and the greater region in northern and eastern Africa, southern and central Europe and Asia (Botschantzev 1969a, 1969b). Only naturalised alien species are found in America and Australia (Botschantzev 1969a). In recent years almost 90 species of *Salsola* were recognised in southern Africa, mostly from the arid to semi-arid regions of Namibia, the greater part of the Northern Cape, the northern parts of the Western and Eastern Cape, as well as the western part of the Free State (Arnold & De Wet 1993) (see Figure 1). The genus is most conspicuous under karroid conditions (Dyer 1975).

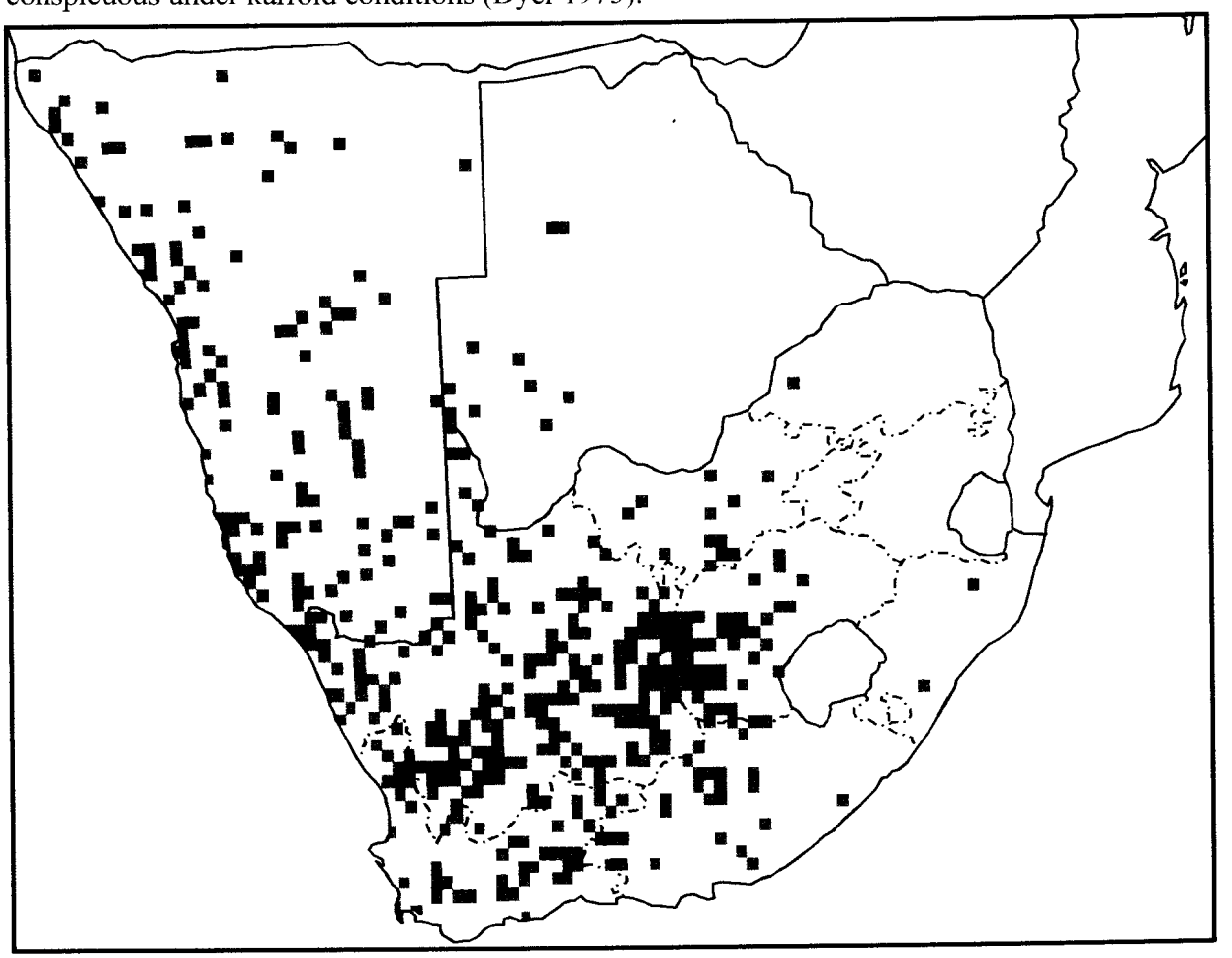


FIGURE 1: Distribution map of the genus *Salsola* in southern Africa.

1.2 CLASSIFICATION OF *SALSOLA* IN SOUTHERN AFRICA

There are several important characters separating *Salsola* from other related genera in Chenopodiaceae. Flowers of *Salsola* are bi-bracteolate (Bentham & Hooker 1880; Botschantzev

1969a; Dyer 1975) and all segments of the fruit perianth usually develop a broad horizontal wing (Bentham & Hooker 1880; Ulbrich 1934; Botschantzev 1969a; Dyer 1975). Anthers bear appendages of various shapes at the tip (Botschantzev 1969a). Flowers nearly always contain a disc, which surrounds the pistil (Ulbrich 1934; Botschantzev 1969a). Seeds are usually horizontal (Bentham & Hooker 1880; Ulbrich 1934; Botschantzev 1969a), orbicular (Bentham & Hooker 1880; Dyer 1975), do not contain endosperm and most frequently have a membranous testa (Bentham & Hooker 1880; Botschantzev 1969a; Dyer 1975).

There are 88 indigenous shrub species of section *Caroxylon* reported from southern Africa (Arnold & De Wet 1993). Two naturalised alien species of section *Salsola*, namely *S. kali* L. and *S. caroliniana* Walter, were also identified in the region (Botschantzev 1974c). The 88 indigenous species recognised by V.P. Botschantzev (1910–1991) (1974c, 1978, 1981, 1983) are divided into three subsections. Subsection *Caroxylon* is characterised by shrubs or suffricates with alternate branches, leaves and flowers (Botschantzev 1974d) and contains 74 species (Botschantzev 1974c, 1978, 1981, 1983). Subsection *Distichae* Botsch. is characterised by alternate, distichous leaves and flowers and comprises of one species (Botschantzev 1974c). Subsection *Tetragonae* (Ulbrich) Botsch. is characterised by shrubs or under-shrubs with opposite branches, leaves and flowers (rarely only the stems and leaves of the young shoots opposite and the rest alternate) (Botschantzev 1972) and contains 13 species (Botschantzev 1974c, 1978) (see Table 1).

1.3 SYSTEMATIC PROBLEMS OF *SALSOLA* IN SOUTHERN AFRICA

Because of the variable ecological and agricultural importance of different species of *Salsola* and the occurrence of harmful and beneficial species within the same area (see Chapter 3), correct identification of plants is of considerable importance. However, almost all the southern African *Salsola* species are morphologically strikingly similar, making reliable identification almost impossible, especially in herbaria. This is a cause of major concern and presents many difficulties during the classification of the genus. Specimens of *Salsola* are mostly sterile due to the fact that plants only flower briefly during favourable climatic conditions. Hence, the identification key for southern African *Salsola*, provided by Botschantzev (1974c), is not very practical for quick routine identification, because the fruit and flower characters that form an integral part of the key can not be observed in the usually sterile plants.

Table 1: Classification of the genus *Salsola* in southern Africa (Botschantzev 1974c; 1978; 1981; 1983; Arnold & De Wet 1993)
(Species investigated during this study typed in bold)

Genus *Salsola* L.

Section *Salsola* — ***S. kali* L.**

Section *Caroxylon* (Thunb.) Fenzl

Subsection *Caroxylon*

***S. acocksii* Botsch.**
***S. albida* Botsch.**
S. albisepala Aell.
S. angolensis Botsch.
***S. aphylla* L.f.**
S. apiciflora Botsch.
***S. apterygea* Botsch.**
***S. araneosa* Botsch.**
S. arborea C.A. Sm. ex Aell.
S. armata C.A. Sm. ex Aell.
S. aroabica Botsch.
S. atrata Botsch.
S. barbata Aell.
***S. calluna* Fenzl ex C.H. Wr.**
S. campyloptera Botsch.
S. capensis Botsch.
***S. cauliflora* Botsch.**
***S. ceresica* Botsch.**
S. columnaris Botsch.
S. cryptoptera Aell.
***S. dealata* Botsch.**
***S. denudata* Botsch.**
***S. dinteri* Botsch.**
S. dolichostigma Botsch.
S. esterhuyseniae Botsch.
***S. etoshensis* Botsch.**
S. garubica Botsch.
***S. gemmata* Botsch.**
***S. gemmifera* Botsch.**
S. gemmipara Botsch.
***S. giessii* Botsch.**
***S. glabra* Botsch.**
***S. glabrescens* Burtt Davy**
S. hoanibica Botsch.
S. hottentottica Botsch.
***S. huabica* Botsch.**
S. kalaharica Botsch.
***S. kleinfonteini* Botsch.**
***S. koichabica* Botsch.**
S. luederitzensis Botsch.
***S. marginata* Botsch.**
***S. melanantha* Botsch.**
***S. merxmuelleri* Aell.**
***S. microtricha* Botsch.**
S. namaqualandica Botsch.
S. namibica Botsch.
S. nollothensis Aell.
***S. okaukuejensis* Botsch.**
S. omaruruensis Botsch.
S. parviflora Botsch.
***S. patentipilosa* Botsch.**
S. pearsonii Botsch.
S. phillipsii Botsch.
S. pillansii Botsch.
S. procera Botsch.
S. ptiloptera Botsch.
***S. rabieana* Verdoorn**
***S. robinsonii* Botsch.**
S. ruschii Aell.
S. schreiberae Botsch.
***S. scopiformis* Botsch.**
***S. seminuda* Botsch.**
***S. sericata* Botsch.**
S. seydelii Botsch.
S. spenceri Botsch.
S. squarrosula Botsch.
S. swakopmundi Botsch.
S. tetramera Botsch.
***S. tuberculata* (Moq.) Fenzl**
***S. tuberculatiformis* Botsch.**
S. ugabica Botsch.
S. unjabica Botsch.
***S. warmbadica* Botsch.**
***S. zeyheri* (Moq.) Bunge**

Subsection *Distichae* Botsch.
S. verdoorniae Tölken

Subsection *Tetragonae* (Ulbrich) Botsch.
S. adisca Botsch.
S. adversariifolia Botsch.
***S. aellenii* Botsch.**
S. contrariifolia Botsch.
***S. decussata* C.A. Sm. ex Botsch.**
***S. exalata* Botsch.**
S. geminiflora Fenzl ex C.H. Wr.
***S. henriciae* Verdoorn**
***S. humifusa* A. Brückn.**
***S. inaperta* Botsch.**
***S. minutifolia* Botsch.**
S. mirabilis Botsch.
***S. smithii* Botsch.**

Furthermore, there exists great uncertainty as to the exact identity and taxonomic status of most of the 69 indigenous *Salsola* species newly described by Botschantzev (see Chapter 4). Many species were described on the basis of very limited material and for 25 species only the type specimens are available (Botschantzev 1978). This causes doubt to arise about the reality of some of these species. For this reason, many of these names have not been taken up and applied by southern African botanists. The possibility of hybridisation between species causes further taxonomic problems. For example, *S. glabrescens* is said to be very polymorphic. This is attributed to the fact that it apparently hybridises with *S. albida*, as these two species are linked by an uninterrupted series of transitional forms. *S. rabieana* is most probably a hybrid between *S. glabrescens* and *S. albida* and its type has been chosen so as to occupy an intermediate position between these two species (Botschantzev 1978).

A clear delimitation of the different character states within the genus would greatly facilitate and enhance the process of solving the systematic problems that exist within the group. Botschantzev himself has stated that the time has come to start the study of *Salsola* in southern Africa under natural conditions. By studying plants in the field more material would be available for investigation. Thus it would be possible to delimit the species more accurately and to define their characters more precisely (Botschantzev 1978).

Botschantzev (1969a) places particular emphasis on two important characters to be used in separating groups within family Chenopodiaceae and also for dividing *Salsola* into sections. These two characters are form and shape of the foliage leaves and hair distribution. Therefore, anatomical and morphological characters of leaves may provide additional evidence to assist with the delimitation of infrageneric taxa in *Salsola*.

1.4 AIMS OF THIS STUDY

Plant systematics is fundamental to all areas of applied botany. The name of a species is the key to all the information that has been gathered about the species by different scientists. Without a correct name none of this information can be utilised. The present uncertainties in the systematics of the genus *Salsola* is therefore a cause for concern, as it hampers research and management efforts where members of *Salsola* are involved.

The principle aim of this study is to make a contribution towards the systematics of the genus *Salsola* in southern Africa, in particular to find additional characters that may facilitate the identification of the different species.

Additional aims are to:

- identify the taxonomic problems occurring in southern African *Salsola*;
- compile distribution maps for the genus in southern Africa, as well as for each investigated species;
- review the agricultural, economic and ecological importance of the genus;
- review the taxonomic history of the genus;
- study the leaf anatomical characters and assess their possible taxonomic significance;
- study aspects of leaf macro-morphology, especially the indumentum, and assess its taxonomic significance.

CHAPTER 2

THE KAROO REGION

'Karoo' is a Khoikhoi word meaning 'dry' or 'barren' (Adamson 1938; Cowling *et al.* 1997). The Karoo is a vast arid plain that covers the greater part of the Northern Cape, and the northern parts of the Western and Eastern Cape, mainly north of 33°S and between 17°E and 25°E (White 1983). Its borders can be roughly described as the Orange River in the north, Oudtshoorn in the south, Somerset East in the east and the Cape west coast (Cowling *et al.* 1997). It occupies approximately 430 000 km^2, thus covering about 35% of the surface area of South Africa (Cowling 1986; Rutherford & Westfall 1994). The Karoo region is extremely variable in all aspects. Selected environmental aspects of the region are depicted in Figures 2.1–2.4.

2.1 CLIMATE

Annual minimum and maximum temperature of the Karoo can vary between -12°C and 45°C (Du Preez 1986; Du Toit van der Merwe 1986; Meyer 1986; Schulze 1994; Watkeys 1999). The most notable climatic feature of the Karoo is its great daily and seasonal temperature variation, which can be as severe as a 28°C difference between day maximum and night minimum temperature (Schulze 1994). Daily and annual temperature variation is greatest in the Upper Karoo (Cowling 1986). Desiccating winds in the summer months and severe frost in winter are fairly common throughout the region and periodical droughts are an important phenomenon (Adamson 1938; Anon 1986; Du Preez 1986; Du Toit van der Merwe 1986; Kirsten 1986; Meyer 1986; Venter *et al.* 1986; Desmet & Cowling 1999).

The Karoo is mainly a summer rainfall area and receives 60–70% of its rain during October to March. However, the far western part can receive up to 60% of its annual rain from cyclonic fronts during the winter months (Bosch 1978; Werger 1978; White 1983; Anon 1986; Cowling 1986; Du Preez 1986; Du Toit van der Merwe 1986; Kirsten 1986; Venter *et al.* 1986; Schulze 1994; Low & Rebelo 1996; Desmet & Cowling 1999). Rainfall decreases from east to west, and inland from the coastal mountains (Adamson 1938). Annual rainfall in the region varies between 100 mm in the west and 400 mm in the east, whilst the mountainous areas can receive up to 600 mm per annum (see Figure 2.1) (Bosch 1978; Werger 1978; White 1983; Anon 1986; Cowling 1986; Du Preez 1986; Du Toit van der Merwe 1986; Kirsten 1986; Meyer

1986; Venter *et al.* 1986; Low & Rebelo 1996; Desmet & Cowling 1999). Reliability of precipitation is directly linked with the amount of annual rainfall. Rainfall reliability is thus greatest in the southern and eastern parts and diminishes rapidly towards the northern and western parts of the region (Werger 1978; Cowling 1986; Venter *et al.* 1986; Cowling *et al.* 1997; Desmet & Cowling 1999). Due to certain factors, including the El Niño phenomenon, rainfall reliability is on average 1.15 times higher in the winter-rainfall Karoo than corresponding rainfall in the summer-rainfall Karoo (Desmet & Cowling 1999).

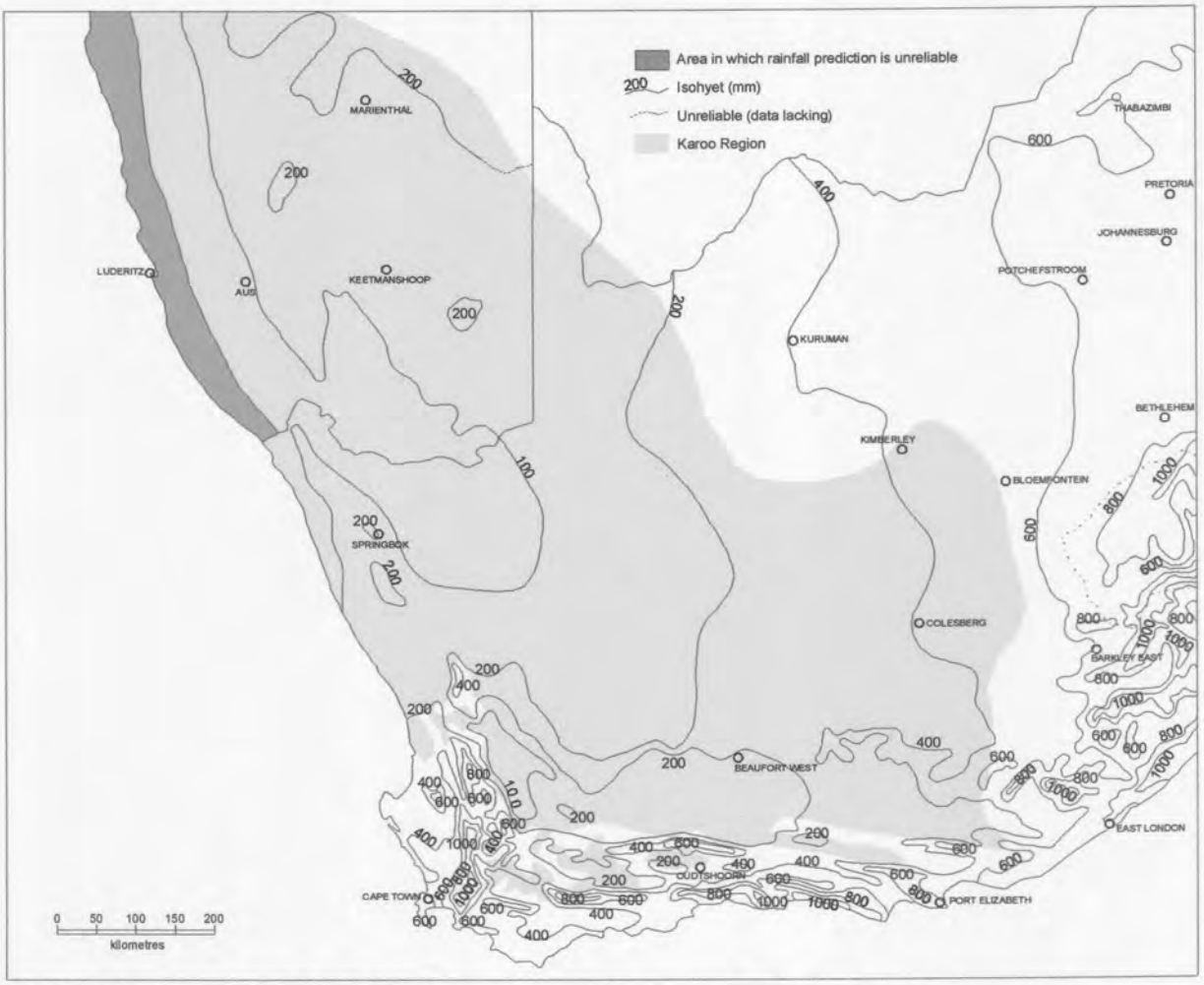


FIGURE 2.1: Rainfall map of the Karoo Region (shaded) (adapted from Richardson & Midgley 1979; Tainton 1988).

2.2 GEOLOGY AND TOPOGRAPHY

The Karoo contains a wide variety of geological formations, topographic characters, soil types and soil depths (Bosch 1978; White 1983; Du Toit van der Merwe 1986; Kirsten 1986; Meyer 1986; Rutherford & Westfall 1994; Low & Rebelo 1996). Ages of the lithostratigraphic units underlying the Karoo vary from Early Precambrian (Archaean) (± 4 600–2 500 million years

ago) to Recent and form a full series from highly deformed formations to unconsolidated sediments (Visser 1986; Watkeys 1999) (see Figure 2.2). Because of the extent of the large variety of rock types occurring in the Karoo, various geomorphological characteristics can be found in this region: along the West Coast a narrow coastal plain covered with Quaternary (from around 2 million years ago) and Recent sands; to the extreme south and west a low mountainous landscape with active incision by streams; south of the escarpment an undulating landscape; a vast plateau where incision by rivers has reached a mature stage stretches above the escarpment; and the north-western corner is characterised by an inselberg landscape (Visser 1986). It is, however, important to note that the geology of the area plays a fairly indirect role in the distribution of Karoo vegetation (Visser 1986), since the Karoo region is primarily determined by rainfall (Low & Rebelo 1996).

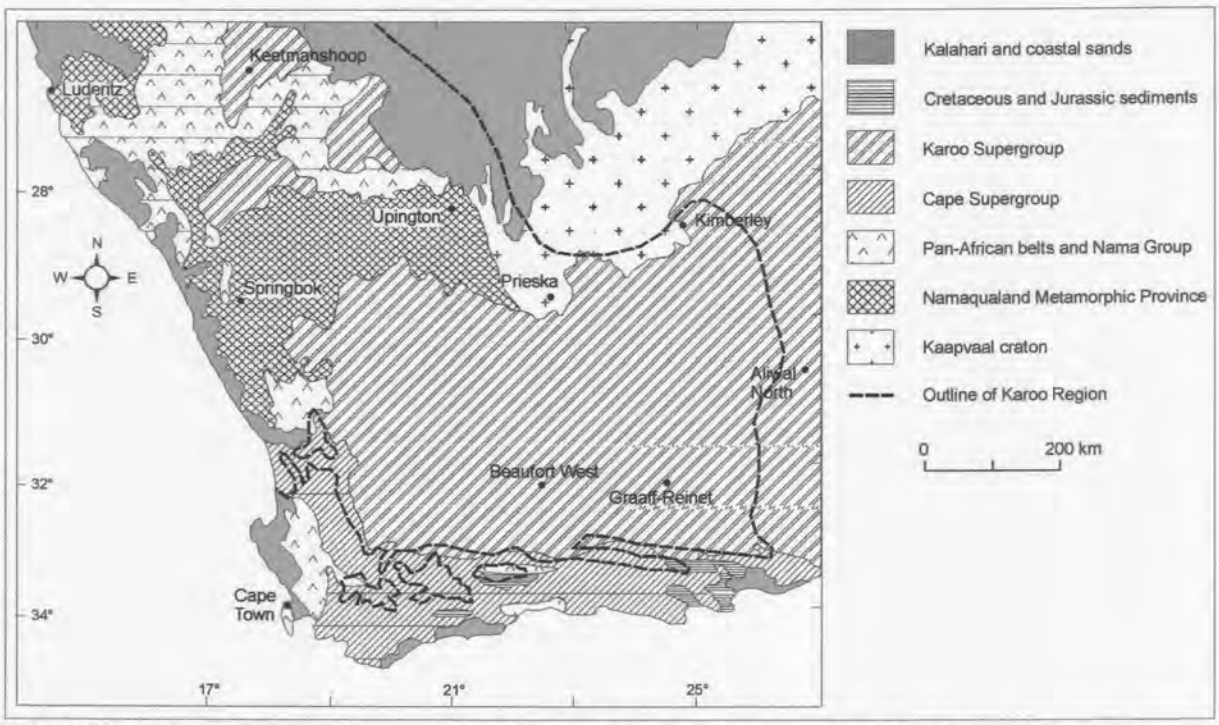


FIGURE 2.2: Geological map of the Karoo Region (outlined in bold stippling) (adapted from Meadows & Watkeys 1999).

Five main soil regions have been identified in the Karoo region, namely the West Coast and Namaqualand, the Upper Karoo, the Escarpment, the Great Karoo and the Little Karoo (Ellis & Lambrechts 1986) (see Figure 2.3). Alkaline and saline soils are fairly common throughout the region (Anon 1986) and most soils can be described as lime-rich, weakly developed soil on rock (Rutherford & Westfall 1994; Low & Rebelo 1996; Dean & Milton 1999). Therefore, the soil over most of the Karoo region is not very deep (less than 0.3 m), and varies from very shallow on the hills to deeper in the valleys, with the deepest soil

occurring in and along water courses (Du Toit van der Merwe 1986; Cowling *et al.* 1997). Highest topsoil clay content is found in soils along the Escarpment, while sandy soils occur along the West Coast, in the inland areas of the Upper Karoo where dunes are present and in the mountain ranges of the Little Karoo to the south (Ellis & Lambrechts 1986). Throughout most of the Karoo there is little organic material to provide organic topsoil (Watkeys 1999). Therefore, organic carbon content of the soil is low and averages at 0.38% C, ranging from 4.1% C on the Escarpment to zero along the West Coast, in Namaqualand and the Upper Karoo (Ellis & Lambrechts 1986).

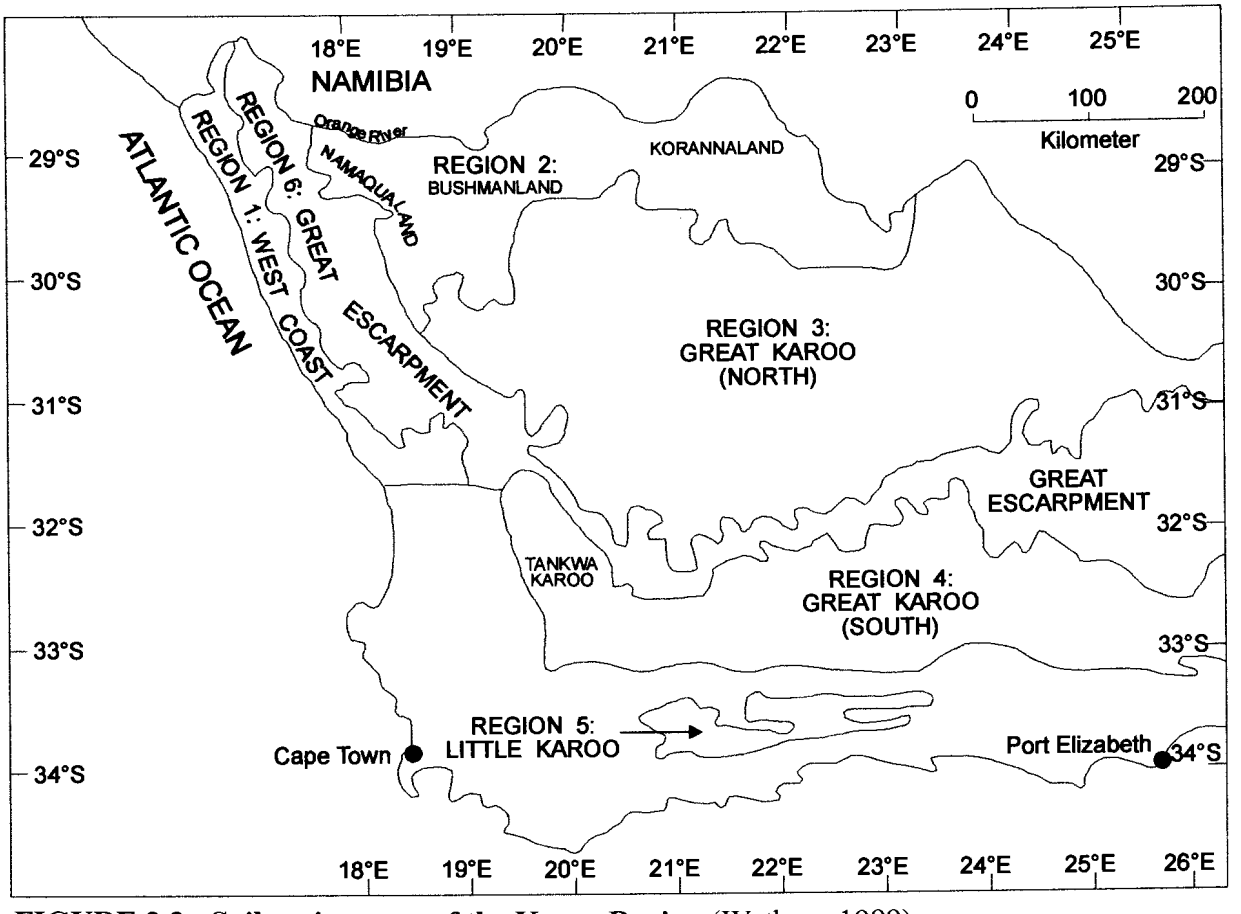


FIGURE 2.3: Soil region map of the Karoo Region (Watkeys 1999).

2.3 VEGETATION AND FLORA

Diversity in the physical characteristics of the Karoo region enhances the biodiversity and floristic variability within the region. Karoo vegetation is predominantly Karoo bushes with the grass component increasing from west to east (White 1983; Anon 1986). The southern parts consist mainly of arid bushveld, while the mountains and hills are mainly covered in shrubs and grasses (Anon 1986). However, despite its apparent uniform vegetation structure, the Karoo region has a rich floristic diversity. Hence, the commonly accepted idea of the Karoo as being

bare soil dotted with Karoo bushes and occasionally covered with annual grasses and succulents, is a false perception (Bosch 1978; Acocks 1988). Annuals are very common and a great number of plants possess interesting modifications correlated with environmental conditions. The number of species and their great variety in form are probably greater in the Karoo than in any other part of the world with a similar climate (Adamson 1938). The richness of the Karoo flora is estimated at between 3 500 and 7 000 species of which 35% to 50% are endemic to the region (White 1983; Cowling 1986; Hilton-Taylor 1987; Cowling & Hilton-Taylor 1999). Since many taxa, including the genus *Salsola,* are in need of revision, the full compliment of the Karoo flora can not yet be reliably assessed (Cowling 1986; Hilton-Taylor 1987).

The Karoo region can be divided into the Nama-Karoo and the Succulent Karoo Biomes (Rutherford & Westfall 1994; Low & Rebelo 1996) (see Figure 2.4). The Nama-Karoo Biome is the second largest Biome south of 22°S. It mainly covers the central plateau of the Northern Cape, the Western and Eastern Cape north of the east-west Cape Fold Belt mountains, the southwestern Free State and the southern interior of Namibia. The Succulent Karoo Biome is the fourth largest Biome in southern Africa. It is found mostly west of the Great Escarpment, from the Lüderitz District in Namibia through the western belt of the Northern and Western Cape and inland of the Fynbos Biome to the Little Karoo (Rutherford & Westfall 1994). This Biome has the highest species richness recorded anywhere in the world for a semi-arid vegetation type and more than 50% of its species are endemic (Cowling *et al.* 1997). One of its most unusual features is the enormous concentration of leaf succulents (Cowling *et al.* 1997) and it probably harbours about one third of the world's approximately 10 000 succulent species (Cowling & Hilton-Taylor 1999).

Each of these two Biomes can be variously divided into numerous vegetation (veld) types. Low & Rebelo (1996) recognise ten vegetation types (six in the Nama-Karoo Biome and four in the Succulent Karoo Biome), while 25 of the 70 vegetation types described by Acocks (1988) in South Africa, occur wholly or partly within the Karoo region (Vorster 1986). These vegetation types vary from xerophytic succulent veld and desert grassland in the west, through mixed Karoo bushes and grass, to semi-mesophytic grassland in the east (Bosch 1978, Vorster 1986). Taller shrubs occur in varying quantities throughout the plains, whilst the mountainous areas are characterised by shrubs, high-fibre grasses, perennial sweet grasses and Karoo bushes

(Vorster 1986). Species of *Salsola* are prominent in at least eight of these 25 vegetation types (Acocks 1988), most of them belonging to the Nama-Karoo Biome.

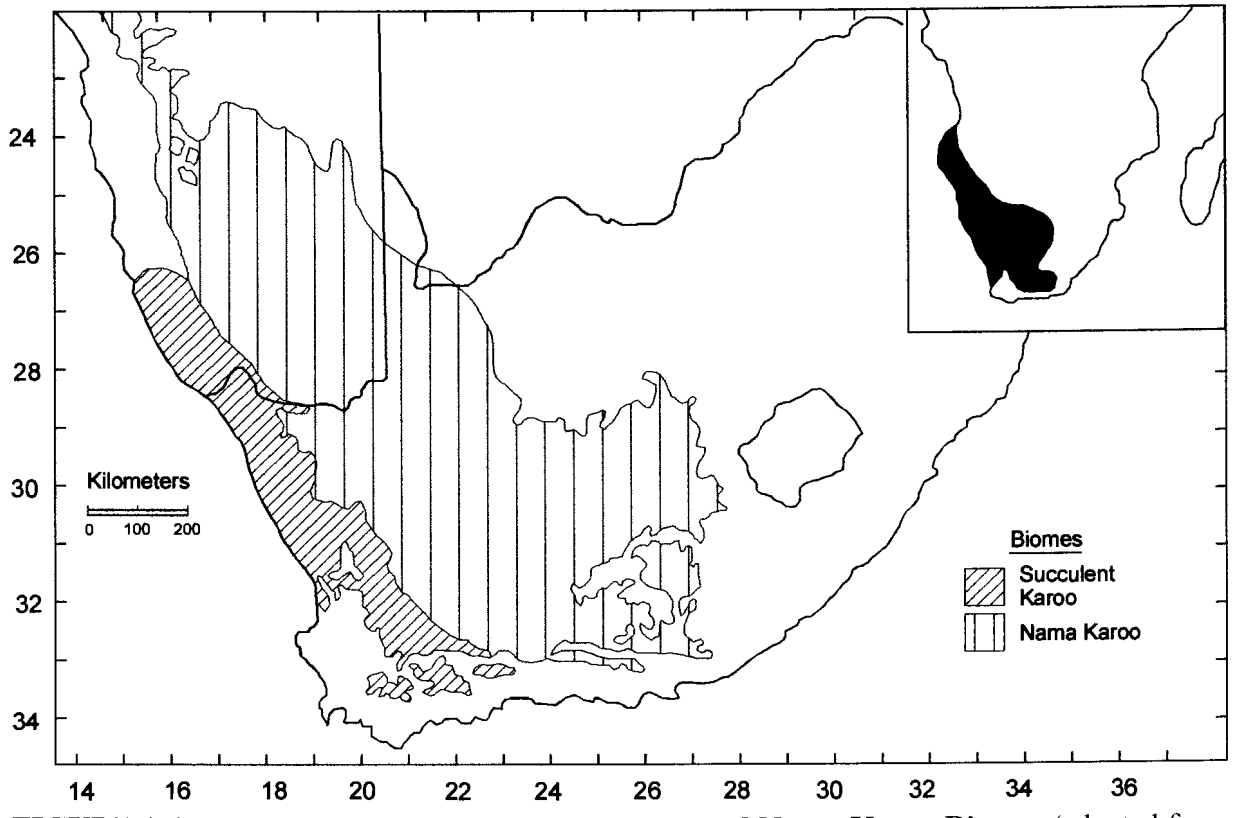


FIGURE 2.4: Distribution of the Succulent Karoo and Nama-Karoo Biomes (adapted from Cowling 1986).

2.4 AGRICULTURE

The Succulent Karoo is of little agricultural importance as the paucity of grasses limits the carrying capacity of the land, which can be as low as 9 ha per sustainable stock unit (ha/ssu) (Rutherford & Westfall 1994), making extensive supplementary feeding necessary (Low & Rebelo 1996). Therefore, most of the agricultural activities within the Karoo region occur in the Nama-Karoo (Low & Rebelo 1996), where the carrying capacity varies from 1 ha/ssu in the more moist east to 5 ha/ssu in the arid Bushmanland (Rutherford & Westfall 1994).

Cultivation of crops is strictly limited to areas where irrigation is possible (Rutherford & Westfall 1994). Thus the agricultural activities in the Karoo comprise mainly of small-stock farming, especially Dorper sheep, Boer goats, Angora goats, Merino and Karakul sheep, and to a lesser extend cattle, in certain areas (Du Toit van der Merwe 1986; Meyer 1986; Vorster 1986; Low & Rebelo 1996; Hoffman *et al.* 1999). The Karoo is the main extensive small stock farming area in South Africa. The southern and eastern parts, where the grass component is

greatest, are the hub of the woollen sheep industry. In the arid western parts non-woollen mutton breeds predominate, whereas Angora goats are preferred in the arid bushveld and thicket regions of the southern Karoo (Anon 1986; Hoffman *et al.* 1999).

A large percentage of the total gross national income derived from small stock farming is generated in the Karoo Region, e.g. 36% of the wool, 48% of the mutton, 60% of the mohair and 60% of the goat meat. This considerable contribution to the gross domestic product of South Africa is dependent on natural vegetation as a primary source of fodder for small stock (Cowling 1986).

CHAPTER 3

ECONOMIC AND ECOLOGICAL IMPORTANCE OF *SALSOLA*

3.1 AGRICULTURAL IMPORTANCE

Fodder production and nutritional value of Karoo vegetation fluctuate greatly over several years, as well as between different seasons of the same year. This has an important influence on the carrying capacity of the veld. During the growing season the grass component has a higher nutritional value and thus a higher carrying capacity than the Karoo bush component. Grasses, however, show a greater decrease in nutritional value, especially in protein content, during the winter than Karoo bushes (Vorster 1986; Palmer *et al.* 1999). Hence, Karoo bushes, such as *Salsola* species, are an extremely important part of the grazing component within the Karoo agricultural region (Vorster 1986).

Palatability and the extent to which each species of *Salsola* is utilised by different animals are extremely variable (Botha *et al.* 1983a; Botha *et al.* 1983b; Vorster 1986; Botha *et al.* 1994). *S. calluna* is a palatable Karoo bush that is highly preferred and utilised by stock (Botha *et al.* 1983a; Botha *et al.* 1983b). *S. tuberculata* and *S. zeyheri* are important, highly utilised plants, especially in the western parts of the Karoo (Du Toit van der Merwe 1986; Vorster 1986). *S. aphylla* and *S. glabrescens* are reasonably palatable species with high protein values and good drought resistance (Hobson & Jessop 1975; Vorster 1986). *S. aphylla* is relished by all livestock, including ostriches (Burtt Davy 1926). *S. glabrescens* is highly preferred by stock (Bosch 1987). *S. humifusa* is often well eaten down by game and livestock (Bruce *et al.* 1951). *S. tuberculatiformis* is said to be very drought resistant and even though it has a salty or slightly bitter taste, it is regarded as a valuable pasture plant in the dry, lime-rich and brackish habitats where it occurs (Kellerman *et al.* 1988). The chemical composition of this species has been found to compare favourably with that of lucerne hay (Morgenthal 1988).

Although somewhat noxious in the mature stage, the alien annual herbaceous *S. kali* is a very useful fodder plant that is readily grazed while still young, but it is avoided by stock as it becomes older and spiny (Watt & Breyer-Brandwijk 1962; Botha *et al.* 1983a; Botha *et al.* 1983b; McBarron 1983; Milton *et al.* 1999a). This ephemeral with its high invasive potential,

has been used to maintain livestock on overgrazed range land during periods of drought in the USA and in South Africa (Milton *et al.* 1999a). In general *Salsola* species are well utilised in mixed veld, but in monoculture utilisation is very poor (Bosch 1987). Most species, such as *S. aphylla* and *S. glabrescens*, are not favoured when other more palatable grazing is available, but are readily grazed during drought or when grazing pressure is heavy (Hobson & Jessop 1975).

The agricultural importance of a plant can be represented by a numeric value on a scale from one to ten, with ten being very important. According to the ecological index method (EIM) plants are awarded an ecological index value (EIV). In this system Karoo bushes are scored according to their relative palatability, and can obtain a value of between 0.7 and 7.7. With the implementation of this system it was argued that Karoo bushes cannot obtain a full score of ten, as they are not as productive or adaptable to high rainfall as grasses. EIV values of ten southern African members of *Salsola* are available, of which only one indigenous species as well as the alien annual *S. kali* has a value below seven (see Table 3.1).

TABLE 3.1: Ecological index values (EIV), grazing index values (GIV) and objective grazing index values (OIV) for southern African members of *Salsola* (Botha *et al.* 1994; Du Toit 1996)

Species	EIV	GIV	OIV
Salsola aphylla L. f.	7.0	5.5	-
Salsola barbata Aell.	7.0	5.0	-
Salsola calluna Fenzl ex C.H.Wr.	7.0	7.2	5.11
Salsola gemmifera Botsch.	4.0	3.6	-
Salsola glabrescens Burtt Davy	7.0	6.0	-
Salsola humifusa A. Brückn.	7.0	4.5	-
Salsola kali L.	1.0	1.5	-
Salsola rabieana Verdoorn	7.0	6.7	3.39
Salsola tuberculata (Moq.) Fenzl	7.0	6.9	4.21
Salsola zeyheri (Moq.) Bunge	7.0	5.9	-

- Values not available

In estimating the grazing capacity of veld, which is an agronomic value, EIM is not very appropriate, as it combines both ecological and agronomic attributes of plants. Furthermore, the theory of succession, which is incorporated into EIM, has been poorly tested in the Karoo. For these reasons, the grazing index method (GIM) is preferred when current grazing capacity is to

be calculated. GIM makes use of grazing index values (GIV) which are calculated in such a way as to ensure comparability of individual species, and also that the estimated value is relatively free of subjectivity (Du Toit 1996). When calculating GIV, six agronomic factors that affect the grazing value of a plant is taken into account, namely: ability of the plant to produce forage (dry material production); nutritional value of the produced material during the growing season; nutritional value of the produced material during the dormant season; relative ease with which the plant can be grazed; degree of perenniality; and ability to protect the soil against erosion (Botha *et al.* 1994; Du Toit 1996). GIV values for nine indigenous *Salsola* species as well as for *S. kali* are available; of these only two indigenous species and *S. kali* have values below five (see Table 3.1).

Despite its aim at objectivity, GIV are still awarded with some degree of subjectivity. A system has been proposed whereby objective grazing index values (OIV) can be obtained for plants. OIV are calculated using palatability, as expressed by chemical constituents, and vegetative characters, such as canopy spread cover and available forage production (Du Toit 1996). OIV values for three indigenous *Salsola* species are available (see Table 3.1). These OIV values are lower than the EIV and GIV values for the same species.

3.2 MEDICINAL AND ECONOMIC IMPORTANCE

Some species of *Salsola* can be very useful for purposes other than grazing or fodder for stock. Many *Salsola* species contain alkaloids and can be used as a source of medicinal compounds, such as salsolin (Botschantzev 1969a). In Malesia *S. kali* has been used as an anthelmintic (Watt & Breyer-Brandwijk 1962). *S. tuberculatiformis* is mentioned in Bushman folklore for contraceptive purposes and has also been shown to be contraceptively active in rats (Morgenthal 1988; Louw *et al.* 1996; Swart *et al.* 1996). Feeding experiments on female rats showed that *S. tuberculatiformis* has a luteotrophic effect on both the oestrus cycle and gestation. The oestrus cycle of rats fed on the shrub was longer than normal, as the cycle was arrested in dioestrus. The higher the dosage, the longer it took for the rat to return to a normal cycle after withdrawal of the plant from the diet. The gestation period in rats fed on the shrub was also significantly longer than normal (Basson *et al.* 1969).

Because of their high alkali content, *S. aphylla* and *S. kali* have been widely used in the making of soap and glass respectively (Burtt Davy 1926; Watt & Breyer-Brandwijk 1962;

Eckardt 1964; Hobson & Jessop 1[illegible] [illegible] (p[illegible]

and/or *S. tuberculatiformis*) and c[illegible]r *S. arborea*) make excellent fire wood, providing a warm fire and forming good coals that radiate heat for a long time. Due to these characters cattle ganna have been decimated on many farms in the Karoo. Other species are also used as fuel in many parts of the world (Botschantzev 1969a).

S. kali is a so-called tumbleweed. At the completion of their annual life cycle, dead plants break off at ground level and are blown over the countryside (Hobson & Jessop 1975; Bromilow 1995), thus spreading their seed (Milton *et al.* 1999a). Sometimes these plants pack up against a fence to such an extend that they offer considerable wind resistance and the fence can thus be pushed over (Hobson & Jessop 1975). It is important for farmers that their fences are in good condition at all times to prevent unnecessary loss of livestock. The costs of repairing such a fence can be extremely high and time consuming.

3.3 ECOLOGICAL IMPORTANCE

An important role played by the genus is as sand stabilisers and anti-erosion agents (Botschantzev 1969a; Bromilow 1995). It also provides a suitable habitat for certain Karoo animals. Tall, dense *Salsola* thickets found on deep alluvium along seasonal water courses are home to the riverine rabbit, *Bunolagus monticularis* (Milton *et al.* 1999b), ranking amongst South Africa's rarest and most endangered mammals (Smithers 1983, 1986; Skinner & Smithers 1990). Riverine rabbits, one of seven endemic Karoo mammals, are the only African lagomorph confined to these thickets (Milton *et al.* 1999b). This dense and discontinuous riverine bush consists mainly of shrubs between 0.5–1 m in height. *S. glabrescens*, at about 11,8%, forms most of the vegetation cover and is also a favoured browse for the riverine rabbit (Skinner & Smithers 1990). Because arable land with access to water is at such a high premium in the Karoo, virtually all alluvium in the region has been ploughed. This habitat destruction almost halved the range of the riverine rabbit and drove it to near extinction (Mills & Hes 1997; Milton *et al.* 1999b). The total population is currently estimated at between 500–1 500 animals (Mills & Hes 1997). The riverine rabbit is listed as endangered in the IUCN *Red Data Book* and in the *South African Red Data Book: terrestrial mammals* (Smithers 1983, 1986; Skinner & Smithers 1990).

Oxalates leached from *S. kali* in the USA have been shown to release soil phosphorous bound to calcium, aluminium and iron, making it available to other plants (Milton & Dean 1999). Due to the rapid growth of this alien it is able to deplete soil water, to the detriment of grasses in areas where water is limited. This species, however, has no competitive advantage in moist conditions (Milton *et al.* 1999a) and is not a problem on well-managed veld, as it cannot stand competition from more palatable plants (Hobson & Jessop 1975). Seasonally it can almost take over veld that has been overgrazed and can thus provide cover and assistance for good plants to re-establish (Hobson & Jessop 1975). In the USA, the presence of *S. kali* during succession of overgrazed rangeland reduced the establishment of shrubs, but facilitated grass establishment. The impact of this species on vegetation re-establishment in the Karoo has not yet been investigated (Milton *et al.* 1999a).

3.4 VETERINARY IMPORTANCE

Although members of *Salsola* are generally regarded as good grazing plants and have other valuable properties, not all species are purely beneficial. *S. tuberculatiformis*, for example, causes a syndrome locally known as *grootlamsiekte*, characterised by prolonged gestation and foetal post-maturity (Basson *et al.* 1969; Joubert *et al.* 1972; Kellerman *et al.* 1988; Morgenthal 1988; Vahrmeijer 1987; Louw *et al.* 1996; Swart *et al.* 1996). This syndrome occurs particularly in Karakul and Karakul-Persian crossbreeds. The pelts from lambs born after prolonged gestation is of low quality and often unacceptable to furriers. Many ewes have to be slaughtered for humane reasons to relieve them from the severe suffering they undergo due to the big size of their lambs. These facts have severe financial implications for farmers. Outbreaks of *grootlamsiekte* are almost invariably associated with severe droughts (Basson *et al.* 1969; Joubert *et al.* 1972; Kellerman *et al.* 1988; Morgenthal 1988), times when *Salsola* species are readily utilised as a pasture plant. *S. tuberculatiformis* possibly contain more of the toxic ingredient causing *grootlamsiekte* in its dormant stage during droughts, than at periods of higher rainfall (Joubert *et al.* 1972). At least five other species of *Salsola* may also produce this syndrome when eaten in sufficient quantities (Kellerman *et al.* 1988).

During extensive investigations on *grootlamsiekte*, experiments have indicated that the last 50 days of gestation are the most susceptible period (Basson *et al.* 1969; Morgenthal 1988). Further investigations showed that the gestation period of ewes fed on twigs of *S. tuberculatiformis* during the first 50 days of gestation were also increased, whereas leaves were

a bigger problem in causing prolonged gestation during the last trimester. It has been concluded that ewes need to ingest 900 g of the shrub daily for at least 10–50 days during any stage of pregnancy in order to produce the syndrome, with the first and last 50 days being the most vulnerable (Joubert *et al.* 1972; Kellerman *et al.* 1988; Morgenthal 1988). The pathogenesis of the syndrome is not yet clear. Available evidence, however, indicates that it is triggered by a hypothalamic inhibitor in the shrub, which inhibits the hypothalamic releasing factors regulating secretion of most adenohypophysial hormones. This leads to secretory dysfunction and ultimately to atrophy of the pituitary gland. The inhibitory effect of the shrub on secretion of follicle stimulating hormone and luteinizing hormone is also manifested in the suppressive effect it has on the oestrus cycle and the development of Leidig cells (Basson *et al.* 1969; Kellerman *et al.* 1988).

The problem of post-maturity in sheep can be successfully alleviated to some extend by *partus* induction up to 170 days gestation through administering stilboestrol, oxytocin and antibiotics (Joubert *et al.* 1972; Kellerman *et al.* 1988). However, the best 'cure' for *grootlamsiekte* would be prevention. If possible, farmers must prevent pregnant ewes from grazing on veld where *S. tuberculatiformis* is common, especially during the last 50 days of gestation and periods of drought.

A copper deficiency, leading to bone fractures and anaemia in lambs, can occur in animals grazing on veld where *S. tuberculata* is common (Vorster 1986). This species is also low in phosphorous and has a very unfavourable calcium : phosphorous ratio (Bosch 1987). Growing sheep need approximately 0.2–0.5% calcium and 0.2–0.46% phosphorous in their diet. Thus the calcium : phosphorous ratio must be in the region of 1.0 for normal growth and development (Du Toit 1996). This is clearly not the case for *S. tuberculata*, nor for the other two indigenous species for which these values are available (see Table 3.2).

TABLE 3.2: Percentage calcium, percentage phosphorous and calcium : phosphorous ratio for indigenous members of *Salsola* (Du Toit 1996)

Species	% Ca	% P	Ca:P
Salsola calluna Fenzl ex C.H.Wr.	1.27	0.18	7.65
Salsola rabieana Verdoorn	0.86–1.19	0.09–0.12	7.74–13.1.
Salsola tuberculata (Moq.) Fenzl	2.40–2.76	0.08–0.11	30.24–33.05

Circumstantial evidence shows that salt ganna, *S. barbata*, may be the cause of nephrotic syndrome in sheep, in certain areas of the Karoo in the western parts of the Northern Cape Province. This often fatal syndrome has so far only been reported in Dorpers grazing on salt ganna veld (Kellerman *et al.* 1988; De Wet & Bath 1994). Dorpers are probably more suspect to the syndrome because of their non-selective grazing tendencies. Major problems are experienced amongst Dorper ewes with lambs. Due to good rainfall during the 1970s and simultaneous conservation strategies to rehabilitate the veld, the quantity of *S. barbata* increased drastically. During ensuing droughts, Dorper were forced to eat salt ganna, which is unpalatable and not preferred when more suitable grazing is available. Symptoms of poisoning are swelling of the throat and the middle of the jaw, but in more severe cases even the whole face, chest and legs can be swollen. Poisoned animals also have an enlarged abdomen due to the accumulation of fluids in the abdominal cavity. Results of treatment are not very satisfactory, since the kidneys of affected animals are often severely damaged. The best way to prevent poisoning is to constrain animals from grazing on salt ganna. This is, however, not a very viable option during periods of drought. A good way of minimising stock loss is to check animals at least three times a week for symptoms. Affected animals must be removed from the herd immediately and fed in a camp free from *S. barbata*. After two to three weeks most animals would have recovered sufficiently to be returned to the herd. With this method stock loss can be decreased with up to 80% (De Wet & Bath 1994).

The alien species *S. kali*, has sharp spines arming the leaf tips and these can cause severe physical damage. Spines sometimes break off under the skin of an animal, causing festering sores. This species is said to be toxic when potassium nitrate is absorbed from the soil and water (Watt & Breyer-Brandwijk 1962). It is especially when plants are young that they are capable of accumulating dangerous amounts of nitrate. Nitrate poisoning can be treated by an intravenous injection of 1% methylene blue. *S. kali* can also contain poisonous amounts of oxalate, causing rapid death within 8 hours of grazing on young growth. Oxalate poisoning can be treated by an injection of 10–20% calcium borogluconate. This treatment can be supplemented by mouth administration of lime water, chalk in water and Epsom salt in purgative doses, in order to form insoluble magnesium oxalates. Poisoning can be greatly avoided by preventing hungry stock from grazing on young growth. Oxalate and nitrate poisoning due to *S. kali* are more common amongst cattle than amongst sheep (McBarron 1983) and may therefore not be such a big problem in the Karoo, where sheep and goats are the majority stock.

3.5 CONCLUSIONS

Chenopodiaceae is one of the families that have a high potential to transform natural plant communities in arid regions of the world. In general, these plants have had a more positive effect on economies and relatively fewer negative effects on ecosystems (Milton *et al.* 1999a). In southern Africa and the USA, *S. kali* is a good example of an alien plant with the potential of having greater benefits under certain circumstances, than possible detrimental effects.

Clearly most members of *Salsola* are highly beneficial and must be regarded as a natural asset to be properly utilised and conserved. Although some species may be detrimental to the health of livestock, most negative effects can be avoided to a great extend, provided that the culprit species are easily identified and well managed. However, because of the striking similarity between almost all southern African *Salsola* species, a quick and positive identification is virtually impossible.

CHAPTER 4

TAXONOMIC HISTORY

Taxonomic studies on the genus *Salsola* have a long and complicated history. *Salsola* was initially not studied monographically and the genus system was not developed as an entity, but rather in the framework of the whole family. This resulted that many plants belonging to other genera were initially described in *Salsola*, while true members of the genus were ascribed to other genera of the family (Botschantzev 1969a). Many infrageneric classification systems for the genus were proposed, most of which were entirely artificial and rejected by subsequent workers. The following are the more important researchers that worked on the genus and the systems they proposed.

The genus *Salsola* was first described by the Swedish naturalist, Carl Linnaeus, in 1753 in *Species Plantarum*. He then included five species in the genus. In subsequent editions he included more species, up to 12 in 1764 (Linnaeus 1762, 1764).

By 1840, the French botanist, Christian Moquin-Tandon, already ascribed 29 species to *Salsola*. He divided the genus into three sections: *Kali* Dum., *Salsolaria* Moq. and *Soda* Dum. These sections were, however, entirely artificial and were subsequently rejected. In 1849, he produced a monograph of the family, but this publication only served to further complicate the situation. In this publication, the 30 species ascribed to the genus were divided amongst two sections: *Kali* Dum., with 27 species, and *Soda* Dum., with three species. This system was also artificial and has therefore, not gained support (Botschantzev 1969a).

The treatment of the genus and its sections by the Austrian botanist, Eduard Fenzl, in 1857, is substantially closer to the current views. He ascribed 24 species to the genus and divided them into five sections: *Kali* Dum. with four species, *Coccosalsola* Fenzl with one species, *Eusalsola* Fenzl with eight species, *Soda* Dum. with one species, and *Caroxylon* (Thunb.) Fenzl with ten species (Botschantzev 1969a).

The German botanist, Eberhard Ulbrich (1934), reviewed the systematics of the family in a world context. In this work, he recognised more than 100 species in *Salsola*, classified amongst eight sections: *Kali* Dum., *Nitraria* Ulbrich, *Tetragona* Ulbrich, *Arbuscula* Ulbrich,

Ericoides Ulbrich, *Genistoides* Ulbrich, *Pseudonoaea* Ulbrich and *Caroxylon* (Thunb.) Fenzl. Some of these sections were fairly natural and are retained to the present. Other sections, however, were artificial and composite and could not be accepted into a natural system of the genus. Furthermore, many of the southern African species named by Ulbrich were never validly described and thus still remain mere names (Botschantzev 1969a).

Modest Mikhailovich Iljin combined his own ideas with all the best data from the predecessors to formulate his classification system of the genus *Salsola*, which was published in 1936. Iljin divided the genus into ten sections: *Kali* Dum., *Physurus* Iljin, *Brachyphylla* Iljin, *Heterotricha* Iljin, *Anchophyllum* Iljin, *Sphragidanthus* Iljin, *Aleuranthus* Iljin, *Belanthera* Iljin, and *Coccosalsola* Fenzl. This system was the most natural of all the previously proposed systems and was used by Botschantzev (1969a) as the foundation on which he based the current system of the genus *Salsola*. Many of the sections were natural and have been accepted, either entirely, with a few exceptions, or with a change of name, into the current system.

The Russian, Victor Petrovic Botschantzev (1969a), ascribed 114 species to the genus *Salsola* and divided the genus into seven sections: *Caroxylon* (Thunb.) Fenzl, *Malpigipila* Botsch., *Cardiandra* Aellen (=*Aleuranthus* Iljin), *Belanthera* Iljin, *Arbuscula* Ulbrich (=*Anchophyllus* Iljin), *Coccosalsola* Fenzl, and *Salsola* (=*Kali* Dum.). Only one of these sections, *Caroxylon* (Thunb.) Fenzl, which is considered by Botschantzev to be the most primitive section in the genus (Botschantzev 1969a & 1969b), has indigenous representatives in southern Africa. Members of section *Salsola* in southern Africa, the youngest section in the genus (Botschantzev 1969a & 1969b), are all naturalised aliens, for example *S. kali*. Botschantzev ascribed 43 species to section *Caroxylon*, of which 18 were reported for southern Africa (Botschantzev 1969a & 1969b). However, in subsequent papers (Botschantzev 1973, 1974a, 1974b, 1978, 1981, 1983), he described several new species from South Africa and Namibia, mainly using herbarium specimens (Botschantzev 1969a). No less than 25 of these new species were only known to Botschantzev from their type location (Botschantzev 1978). This casts doubt on the actual reality of these species.

The most recent taxonomic revision of the genus *Salsola* in southern Africa is that of Botschantzev (1974c). He recognised 69 species, including two naturalised aliens from section *Salsola*. The 67 indigenous species all belong to section *Caroxylon*, which he divided into

subsection *Caroxylon* with 54 species, subsection *Distichae* with one species and subsection *Tetragonae* with 12 species. In this synopsis of the species of *Salsola* from South Africa and Namibia, a key to their identification is provided. This key relies heavily on flower and fruit characters, but as specimens of *Salsola* are usually sterile, it is rendered of little or no importance for routine identification. Members of *Salsola* only flower for a very brief period each year and may not flower at all during long periods of drought. Furthermore, 21 new species were described since the publication of this key (Botschantzev 1979, 1981, 1983). This key can thus not be used to identify almost a quarter of the species currently proposed for southern Africa.

The total number of *Salsola* species currently listed for southern Africa amounts to 89, of which no less than 69 were described by Botschantzev (Arnold & De Wet 1993). These new species were mainly published in Latin and Russian in publications not readily available in South Africa and therefore, many of the names have hardly been taken up and applied by southern African botanists. This situation further hampers the systematics of the genus.

CHAPTER 5

MATERIALS AND METHODS

5.1 MATERIALS

Material used in this study were either collected in their natural habitat [voucher specimens deposited in the HGWJ Schweickerdt Herbarium (PRU), University of Pretoria] or were obtained from herbarium specimens housed in the National Herbarium, Pretoria (PRE). Where available, mostly type specimens and specimens determined by Botschantzev were used due to the uncertainty that exists as to the taxonomic status of many species. Unfortunately, material of the only member of subsection *Distichae*, namely *S. verdoorniae*, is very scant. Thus only members from subsections *Caroxylon* and *Tetragonae* could be studied. Voucher specimens are listed in Table 5.

TABLE 5: Specimens of *Salsola* investigated [Localities are given as quarter-degree grid references (Edwards & Leistner 1971). Herbarium acronyms follow Holmgren *et al.* (1990)]

Species	Collector	Grid	Herbarium
S. acocksii	Acocks 18809, Isotype	2819BB	PRE
S. aellenii	Acocks 13198, Isotype	3119BD	PRE
	Geo Potts (Bloemfontein University 6613)	2926AA	PRE
S. albida	Lang (sn 31718)	2723AD	PRE
	Leistner 2170, Syntype	2824BA	PRE
S. aphylla	Bohnen 8406	3321CC	PRE
	Burger 600	2427AB	PRE
	Collins 26	2722DD	PRE
	Giess 8310	2418AB	PRE
	Van Zinderen Bakker 1000	2827AC	PRE
S. apterygea	Theron 1645, Isotype	3120BD	PRE
S. araneosa	Dinter 4017, Isolectotype	2715BC	PRE
S. calluna	RR Klopper & AW Klopper 33	3023DA	PRU
	Smith 5305, Holotype	2925AC	PRE
	Smith 5355	2925CB	PRE
	Verdoorn 2301	2925CB	PRE
S. cauliflora	Giess 10311, Type	2516DD	PRE
S. ceresica	Acocks 14455, Isotype	3219DA	PRE
S. dealata	Acocks 17827	3124AB	PRE
	Acocks 17830, Isotype	3124AB	PRE
S. decussata	Schlechter 8091, Isotype	3118DA	PRE
S. denudata	Giess 8362, Isotype	2619CA	PRE
S. dinteri	Dinter 4972, Isotype	2718CA	PRE

Species	Collector	Grid	Herbarium
S. etoshensis	De Winter 3610, Isotype	1915BB	PRE
	Van Son (sn 28789)	2419BD	PRE
S. exalata	Henrici 3886b	2925AC	PRE
	Verdoorn 1599, Holotype	2924DB	PRE
S. gemmata	Giess & Robinson 13221, Isotype	2514DB	PRE
S. gemmifera	Dinter 4049	2715BC	PRE
	Dinter 6456, Isotype	2715DD	PRE
S. giessii	Giess 3770, Isotype	2216DC	PRE
S. glabra	Giess 9139, Isotype	2115BD	PRE
S. glabrescens	Burtt Davy 1496, Isotype	2725DA	PRE
	Henrici 3909	2925CB	PRE
	RR Klopper & AW Klopper 188	3021BC	PRU
	Smith 3901	2925CB	PRE
S. henriciae	Henrici 3897, Holotype	3022CA	PRE
	Sidey 533	3022CA	PRE
S. huabica	Giess 7947, Isotype	2014AC	PRE
S. humifusa	Acocks H1282	2824DB	PRE
	Smith 4514, Holotype	2925AC	PRE
S. inaperta	Story 5298, Syntype	1920DC	PRE
S. kali	RR Klopper & AW Klopper 164	3118DA	PRU
S. kleinfonteini	Giess 8312, Isotype	2516BB	PRE
S. koichabica	Merxmüller & Giess 28451, Isotype	2615BC	PRE
S. marginata	Giess 8342, Isotype	2218CA	PRE
S. melanantha	Leistner 1486, Isotype	2824BA	PRE
S. merxmuelleri	Acocks 14228	2916BD	PRE
	Merxmüller & Giess 2289, Isotype	2615CA	PRE
S. microtricha	Acocks 16291, Isotype	3125DB	PRE
S. minutifolia	Coetzer 53, Holotype	3121DC	PRE
S. okaukuejensis	Giess 15462, Isotype	1915BB	PRE
S. patentipilosa	Acocks 13204, Holotype	3019CD	PRE
	Breuckner 1159	2623DB	PRE
	RR Klopper & AW Klopper 160	3118DA	PRU
S. rabieana	Breuckner 165	2824DA	PRE
	Herman 366	2924DD	PRE
	RR Klopper & AW Klopper 53	3021DB	PRU
	Verdoorn 2297	2925CB	PRE
S. robinsonii	Giess & Robinson 13237, Isotype	2615CA	PRE
S. scopiformis	Merxmüller & Giess 28891, Isotype	2618CA	PRE
S. seminuda	De Winter 3257, Isotype	2618CA	PRE
S. sericata	Acocks 19585, Holotype	3017BA	PRE
S. smithii	RR Klopper & AW Klopper 57	3021DB	PRU
	Smith 5347	2924DB	PRE
	Smith 5439, Isotype	2925CD	PRE

Species	Collector	Grid	Herbarium
S. tuberculata	Henrici 4923	2925CB	PRE
	Pole-Evans 2245	2921AC	PRE
	RR Klopper & AW Klopper 179	3020AD	PRU
	Story 1109	2921AC	PRE
S. tuberculatiformis	Acocks 14443	3319AD	PRE
	Leistner 3035	2721AD	PRE
	RR Klopper & AW Klopper 174	3019CD	PRU
S. warmbadica	Acocks 18805, Isotype	2819DA	PRE
S. zeyheri	Acocks 13206	3019CD	PRE
	RR Klopper & AW Klopper 162	3118DA	PRU
	Zeyher 1447 (*planta alternifolia*), Isolectotype	3418AD	PRE

Distribution maps for all investigated species can be found in the Appendix. These maps were compiled according to specimens housed at the National Herbarium in Pretoria (PRE), the HGWJ Schweickerdt Herbarium at the University of Pretoria (PRU) and the herbarium of the Grootfontein Agricultural College in Middelburg, Eastern Cape Province.

5.2 METHODS

Fresh material was immediately fixed in a formalin-acetic acid-alcohol (FAA) mixture (Johansen 1940). Dried material from herbarium specimens was rehydrated by heating in distilled water. Material was slowly heated to boiling point in a water bath for approximately one hour and allowed to cool to room temperature. Rehydrated material was fixed and preserved in FAA.

5.2.1 Methods for LM study

Material fixed in FAA was used for LM studies. For preparation of semi-thin sections, leaves were removed from stems with a sharp blade, dehydrated and embedded in the monomer mixture, glycol methacrylate (GMA), basically according to the method of Feder and O'Brien (1968).

96% ethanol	2×	8–12 hours between changes
↓		
100% ethanol	2×	8–12 hours between changes
↓		
n-propanol	2×	8–12 hours between changes
↓		
n-butanol	2×	8–12 hours between changes
↓		
monomer mixture (GMA)	3×	24 hours between changes (Left in GMA mixture for 7–10 days after third infiltration before embedding.)

This dehydration and infiltration procedure was carried out at room temperature. For embedding the infiltrated material was transferred to labelled weighing dishes, covered with GMA mixture and another weighing dish placed on top of the GMA mixture with the material to minimise contact with air. This is necessary since oxygen inhibits the polymerisation of GMA. The weighing dishes were placed in an oven at about 59°C for 25 hours to polymerise.

GMA polymerises into a hard block. Material was sawn out and the blocks trimmed. Transverse sections, 3 µm thick, were cut with glass knives on a Jung Multicut 2045 ultra-microtome. Sections were placed on drops of distilled water on chemically clean slides and left on a slide warmer for about 24 hours to adhere firmly to the glass. Sections were then stained with Schiff's reagent, according to the Periodic Acid-Shiff Reaction (PAS) as proposed by Feder and O'Brien (1968). Sections were counter-stained with 0.05% Toluidine blue in benzoate buffer at pH 4.4 (Sidman *et al.* 1961). The staining procedure is summarised below.

saturated 2,4 - dinitrophenylhydrazine	30 minutes (This was used to carry out the aldehyde blockade.)
↓	
running water	10 minutes
↓	
1% periodic acid solution	10 minutes
↓	
running water	5 minutes
↓	
Schiff's reagent	30 minutes
↓	
running water	10 minutes
↓	
distilled water	1–2 minutes
↓	
slide warmer	until dry
↓	
Toluidine blue	1 minute
↓	
running water	until background plastic is more or less clear
↓	
distilled water	1–2 minutes
↓	
slide warmer	until dry

With this procedure starch and polysaccharides of the cell wall stain red or magenta, collenchyma and parenchyma stain a reddish purple, lignified tissue stains green or blue-green, and callose and cellulose remain unstained (Feder & O'Brien 1968; O'Brien & McCully 1981).

After staining, coverslips were applied to the dried slides with the mountant Entellan (Product 7961, E. Merck, Darmstadt). A complete set of slides is housed at the Department of Botany, University of Pretoria. Photos were taken with an Olympus BH-2 microscope using Kodak Technical Pan film.

In order to investigate trichome structure and length, epidermal peels of leaves fixed in FAA were made. The epidermal peels were stained with 0.05% Toluidine blue in benzoate buffer at pH 4.4 (Sidman *et al.* 1961) for ± 1 minute. Stained material was mounted in distilled water and viewed with a light microscope.

Measurements of leaves were taken using:
- uncut leaves fixed in FAA, by means of a dissecting microscope,
- uncut critical point dried leaves, using an SEM (see section 5.2.2),
- as well as the coloured semi-thin section slides described above.

Leaf dimensions are given in millimeters in the order *length* × *width* × *thickness*. Cell proportions were taken using the coloured slides by means of a light microscope, and are given in micrometers as *anticlinal dimensions* × *periclinal dimensions*. Measurements mentioned under Leaf Type, Indumentum Type and in all species descriptions are given as (*smallest measurement*–) *range* (–*largest measurement*). The range was calculated by subtracting and adding the standard deviation to the average and then choosing the measurements nearest to these calculated values. For all size calculations, at least ten measurements from each sample were used. Measurements were not made on specimens that appeared distorted due to poor rehydration. Where cell proportions are not given, none of the available material was sufficiently rehydrated to permit measurements to be taken.

5.2.2 Methods for SEM study

For study with SEM, the material fixed in FAA was used. The material was dehydrated using an ethanol sequence and thereafter critical point dried.

100% ethanol	at 10°–12° C	
↓		
liquid CO_2	3×	5 minutes between changes
↓		
liquid CO_2	3×	15 minutes between changes
↓		
liquid CO_2	3×	1 hour between changes
↓		

heated to 32°–35° C to dry samples completely

Dried material was mounted on SEM plates with silver paint, sputter coated with gold and viewed and photographed with a Joel 480 scanning electron microscope.

CHAPTER 6

ANATOMICAL CHARACTERS

6.1 INTRODUCTION

Leaves of the Chenopodiaceae show a number of anatomical characters that can be correlated to the xerophytic habitat of so many members of this family (Solereder 1908). The availability of water is an important factor affecting the form and structure of plants (Esau 1977; Fahn & Cutler 1992). In the arid Karoo the restricted possibilities of plant life have induced a large variety of growth and life forms, well suited to tolerate the severity of the climate and habitat and to survive unfavourable periods (Werger 1978). Nutrient deficiency, extreme cold, high light intensity, as well as a high content of dissolved mineral substances, as found in the saline habitats of halophytes, may also lead to the expression of xeromorphic characters in plants (Esau 1977; Metcalfe & Chalk 1983; Fahn & Cutler 1992).

Xerophytic plants possess many characters that minimise transpiration and thus protect the aerial parts from excessive water loss (Esau 1977; Fahn & Cutler 1992). Xerophytism can be recognised by characters like narrow leaves, hairy surfaces, sclerophylly and desiccation-tolerant foliage (Werger 1978). The most prevalent xeromorphic character is a high surface to volume ratio and leaves of xeromorphic plants are thus small and compact (Esau 1977; Metcalfe & Chalk 1983; Fahn & Cutler 1992). This is the case with many of the, mostly leaf succulent, members of the Chenopodiaceae, including species of *Salsola* (Werger 1978) with their small mostly terete leaves (Solereder 1908). These small leaves usually have a thick mesophyll and therefore the internal tissue of the leaf mainly consists of centrally placed aqueous tissue, enclosing the median vascular bundle and its branches (Solereder 1908; Esau 1977). In the aqueous mesophyll of xerophytic plants the palisade parenchyma is often more strongly developed than the spongy parenchyma, or sometimes present alone (Esau 1977; Metcalfe & Chalk 1983). If spongy parenchyma is present, its intercellular spaces are usually very small (Esau 1977). The Chenopodiaceae is characterised by the absence of typical spongy tissue in its leaves (Solereder 1908). Mineral salts are often dissolved in the aqueous tissue of this family (Solereder 1908).

Some xeromorphic plants do, however, possess characters that are thought to promote transpiration, for example large intercellular spaces, abundant chloroplasts and a large amount of widely distributed stomata. These are also characters promoting photosynthesis. The predominance of such characters in a number of South African xerophytes indicates that the survival of these species depends on storing as many resources as possible during times when water is abundant. These stored resources are then used during periods of drought, when photosynthesis is minimised by the closing of stomata. During these dry times, water absorption through trichomes may play a significant role in the plant's water economy. Simultaneously, characters such as, amongst other, a thick indumentum may play a role in the reduction of transpiration (Jordaan & Kruger 1992).

The Chenopodiaceae is one of the families most frequently quoted as showing Kranz-type anatomy (Metcalfe & Chalk 1979). Kranz anatomy is an anatomical pattern that was first identified by German botanists (Laetsch 1974) and is commonly associated with the C4-carbon fixation pathway. Typical Kranz-anatomy is characterised by a layer of parenchymatous bundle sheath cells that usually envelope the vascular bundles, surrounded by chlorenchymatous mesophyll cells that are most often palisade in form. The chloroplasts of the bundle sheath cells are usually much larger than those of the mesophyll cells (Laetsch 1974; Shomer-Ilan *et al.* 1975; Metcalfe & Chalk 1979).

In leaves of *Salsola* the palisade surrounds a parenchyma of large, colourless, presumably water storage cells containing the centrally placed main vascular bundle (Esau 1977; Carraro *et al.* 1993; Patrignani *et al.* 1993). The vascular branches lie at the periphery of this aqueous tissue and are often surrounded by a special starch-sheath (Solereder 1908; Carraro *et al.* 1993; Patrignani *et al.* 1993). The presence of small vascular bundles at the periphery of the aqueous tissue, indicates that the inner chlorenchymatous tissue or starch-sheath is a true bundle sheath (Shomer-Ilan *et al.* 1975). This type of structure, where the Kranz- and palisade mesophyll cells and their associated network of secondary vascular bundles tend to form a complete layer around the leaf with the main vascular bundle in a central position separated from the Kranz-cells by aqueous tissue (Carraro *et al.* 1993; Patrignani *et al.* 1993), has been coined by Carolin *et al.* (1975) as the Salsoloid-type Kranz-anatomy. This type of Kranz-anatomy might seem strange when compared with the typical Kranz-type (Laetsch 1974). The differentiated chlorenchyma, with the inner layer attached to

the vascular tissue, is commonly believed to be necessary for the operation of the C4-photosynthetic pathway. It has, however, been shown that the two types of chlorenchymatous cells may be necessary for successful operation of the C4-pathway, but that it is not essential for the Kranz-cells to be associated with the vascular bundles (Shomer-Ilan *et al.* 1975).

Cells in the leaves of xerophytic plants, with the obvious exception of large water storage cells, are often conspicuously smaller than corresponding cells in mesophytes and hydrophytes, this pertains especially to epidermal cells (Metcalfe & Chalk 1983). The epidermis of xerophytic plants often has thick cell walls, particularly the outer periclinal ones. Thick cuticles are also very common, although the latter can be extremely variable (Esau 1977; Metcalfe & Chalk 1983; Fahn & Cutler 1992). In the Chenopodiaceae the leaf epidermis is usually a single layer of cells and the cuticle rarely attains a considerable thickness (Solereder 1908). It has been stated that the chemical composition of the cuticle is important in limiting cuticular transpiration. Due to this fact, thin cuticles are often very effective in preventing excessive transpiration through the cuticle (Mèrida *et al.* 1981; Jordaan & Kruger 1992, 1998). In arid regions where resources are limited, there is a high premium on energy conservation. In this respect, forming thin, effective cuticles as opposed to thick cuticles can drastically decrease the costs involved in cuticular construction (Jordaan & Kruger 1998).

To help prevent water loss, stomata of xerophytic plants are often located in cavities, stomatal crypts or grooves, lined with epidermal hair (Esau 1977) or surrounded by protrusions of cuticle (Metcalfe & Chalk 1983). In xerophilous species of the Chenopodiaceae the stomata are commonly depressed below the surface. However, a very noteworthy feature in the leaf structure of the Chenopodiaceae is the diversity of stomatal types in the family. In the narrow, terete, succulent leaves of the family, guard cells are often parallel to one another with their pores arranged transversely to the median vein of the leaf (Solereder 1908).

Xerophytic flora has a high proportion of representatives with leaves having a hypodermis (Esau 1977). A hypodermis is one or more layers of cells lying immediately beneath the epidermis and differs morphologically from the underlying tissues. The hypodermis often contains large quantities of sclerenchyma, presumably enabling it to act as a strengthening tissue (Tootill 1984). The abundant development of sclerenchyma for

mechanical strengthening of leaves is common amongst xerophytes and is thought to reduce the injurious effects of wilting (Esau 1977; Metcalfe & Chalk 1983). The hypodermis may fulfil an important function in this regard. A hypodermis has been observed in the leaves of some species with the Salsoloid-type Kranz-anatomy, including a number of *Salsola* species (Carolin *et al.* 1975; Carraro *et al.* 1993; Patrignani *et al.* 1993). It has, however, been stated that the presence or absence of a hypodermis layer appears to have no taxonomic significance (Carolin *et al.* 1975). In certain members of the Chenopodiaceae, including *Salsola* species, clustered crystals are found in a loose layer of colourless, roundish cells between the epidermis and the palisade parenchyma. Functionally this sheath of crystals can be interpreted as a possible protective measure against small herbivores (Solereder 1908).

Plant anatomy is a basic science and a classical source of information to the botanist (Fahn 1990; Stuessy 1990). It is thus of primary importance for all lines of research in plant science (Fahn 1990). As the internal parts of plants tend to be less affected by the environment than exposed/superficial parts, anatomical characters can be of great taxonomic importance (Stace 1989). Since the leaf is often the most conspicuous and also a very important functional part of a plant, leaf characters can be especially important.

Vegetative features are very useful for outlining natural groups within the Chenopodiaceae as well as in the genus *Salsola*. Leaf shape is considered to be one of the most important characters for dividing the genus into natural groups (Botschantzev 1969a). This and other leaf anatomical characters were investigated to assess the taxonomic significance of the different character states within *Salsola* section *Caroxylon* in southern Africa.

In this chapter a key to the leaf types are given, followed by a detailed description of each leaf type with an indication of its associated indumentum types. A list of species for each leaf type is given, whereafter each species is shortly described. In both the list of species and the species description indumentum types are again mentioned. For a detailed description of indumentum types see Chapter 7.

6.2 RESULTS

Viewed in transverse section, two main leaf types can be identified, namely: leaves with an adaxial hypodermis and leaves without an adaxial hypodermis. These leaf types have been used as a primary division of the investigated species into two groups. In the leaf type without an adaxial hypodermis, one species (*S. inaperta*) can be distinguished from the others in the group, by the fact that the palisade mesophyll and bundle sheath layers are absent over the midrib section of the leaf (see Figures 6.1 & 6.2).

KEY TO LEAF TYPES

Leaves with a uniseriate hypodermis underlying adaxial epidermis.....*Leaf Type H+*

Leaves without a hypodermis underlying adaxial epidermis.....*Leaf Type H-*

DESCRIPTION OF LEAF TYPES

Leaf Type H+

OUTLINE in transverse section ± semi-circular; ± (0.78–) 1–2.08 (–3.58) mm × (0.55–) 1.07–1.75 (–2.7) mm × (0.3–) 0.5–1.2 (–1.87) mm, thickest at midrib; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 2 µm) adaxially; thin (± 2 µm) to medium thick (± 4 µm) abaxially. ADAXIAL EPIDERMIS uniseriate; periclinal cell walls longer than anticlinal cell walls, ± (5–) 10–18 (–33) µm × (15–) 23–38 (–64) µm, cell size often decreases towards leaf margin; cell walls usually ± equally thickened, outer periclinal cell walls sometimes thicker than inner periclinal or anticlinal cell walls, inner periclinal cell walls only rarely thicker than outer periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS uniseriate; periclinal cell walls usually longer than anticlinal cell walls, cells only rarely ± isodiametric to anticlinal cell walls longer than periclinal cell walls, ± (9–) 17–31 (–47) µm × (15–) 23–39 (–65) µm, cell size often decreases towards leaf margin; outer periclinal cell walls usually thicker than inner periclinal and anticlinal cell walls, cell walls sometimes ± equally thickened. STOMATA paracytic; only occur abaxially (leaves hypostomatic) in area where palisade mesophyll and bundle sheath layers are present; mostly abundant, only sometimes rare; ± sunken to not sunken; often with a thick cuticle; guard cells parallel to one another, pores arranged transversely to median vein of leaf. ADAXIAL HYPODERMIS present; uniseriate; cell walls lignified; often contains cubic crystals near inner periclinal cell walls. ABAXIAL HYPODERMIS present; uniseriate, rather weakly differentiated; cells ± isodiametric, often contains cubic crystals. PALISADE MESOPHYLL present; uniseriate, placed abaxially; cells

cylindrical, ± (31–) 41–66 (–94) µm × 5–10 (–17) µm, cell size sometimes decreases slightly towards leaf margin. SPONGY MESOPHYLL present; cells large, thin-walled; cell size sometimes decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER present; comprising a single layer underlying palisade mesophyll; anticlinal cell walls usually longer than periclinal cell walls, cells sometimes ± cubic, ± (11–) 22–37 (–54) µm × (11–) 16–27 (–45) µm; cell walls not thickened. VASCULAR BUNDLES one to many; main vascular bundle centrally placed, often closer to adaxial epidermis, usually with a large to very large sclerenchym cap; secondary vascular strands several, small, associated with bundle sheath layer. INDUMENTUM TYPE 1, 2, 3a.i, 3a.ii, 3b.i, 3b.ii, 4a.

SPECIES POSSESSING LEAF TYPE H+ (Indumentum Type in brackets)

S. acocksii (3b.ii)	*S. etoshensis* (3b.i)	*S. koichabica* (3b.i)	*S. robinsonii* (3b.i)
S. albida (3b.i)	*S. exalata* (4a)	*S. marginata* (3a.i)	*S. scopiformis* (2)
S. aphylla (3a.ii)	*S. gemmifera* (4a)	*S. merxmuelleri* (3a.i)	*S. sericata* (2)
S. apterygea (4a)	*S. giessii* (3b.i)	*S. microtricha* (3b.i)	*S. tuberculata* (3a.i)
S. araneosa (1)	*S. glabrescens* (4a)	*S. okaukuejensis* (3b.i)	*S. tuberculatiformis* (3a.i)
S. ceresica (3a.ii)	*S. huabica* (3b.i)	*S. patentipilosa* (3b.i)	*S. warmbadica* (3b.i)
S. dealata (4a)	*S. kleinfonteini* (3a.i)	*S. rabieana* (4a)	*S. zeyheri* (1)

LEAF ANATOMICAL DESCRIPTION OF SPECIES

S. acocksii

OUTLINE ± 1–1.12 mm × (1–) 1.13–1.25 (–1.3) mm × 0.4–0.8 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (14–) 18–20 (–23) µm × (28–) 32–42 µm; outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (21–) 23–28 (–30) µm × (26–) 28–35 (–39) µm, cell size decreases towards leaf margin; cells walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (54–) 58–70 (–75) µm × 6–9 (–11) µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls,

± (37–) 40–51 (–54) µm × 20–29 (–39) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 3b.ii.

S. albida

OUTLINE ± 1.44–1.64 (–1.7) mm × (1.14–) 1.38–2 (–2.2) mm × (0.85–) 1.08–1.32 (–1.62) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 2 µm) adaxially; medium thick (± 3 µm) to thick (± 6 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 14–17 µm × (28–) 33–42 (–45) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (17–) 23–34 (–36) µm × (27–) 35–50 (–52) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA abundant; sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (45–) 60–76 (–83) µm × (6–) 8–10 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (30–) 34–43 (–45) µm × 21–26 (–31) µm. MAIN VASCULAR BUNDLE centrally placed, with a very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. aphylla

OUTLINE ± 1.13–1.65 (–1.86) mm × (0.73–) 1–1.6 (–1.94) mm × 0.5–0.76 (–0.87) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 1–3 µm) adaxially; thin (± 2 µm) to thick (± 5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (8–) 10–14 µm × (17–) 25–39 (–53) µm, cells size decreases towards leaf margin; cell wall ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (10–) 18–32 (–47) µm × (21–) 26–40 (–55) µm, cells size decreases towards leaf margin; cells walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. STOMATA ± abundant; ± sunken to not sunken; often with thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (34–) 39–60 (–94) µm × 6–10 (–13) µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (17–) 22–33 (–37) µm × (13–) 17–29 (–37) µm. MAIN VASCULAR

BUNDLE centrally placed closer to adaxial epidermis, with a large to very large sclerenchym cap. INDUMENTUM TYPE 3a.ii.

S. ceresica

OUTLINE ± 1.2–2.33 (–2.4) mm × (1.3–) 1.6–1.67 (–1.75) mm × 0.73–0.9 (–1.1) mm; margin thinly tapering. CUTICLE thin (± 1 µm) adaxially; thin (± 1–2 µm) to medium thick (± 2–3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (11–) 13–15 (–18) µm × (15–) 24–40 (–46) µm; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 18–25 (–29) µm × (24–) 27–35 (–46) µm; outer periclinal cell walls thicker than inner periclinal walls. STOMATA abundant; ± sunken to not sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (34–) 39–43 (–46) µm × 4–5 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal walls longer than periclinal walls, ± (18–) 23–30 (–32) µm × 15–22 (–24) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 3a.ii.

S. dealata

OUTLINE ± 0.8–1.16 mm × (0.77–) 0.9–1.3 mm × 0.35–0.54 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) to thick (± 6 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (8–) 10–12 µm × 20–34 (–44) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 17–22 µm × 24–29 (–33) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± 34–39 (–41) µm × 4–6 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (24–) 26–30 (–36) µm × (13–) 15–20 (–22) µm. MAIN VASCULAR BUNDLE centrally placed. INDUMENTUM TYPE 4a.

S. etoshensis

OUTLINE ± (1.08–) 1.4–1.85 (–1.9) mm × (1.35–) 1.47–1.7 mm × 0.75–1.7 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) to thick (± 5–6 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 12–15 (–18) µm × (29–) 33–44 (–49) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (9–) 16–22 (–33) µm × (25–) 29–32 (–39) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. STOMATA abundant; ± sunken to not sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (60–) 66–74 (–78) µm × 8–14 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal walls longer than periclinal walls, ± 28–32 (–40) µm × (16–) 18–24 (–26) µm. MAIN VASCULAR BUNDLE centrally placed, with a very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. exalata

OUTLINE ± 1.7–1.15 mm × 1.1–1.5 (–2.7) mm × 0.44–0.63 mm; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 7–10 µm × (16–) 19–26 (–28) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (13–) 16–22 µm × (20–) 23–30 µm, cell size decreases slightly towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL cells cylindrical. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER present. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis. INDUMENTUM TYPE 4a.

S. gemmifera

OUTLINE ± 0.95–1.75 mm × 1.3–1.88 mm × 0.57–0.7 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 1–2 µm) adaxially; thin to medium thick (± 2–3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (9–) 11–16 µm × (21–) 24–35 (–43) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than

anticlinal cell walls, ± (16–) 18–23 (–26) µm × (21–) 25–37 (–42) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (31–) 39–45 (–54) µm × 5–7 µm. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER cells ± cubic, ± 18–25 (–32) µm × (16–) 21–25 (–29) µm. MAIN VASCULAR BUNDLE centrally placed. INDUMENTUM TYPE 4a.

S. giessii

OUTLINE ± (1.2–) 1.5–1.64 mm × (1–) 1.2–1.79 mm × 0.5–0.7 (–1) mm; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 15–18 (–23) µm × (20–) 22–30 (–32) µm; cell walls ± equally thickened. ABAXIAL EPIDERMIS cells ± isodiametric to periclinal cell walls longer than anticlinal cell walls, ± 18–26 (–32) µm × (15–) 23–31 µm; outer periclinal walls thicker than inner periclinal walls. STOMATA abundant; ± sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (40–) 45–55 µm × 5–7 (–9) µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (30–) 32–42 (–44) µm × (11–) 14–17 µm. MAIN VASCULAR BUNDLE centrally placed, with a very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. glabrescens

OUTLINE ± (1.15–) 1.17–1.46 (–1.8) mm × (0.75–) 0.95–1.35 (–1.5) mm × 0.6–0.83 (–0.98) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 1–2 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (9–) 11–15 (–17) µm × (23–) 25–33 (–38) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 17–28 (–40) µm × (20–) 26–38 (–43) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. STOMATA rare to abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (39–) 42–50 (–54) µm × (5–) 7–9 (–11) µm. SPONGY MESOPHYLL cell size decreases slightly towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE

SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (15–) 20–30 (–33) µm × (14–) 19–26 (–31) µm, cell size decreases slightly towards leaf margin. MAIN VASCULAR BUNDLE centrally placed, with a very large sclerenchym cap. INDUMENTUM TYPE 4a.

S. huabica

OUTLINE ± 1.3–1.7 mm × (1–) 1.35–2 mm × 0.8–0.95 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 15–19 (–22) µm × (22–) 27–37 (–40) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 25–41 µm × 30–44 (–54) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; ± sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (41–) 55–65 µm × (5–) 7–12 (–17) µm. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (20–) 30–34 (–40) µm × (17–) 19–29 (–32) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with medium to large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. kleinfonteini

OUTLINE ± 0.9–1.82 mm × 1.05–1.48 (–1.55) mm × 0.8 mm; margin very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell wall longer than anticlinal cell walls, ± (12–) 14–18 µm × (21–) 24–34 (–39) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 20–29 (–33) µm × (25–) 29–39 (–51) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (51–) 55–64 (–73) µm × 6–8 (–13) µm. SPONGY MESOPHYLL cell size decreases towards leaf margin. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± 24–34 (–38) µm × (14–) 17–19 (–26) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with medium to large sclerenchym cap. INDUMENTUM TYPE 3a.i.

S. koichabica

OUTLINE ± 1–1.25 (–1.3) mm × (0.82–) 0.93–1.24 (–1.3) mm × 0.74–0.92 (–1) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (10–) 12–19 (–22) µm × (29–) 33–43 µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (14–) 17–24 (–27) µm × (19–) 24–31 µm, cell size decreases very slightly towards leaf margin; cell walls ± equally thickened. STOMATA abundant; ± sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (62–) 65–72 (–81) µm × 9–14 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal walls longer than periclinal walls, ± (33–) 36–42 (–51) µm × (17–) 21–27 µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, with a very small sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. marginata

OUTLINE ± 1.4–1.5 mm × (1–) 1.27–1.76 mm × 0.6–0.8 mm; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2 µm) to medium thick (± 3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 16–21 µm × (23–) 25–35 (–42) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (17–) 23–31 (–33) µm × (24–) 26–40 (–42) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (40–) 49–60 (–63) µm × 5–11 (–17) µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER cells ± cubic to anticlinal cell walls longer than periclinal cell walls, ± (18–) 23–30 (–33) µm × (13–) 18–28 µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with very large sclerenchym cap. INDUMENTUM TYPE 3a.i.

S. merxmuelleri

OUTLINE ± 1.38–1.7 (–1.75) mm × (1.16–) 1.37–1.8 mm × (0.76–) 0.78–1.05 (–1.2) mm; margin tapering. CUTICLE thin (± 1–2 µm) to medium thick (± 3–4 µm) adaxially; medium thick (± 3–4µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (8–) 17–26 µm × (30–) 33–54 (–64) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (20–) 25–39 (–44) µm × (30–) 35–57 (–65) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker that inner periclinal and anticlinal walls. STOMATA abundant; ± sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (37–) 40–47 (–50) µm × 10–12 (–14) µm, cell length decreases slightly towards leaf margin. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER periclinal cell walls longer than anticlinal cell walls, ± (15–) 20–29 (–33) µm × 24–36 (–44) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, without sclerenchym cap. INDUMENTUM TYPE 3a.i.

S. microtricha

OUTLINE ± 1–1.4 (–1.55) mm × (1.18–) 1.22–1.3 (–1.35) mm × (0.52–) 0.75–0.98 mm; margin thinly tapering. CUTICLE thin (± 1–2 µm) adaxially; thin (± 2–3 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 12–15 µm × (19–) 21–32 (–36) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (12–) 16–21 µm × 22–27 (–29) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. STOMATA abundant; ± sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (40–) 45–50 µm × 5–7 µm. SPONGY MESOPHYLL cell size decreases slightly towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (20–) 28–34 (–36) µm × (11–) 15–21 µm. MAIN VASCULAR BUNDLE centrally placed very close to adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. okaukuejensis

OUTLINE ± 1.15–1.65 mm × 1.35–2.08 (–2.2) mm × 0.78–0.9 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) to thick (± 5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (11–) 13–15 µm × (25–) 28–40 (–43) µm; cell walls ± equally thickened. ABAXIAL EPIDERMIS cells ± isodiametric to anticlinal cell walls longer than periclinal cell walls, ± (24–) 28–38 (–40) µm × (18–) 24–32 (–40) µm; cell walls ± equally thickened. STOMATA ± abundant; sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (47–) 64–70 (–72) µm × (6–) 8 – 12 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (20–) 26–36 (–40) µm × (13–) 15–20 (–25) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. patentipilosa

OUTLINE ± 1.2–1.35 (–1.42) mm × (1.23–) 1.44–1.68 (–1.82) mm × 0.53–0.7 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 11–14 µm × (24–) 27–35 (–40) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (16–) 20–26 (–30) µm × 23–34 µm; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (55–) 60–70 µm × (5–) 7–9 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± 31–40 (–50) µm × (14–) 18–23 µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. rabieana

OUTLINE ± 0.9–1.66 (–2) mm × (0.55–) 1–1.62 (–1.9) mm × (0.53–) 0.56–0.83 (–0.88) mm; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 2–3 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell

walls longer that anticlinal cell walls, ± (8–) 10–18 (–23) µm × (20–) 23–34 (–40) µm; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (13–) 19–31 (–39) µm × (22–) 28–35 (–38) µm, cell size decreases towards leaf margin; cells walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (33–) 37–60 (–72) µm × 5–8 (–10) µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (23–) 26–33 (–40) µm × (12–) 16–27 (–32) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 4a.

S. robinsonii

OUTLINE ± 1.5–1.77 mm × (1.43–) 1.5–0.9 mm × 0.9–1 mm; margin thinly tapering. CUTICLE thin (± 1–2 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (22–) 24–30 (–33) µm × (27–) 36–42 (–51) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS cells ± isodiametric to anticlinal cell walls longer than periclinal cell walls, ± (25–) 32–42 (–44) µm × (23–) 30–42 (–46) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; sunken; with a thick cuticle. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (46–) 57–66 (–71) µm × 7–10 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (25–) 30–40 (–47) µm × (17–) 21–27 µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with medium to large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. scopiformis

OUTLINE ± (1.15–) 1.5–2.25 mm × (1.18–) 1.8–2.28 mm × (0.65–) 0.88–1 mm; margin very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 14–16 (–18) µm × 20–34 (–44) µm, cell size decreases towards leaf margin; cell walls ± equally thickened to outer

periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (16–) 19–28 (–31) µm × (24–) 28–35 (–44) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA abundant; does not appear to be sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (52–) 56–72 (–78) µm × 5–8 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin. BUNDLE SHEATH LAYER cells ± cubic to anticlinal cell walls longer than periclinal cell walls, ± (11–) 20–31 µm × (14–) 22–27 µm. MAIN VASCULAR BUNDLE centrally placed. INDUMENTUM TYPE 2.

S. sericata

OUTLINE ± (1.22–) 1.28–1.4 (–1.5) mm × (1.25–) 1.4–1.82 (–1.98) mm × 0.9–1 (–1.7) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 9–13 µm × (20–) 23–32 (–39) µm; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 16–20 (–22) µm × (23–) 30–35 (–40) µm; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA rare; does not appear sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (56–) 63–73 (–84) µm × 5–8 µm. SPONGY MESOPHYLL cell size decreases slightly towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER cells ± cubic to anticlinal cell walls longer than periclinal cell walls, ± 20–28 (–31) µm × (16–) 18–27 (–30) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, with a large sclerenchym cap. INDUMENTUM TYPE 2.

S. tuberculata

OUTLINE ± (0.88–) 0.98–1.4 (–1.8) mm × (0.92–) 1.05–1.64 (–1.78) mm × 0.5–0.7 (–1.05) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (8–) 10–15 (–17) µm × (18–) 24–34 (–43) µm, cells size decreases towards leaf margin; cell walls ± equally thickened to inner periclinal cell walls thicker than outer periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than

anticlinal cell walls, ± (12–) 15–26 (–33) µm × (18–) 22–27 (–32) µm, cell size decreases towards leaf margin; cells walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. STOMATA ± abundant; ± sunken to not sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (38–) 40–47 (–50) µm × 5–7 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± 23–29 (–31) µm × (11–) 13–18 (–21) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 3a.i.

S. tuberculatiformis

OUTLINE ± (0.78–) 0.88–1.4 mm × 1.05–1.32 (–1.5) mm × 0.3–0.8 (–0.95) mm; margin thinly to very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to thick (± 4–5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 7–12 µm × (18–) 20–28 (–33) µm; cell walls ± equally thickened to outer periclinal cell walls thickener than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (10–) 14–23 µm × (18–) 22–30 (–38) µm; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; ± sunken to not sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± 44–53 (–56) µm × 5–7 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (15–) 22–33 (–40) µm × (12–) 14–20 (–24) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with a very large sclerenchym cap. INDUMENTUM TYPE 3a.i.

S. warmbadica

OUTLINE ± 1–1.15 (–1.36) mm × 1.25–1.48 mm × 0.57–0.8 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (6–) 8–13 µm × (19–) 22–31 (–38) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS cells ± isodiametric, ± (19–) 22–28 (–33) µm × 20–27 (–30) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. STOMATA ± abundant, ± sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE

MESOPHYLL ± (40–) 44–51 (–56) µm × 4–6 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (24–) 28–30 (–33) µm × 11–17 µm. MAIN VASCULAR BUNDLE centrally placed, with very large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. zeyheri

OUTLINE ± (2.24–) 2.6–3.46 (–3.58) mm × (1.34) 1.46–1.85 (–2) mm × 1.28–1.73 (–1.87) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (± 1–3 µm) adaxially; thin (± 1–2 µm) to thick (± 4–6 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (5–) 7–11 (–14) µm × 16–35 (–48) µm, cell size decreases towards leaf margin; cell walls ± equally thickened to inner periclinal walls thickener than outer periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 20–29 (–40) µm × (16–) 19–39 (–65) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. STOMATA rare to abundant; does not appear to be sunken to ± sunken. ADAXIAL HYPODERMIS present. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (36–) 42–52 (–65) µm × 7–11 (–15) µm, cell length decreases towards leaf margin. SPONGY MESOPHYLL cell size decreases towards leaf margin. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (20–) 25–38 (–42) µm × (20–) 23–33 (–45) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, with a small sclerenchym cap. INDUMENTUM TYPE 1.

Leaf Type H-

OUTLINE in transverse section ± semi-circular; ± (0.48–) 0.95–2.5 (–4.8) mm × (0.51–) 0.88–1.85 (–2.54) mm × (0.4–) 0.5–1.16 (–1.9) mm, thickest at midrib; margin thinly to roundly tapering. CUTICLE very thin (> 1 µm) to thin (± 2 µm) adaxially; thin (± 2 µm) to medium thick (± 4 µm) abaxially. ADAXIAL EPIDERMIS uniseriate; periclinal cell walls longer that anticlinal cell walls, ± (5–) 10–19 (–27) µm × (18–) 24–39 (–59) µm, cell size often decreases towards leaf margin; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS uniseriate; periclinal cell walls usually longer than anticlinal cell walls, cells only rarely ± isodiametric to anticlinal cell walls longer than periclinal cell walls, ± (12–) 15–34 (–53) µm × (15–) 21–42 (–63) µm, cell size often decreases towards leaf margin; outer periclinal cell walls usually thicker than

inner periclinal or anticlinal cell walls, cell walls sometimes ± equally thickened. STOMATA paracytic; only occur abaxially (leaves hypostomatic) in area where palisade mesophyll and bundle sheath layers are present; mostly abundant, sometimes rare; mostly does not appear to be sunken, sometimes ± sunken; sometimes with a thick cuticle; guard cells parallel to one another, pores arranged transversely to median vein of leaf. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present; uniseriate, rather weakly differentiated; cells ± isodiametric, often contains cubic crystals. PALISADE MESOPHYLL present; uniseriate, placed abaxially; cells cylindrical, ± (28–) 34–50 (–59) µm × (4–) 6–10 (–14) µm, cell size sometimes decreases slightly towards leaf margin. SPONGY MESOPHYLL present; cells large, thin-walled; cell size sometimes decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER present; comprising a single layer underlying palisade mesophyll; anticlinal cell walls usually longer than periclinal cell walls, cells sometimes ± cubic, periclinal cell walls only rarely longer than anticlinal cell walls, ± (12–) 19–31 (–42) µm × (11–) 14–24 (–35) µm; cell walls not thickened. VASCULAR BUNDLES one to many; main vascular bundle centrally placed, sometimes closer to adaxial epidermis, sometimes with small to large sclerenchym cap; secondary vascular strands several, small, associated with bundle sheath layer. INDUMENTUM TYPE 2, 3a.i, 3a.ii, 3b.i, 4a, 4b.

SPECIES POSSESSING LEAF TYPE H- (Indumentum Type in brackets)

S. aellenii (4a)	*S. denudata* (4a)	*S. henriciae* (3a.i)	*S. minutifolia* (4a)
S. calluna (4b)	*S. dinteri* (2)	*S. humifusa* (4a)	*S. seminuda* (4a)
S. cauliflora (3a.ii)	*S. gemmata* (2)	*S. inaperta* (4a)	*S. smithii* (4a)
S. decussata (2)	*S. glabra* (4a)	*S. melanantha* (3b.i)	

LEAF ANATOMICAL DESCRIPTION OF SPECIES

S. aellenii

OUTLINE ± 1.8–2.4 mm × (1–) 1.2–1.98 mm × 0.8–0.98 mm; margin very thinly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 7–10 (–13) µm × (18–) 22–33 (–43) µm; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (13–) 18–34 (–39) µm × (25–) 30–40 µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal or

anticlinal cell walls. STOMATA abundant; does not appear to be sunken to ± sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL present. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (21–) 23–30 (–34) µm × 12–19 (–21) µm. MAIN VASCULAR BUNDLE centrally placed. INDUMENTUM TYPE 4a.

S. calluna

OUTLINE ± 0.48–2.14 (–2.65) mm × (0.51–) 0.57–0.88 (–1) mm × (0.41–) 0.5–0.62 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (5–) 7–11 (–13) µm × 18–28 (–33) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened to outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 13–18 µm × 18–32 (–42) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened to outer periclinal walls thicker than inner periclinal walls. STOMATA rare to abundant; does not appear to be sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (40–) 43–50 µm × 6–7 µm, cell length decreases slightly towards leaf margin. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± 25–32 (–42) µm × (14–) 16–20 (–22) µm. MAIN VASCULAR BUNDLE centrally placed, with a large sclerenchym cap. INDUMENTUM TYPE 4b.

S. cauliflora

OUTLINE ± 1.11–20.5 mm × 1.3–1.8 mm × 0.65–1 mm; margin tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 9–12 (–15) µm × (21–) 23–30 (–36) µm, cell size decreases towards leaf margin; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 16–24 (–27) µm × (19–) 24–37 (–44) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; ± sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± 30–36 (–42) µm × 8–11 µm. SPONGY MESOPHYLL present. BUNDLE

SHEATH LAYER cells ± cubic to periclinal cell walls longer than anticlinal cell walls, ± (12–) 14–18 (–20) µm × 15–22 (–25) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with large sclerenchym cap. INDUMENTUM TYPE 3a.ii.

S. denudata

OUTLINE ± 1.45–2.04 mm × 1–1.3 (–1.86) mm × 0.6–0.9 mm; margin roundly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 18–25 (–27) µm × (30–) 32–45 (–47) µm; outer periclinal cell walls thicker than inner periclinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (27–) 33–51 (–53) µm × (30–) 38–54 (–63) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (45–) 50–57 (–59) µm × 10–13 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER cells ± cubic to anticlinal cell walls longer than periclinal cell walls, ± (22–) 25–33 (–35) µm × (20–) 24–29 (–35) µm. MAIN VASCULAR BUNDLE centrally placed. INDUMENTUM TYPE 4a.

S. dinteri

OUTLINE ± 2–4.56 (–4.8) mm × 1.75–2 (–2.25) mm × 0.67–1.6 (–1.9) mm; margin tapering. CUTICLE very thin (> 1 µm) adaxially; thin to medium thick (± 2–3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (15–) 18–21 (–24) µm × (26–) 33–42 (–44) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (19–) 21–27 (–34) µm × (24–) 31–45 (–57) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. STOMATA rare, does not appear to be sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL present. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal walls longer than periclinal walls, ± (20–) 24–35 (–40) µm × (16–) 19–26 (–29) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis, with a small sclerenchym cap. INDUMENTUM TYPE 2.

S. gemmata

OUTLINE ± 1.6–2 mm × 2.03–2.52 mm × 0.98–1 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 11–15 (–17) µm × (26–) 29–45 (–59) µm; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (33–) 36–45 (–53) µm × (27–) 32–49 (–59) µm; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± rare; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (35–) 37–44 (–49) µm × 7–11 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin. BUNDLE SHEATH LAYER cells ± cubic to anticlinal cell walls longer than periclinal cell walls, ± 20–25 (–32) µm × (13–) 17–24 (–32) µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis. INDUMENTUM TYPE 2.

S. glabra

OUTLINE ± 1.6–1.75 mm × (1.25–) 1.35–1.69 (–1.75) mm × 0.66–0.71 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) to medium thick (± 3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (7–) 11–18 µm × 35–40 (–46) µm, cell size decreases towards leaf margin; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± 15–26 µm × (18–) 28–35 (–46) µm, cell size decreases towards leaf margin; outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± rare; does not appear to be sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL present. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER present. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with medium sized sclerenchym cap. INDUMENTUM TYPE 4a.

S. humifusa

OUTLINE ± 1.4–2 mm × 0.8–1.16 mm × 0.5–0.8 mm; margin thinly tapering. CUTICLE thin (± 1–2 µm) adaxially; medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 13–19 (–21) µm × (19–) 21–29 (–33) µm, cell size

decreases towards leaf margin; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 19–24 (–26) µm × 20–30 (–36) µm, cell size decreases slightly towards leaf margin; outer periclinal walls thicker than inner periclinal walls. STOMATA abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (45–) 48–55 µm × 5–9 µm. SPONGY MESOPHYLL cell size decreases towards leaf margin; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (22–) 24–26 (–28) µm × (14–) 15–20 (–23) µm. MAIN VASCULAR BUNDLE centrally placed close to adaxial epidermis, with a small sclerenchym cap. INDUMENTUM TYPE 4a.

S. inaperta

OUTLINE ± (1.74–) 1.78–2.68 (–2.73) mm × (1.23–) 1.5–2.14 (–2.25) mm ×v (0.8–) 1–1.52 (–1.8) mm; margin thinly tapering. CUTICLE very thin (> 1 µm) to thin (1–2 µm) adaxially; thin (± 2 µm) to thick (± 5 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 15–20 (–22) µm × (21–) 30–36 (–40) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS anticlinal cell walls longer than periclinal cell walls, ± (13–) 20–29 µm × (20–) 25–34 (–40) µm, cell size decreases towards leaf margin; outer periclinal walls thicker than inner periclinal walls. STOMATA ± abundant; does not appear to be sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL absent over midrib; ± 28–34 (–38) µm × 6–7 µm. SPONGY MESOPHYLL present; cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER absent over midrib; anticlinal cell walls longer than periclinal cell walls, ± 25–32 µm × 16–23 µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis. INDUMENTUM TYPE 4a.

S. melanantha

OUTLINE ± 0.7–0.85 mm × 0.76–1 mm × 0.5–0.73 mm; margin thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2–3 µm) to medium thick (± 3–4 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (11–) 13–18 µm × 23–30 (–33) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. ABAXIAL EPIDERMIS cell ± isodiametric to periclinal cell walls longer than anticlinal cell walls,

± (12–) 17–27 (–29) µm × (15–) 20–25 (–33) µm, cell size decreases slightly towards leaf margin; cell walls ± equally thickened. STOMATA rare to abundant; does not appear to be sunken; with a thick cuticle. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (37–) 40–50 (–56) µm × 5–8 µm. SPONGY MESOPHYLL cells adjacent to bundle sheath often contains cubic crystals. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± (20–) 23–28 (–30) µm × 12–17 µm. MAIN VASCULAR BUNDLE centrally placed, with a large sclerenchym cap. INDUMENTUM TYPE 3b.i.

S. minutifolia

OUTLINE ± (1.08–) 1.15–1.35 (–1.45) mm × 0.98–1.4 mm × 0.88–0.05 (–1.13) mm; margin roundly tapering. CUTICLE very thin (> 1 µm) adaxially; thin to medium thick (± 2–3 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± (11–) 14–17 µm × 25–37 (–44) µm, cell size decreases towards leaf margin; outer periclinal walls thicker than inner periclinal walls. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 20–24 (–27) µm × (23–) 25–34 (–37) µm, cell size decreases towards leaf margin; cell walls ± equally thickened. STOMATA abundant; ± sunken to not sunken; with a thick cuticle. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± (30–) 34–39 (–41) µm × 5–7 µm. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER anticlinal cell walls longer than periclinal cell walls, ± 18–24 (–28) µm × (11–) 14–20 (–22) µm. MAIN VASCULAR BUNDLE centrally placed near adaxial epidermis. INDUMENTUM TYPE 4a.

S. seminuda

OUTLINE ± 1.03–1.14 mm × 0.8–1.3 mm × 0.4–0.5 mm; margin tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 1–2 µm) abaxially. ADAXIAL EPIDERMIS periclinal cell walls longer that anticlinal cell walls, ± 14–16 (–19) µm × (25–) 29–35 (–39) µm; cell walls ± equally thickened. ABAXIAL EPIDERMIS periclinal cell walls longer than anticlinal cell walls, ± (15–) 17–21 (–26) µm × (17–) 22–31 (–39) µm, cell size decreases towards leaf margin; cell walls ± equally thickened to outer periclinal cell walls thicker than inner periclinal and anticlinal cell walls. STOMATA ± rare; does not appear to be sunken. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL present. SPONGY MESOPHYLL present.

BUNDLE SHEATH LAYER present. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis. INDUMENTUM TYPE 4a.

S. smithii

OUTLINE ± 1.81 mm × 1.47 mm × 0.51 mm; margins thinly tapering. CUTICLE very thin (> 1 µm) adaxially; thin (± 2 µm) abaxially. ADAXIAL EPIDERMIS uniseriate. ABAXIAL EPIDERMIS cell ± isodiametric to periclinal cell walls longer than anticlinal cell walls, ± 20.44 µm × 21.89 µm; outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. STOMATA present. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present. PALISADE MESOPHYLL ± 36.44 µm × 8 µm. SPONGY MESOPHYLL present. BUNDLE SHEATH LAYER cells ± cubic, ± 17.67 µm × 17.78 µm. MAIN VASCULAR BUNDLE centrally placed closer to adaxial epidermis, with a large sclerenchym cap. INDUMENTUM TYPE 4a.

6.3 DISCUSSION

The genus *Salsola* possesses a number of adaptive leaf characters that correspond to the xerophytic habitat occupied by these plants in southern Africa. All these characters are suspected to minimise transpiration and thus prevent excessive water loss in an arid environment, and also to protect the plant's vital tissues from extreme heat.

Leaves of the investigated species are all terete and very small. In most species leaves are between 1–2 mm in length, often with the same or slightly smaller width. Leaves are succulent and can be between 0.5–1.5 mm thick. This gives the leaves a high surface to volume ratio, which is one of the most prevalent xeromorphic characters (Esau 1977; Metcalfe & Chalk 1983; Fahn & Cutler 1992).

Corresponding with the findings of other researchers (Solereder 1908; Esau 1977; Metcalfe & Chalk 1983), *Salsola* leaves have a very thick mesophyll. Palisade mesophyll is quite well developed in most species. The features of the spongy mesophyll are not typical, but it is rather characterised by the absence of intercellular spaces and comprises of centrally placed aqueous tissue, enclosing the main vascular bundle and its branches.

Typical Salsoloid-type Kranz-anatomy (Carolin *et al.* 1975) was not found in the investigated material. Instead, all taxa show a variation on this type of Kranz-anatomy. Leaves are inversely-dorsiventral, with the palisade mesophyll and bundle sheath layer, and its associated networks of secondary vascular bundles, only being present abaxially. The reason for this configuration may be the shape of the leaves. The apex of the leaf in *Salsola* species from the Northern Hemisphere, for example *S. kali*, is typically elongated into a spine, which is exposed to the environment on all sides. In a transverse section through one of these spines, the palisade mesophyll and bundle sheath layers form a continuous layer around the leaf. Southern African *Salsola* species do not have such extremely elongated leaves, but leaves typically have a short rounded apex. Leaves are also very densely packed, with their adaxial epidermis adpressed against the stem, thus covering the branches almost completely. This may be the reason for the adaxial absence of the palisade mesophyll and bundle sheath layers. Some leaves of a few indigenous species tend to have an apex that is somewhat elongated, but not as much as in the Northern Hemisphere species. In a transverse section through the apex of such a leaf, the palisade mesophyll and bundle sheath layers do form a continuous layer around the leaf, but it is not as pronounced as in, for instance, *S. kali*.

Epidermal cells of the investigated species are generally small; those of the adaxial epidermis being smaller than those of the abaxial epidermis. The adaxial epidermis is on average ± 10 µm thinner than the abaxial one. Epidermal cell walls are notably thickened, with the outer periclinal cell walls more often thicker than the inner periclinal or anticlinal cell walls. These are common features of xerophytic plants (Metcalfe & Chalk 1983).

The adaxial cuticle is almost always thinner than the abaxial one. Adaxially the cuticle is mostly less than 1 µm thick, while abaxially it averages at 3 µm, exceeding 4 µm in some species. One would expect a thick cuticle in xerophytic plants such as *Salsola*, but cuticle thickness can be an extremely variable character (Esau 1977; Metcalfe & Chalk 1983; Fahn & Cutler 1992) and the foliage cuticle rarely attains a considerable thickness in the Chenopodiaceae (Solereder 1908). The thin cuticle of these *Salsola* species may be due to an effective chemical composition that limits cuticular transpiration just as effectively as a thick cuticle (Mèrida *et al.* 1981; Jordaan & Kruger 1992, 1998). Forming thin, effective cuticles

instead of thick ones can be a way of conserving energy during growth (Jordaan & Kruger 1998).

All the investigated species have hypostomatic leaves with paracytic stomata. As the adaxial epidermis is adpressed against the stem and not readily in contact with the atmosphere, gas exchange through this surface would be extremely difficult. This may be the reason for the total absence of stomata on the adaxial surface. Stomata are abaxially abundant in most species, sometimes with a thick cuticle, and only occur in that area where the palisade mesophyll and bundle sheath layers are present internally. These two layers are necessary for photosynthesis and thus rely on proper gas exchange. The aqueous mesophyll subtending the epidermis of the leaf margins is mostly storage tissue and does not depend on gas exchange. Therefore, this area of the leaf does not need stomata. This explains the pattern of distribution of stomata on the abaxial leaf surface.

In xerophytes one would expect stomata to be depressed below the surface to help prevent water loss (Solereder 1908), but especially in species with a very dense covering of trichomes, this is not always necessary. In some species of *Salsola* the stomata are depressed below the epidermis, but mostly the inner periclinal walls of the epidermal and guard cells are aligned. In the latter case, the stomata still remain below the general surface of the leaf, because the epidermal layer is thicker than the anticlinal dimensions of the stomata. In a few species the stomata are situated at the epidermal surface and not sunken at all. Guard cells are parallel to one another and the stomatal pores are arranged transversely to the median vein of the leaf. This corresponds to an important character found by other researchers in members of the Chenopodiaceae with terete leaves (Solereder 1908).

The presence of a hypodermis is common amongst xerophytic plants (Esau 1977). An abaxial hypodermal layer containing prismatic crystals is present in all species investigated. This hypodermis is a common feature of many members of the Chenopodiaceae, as well as other *Salsola* species (Solereder 1908; Carolin *et al.* 1975; Carraro *et al.* 1993; Patrignani *et al.* 1993).

The presence or absence of an adaxial hypodermis has been used to divide the investigated species into two main groups. There are a greater number of species possessing Leaf Type H+ (with adaxial hypodermis) than there are species possessing Leaf Type H- (without adaxial hypodermis). Cell walls of the adaxial hypodermis are lignified and the layer is sclerenchymatic. This might act as a strengthening tissue to help protect the leaves against the injurious effects of wilting (Esau 1977; Metcalfe & Chalk 1983; Tootill 1984) or to protect the leaf surface against herbivorous insects. Similarly, the abundance of crystals present in the adaxial as well as the abaxial hypodermis, might fulfil a role as a protective measure against insects and other small herbivores (Solereder 1908). *Salsola* species are readily grazed by a large number of animals.

It has been stated that the presence or absence of a hypodermis appears to have no taxonomic significance in Chenopodiaceae (Carolin *et al.* 1975), a statement evidently not supported by the findings of this study. The taxonomic significance of the adaxial hypodermis layer in *Salsola* is not yet clear, but it might be correlated to some other morphological or even ecological character. There is a poor association between leaf type and subsection (see Table 6). In subsection *Caroxylon* (plants with alternate phylotaxis) the majority of investigated species possesses Leaf Type H+, although there are a small number of species in this subsection possessing Leaf Type H-. However, in subsection *Tetragonae* (plants with opposed phylotaxis) only one species, namely *S. exalata*, was found to possess Leaf Type H+. All other investigated species from subsection *Tetragonae* possess Leaf Type H-. This might be taxonomically significant and *S. exalata* needs to be re-investigated in order to confirm its position in subsection *Tetragonae*. This association between leaf type and subsections certainly calls for further investigation.

TABLE 6: Summary of principle leaf anatomical characters in southern African species of *Salsola* (Symbols are explained at the end of the table)

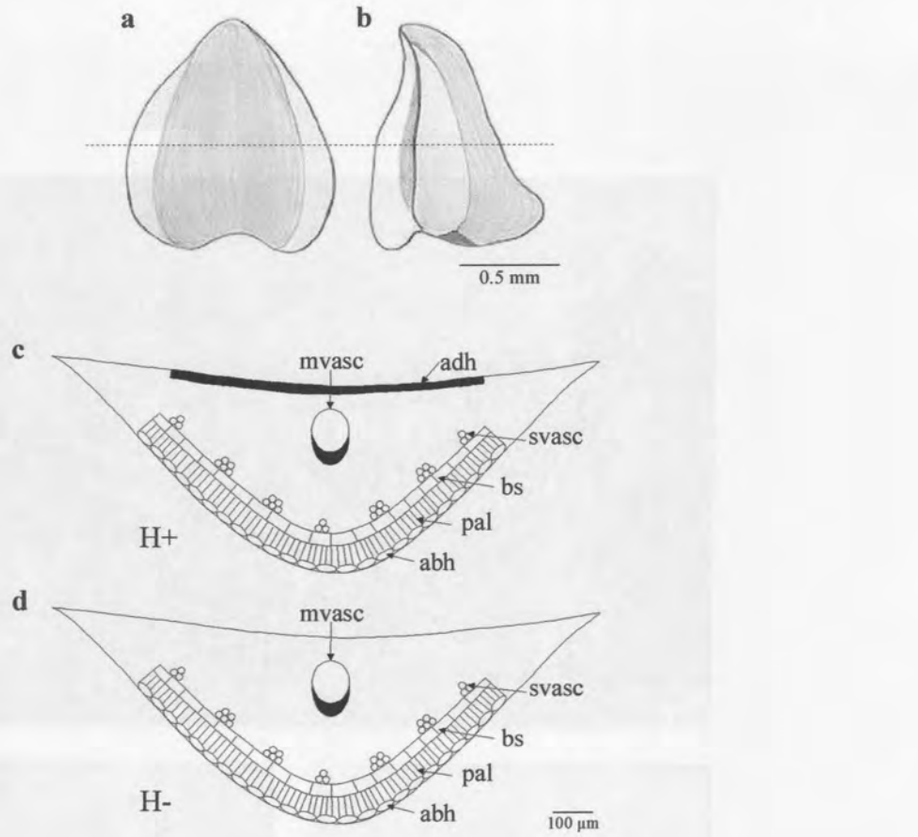
Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	I D Reliability	Species	Leaf type		Indumentum type								Specimens Investigated
			H+	H-	1	2	3a.i	3a.ii	3b.i	3b.ii	4a	4b	
C	1	*S. araneosa*	X		X								**Dinter 4017**
C	1; 2; 3	*S. zeyheri*	X		X								**Zeyher 1447**; **Acocks 13206**; RR & AW Klopper 162
C	1	*S. scopiformis*	X			X							**Merxmüller & Giess 28891**
C	1	*S. sericata*	X			X							**Acocks 19585**
C	1	*S. kleinfonteini*	X				X						**Giess 8312**
C	1	*S. marginata*	X				X						**Giess 8342**
C	1; 2	*S. merxmuelleri*	X				X						**Merxmüller & Giess 2289**; **Acocks 14228**
C	2; 3	*S. tuberculata*	X				X						**Pole-Evans 2245**; Henrici 4923; RR & AW Klopper 179; Story 110
C	2; 3	*S. tuberculatiformis*	X				X						**Acocks 14443**; RR & AW Klopper 174; Leistner 3035
C	3	*S. aphylla*	X					X					Bohnen 8406; Burger 600; Collins 26; Giess 8310; Van Zinderen Bakker 1000;
C	1	*S. ceresica*	X					X					**Acocks 14455**
C	1; 2	*S. albida*	X						X				**Leistner 2170**; **Lang sn (H31718)**
C	1; 2	*S. etoshensis*	X						X				**De Winter 3610**; **Van Son sn (H28789)**
C	1	*S. giessii*	X						X				**Giess 3770**
C	1	*S. huabica*	X						X				**Giess 7947**
C	1	*S. koichabica*	X						X				**Merxmüller & Giess 2289**
C	1	*S. microtricha*	X						X				**Acocks 16291**
C	1	*S. okaukuejensis*	X						X				**Giess 15462**

Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	I D Reliability	Species	Leaf type		Indumentum type								Specimens Investigated
			H+	H-	1	2	3a.i	3a.ii	3b.i	3b.ii	4a	4b	
C	1; 2; 3	*S. patentipilosa*	X						X				**Acocks 13204**; **Breuckner 1159**; RR & AW Klopper 160
C	1	*S. robinsonii*	X						X				**Giess & Robinson 13237**
C	1	*S. warmbadica*	X						X				**Acocks 19905**
C	1	*S. acocksii*	X							X			**Acocks 18809**
C	1	*S. apterygea*	X								X		**Theron 1645**
C	1; 2	*S. dealata*	X								X		**Acocks 17830**; **Acocks 17827**
C	1; 2	*S. gemmifera*	X								X		**Dinter 6456** ; **Dinter 4049**
C	1; 2; 3	*S. glabrescens*	X								X		**Burtt Davy 1496**; **Henrici 3909**; **Smith 3901**; RR & AW Klopper 188
C	2; 3	*S. rabieana*	X								X		**Breuckner 165**; **Verdoorn 2297**; Herman 366; RR & AW Klopper 53
C	1	*S. dinteri*		X		X							**Dinter 4972**
C	1	*S. gemmata*		X		X							**Giess & Robinson 13221**
C	1	*S. cauliflora*		X				X					**Giess 10311**
C	1	*S. melanantha*		X					X				**Leistner 1486**
C	1	*S. denudata*		X							X		**Giess 8362**
C	1	*S. glabra*		X							X		**Giess 9139**
C	1	*S. seminuda*		X							X		**De Winter 3257**
C	1; 2; 3	*S. calluna*		X								X	**Smith 5305**; **Smith 5355**; **Verdoorn 2301**; RR & AW Klopper 33
T	1; 2	*S. exalata*	X								X		**Verdoorn 1599**; **Henrici 3886b**
T	1	*S. decussata*		X		X							**Schlechter 8091**

Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	ID Reliability	Species	Leaf type		Indumentum type								Specimens Investigated
			H+	H-	1	2	3a.i	3a.ii	3b.i	3b.ii	4a	4b	
T	1; 2	*S. henriciae*		X			X						**Henrici 3897**; **Sidey 533**
T	1; 2	*S. aellenii*		X							X		**Acocks 13198**; **Geo Potts sn (Bloemfontein University 6613)**
T	1; 2	*S. humifusa*		X							X		**Smith 4514**; **Acocks H1282**
T	1; 2	*S. inaperta*		X							X		**Story 5298**
T	1	*S. minutifolia*		X							X		**Coetzer 53**
T	1; 2; 3	*S. smithii*		X							X		**Smith 5439**; **Smith 5347**; RR & AW Klopper 57
S	3	*S. kali*	X								X		RR & AW Klopper 164

ID Reliability: 1 = includes type specimen; 2 = includes specimen determined by Botschantzev; 3 = includes other specimen
Subsection: C = *Caroxylon*; T = *Tetragonae;* S = alien species from Section *Salsola*
Leaf type: H+ = with adaxial hypodermis; H- = without adaxial hypodermis
Trichome type: 1 = trichomes long, round in transverse section, entangled; 2 = trichomes round to flattened in transverse section, slightly adpressed to almost entangled; 3a.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin glabrate; 3a.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin glabrate; 3b.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin not glabrate; 3b.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin not glabrate; 4a = Leaves glabrous, trichomes on stems; 4b = leaves and stems glabrous
Specimens Investigated: **Bold & underline** = type specimen; **Bold** = specimen determined by Botschantzev; No bold / underline = other specimen

Section *Caroxylon*



Section *Salsola*

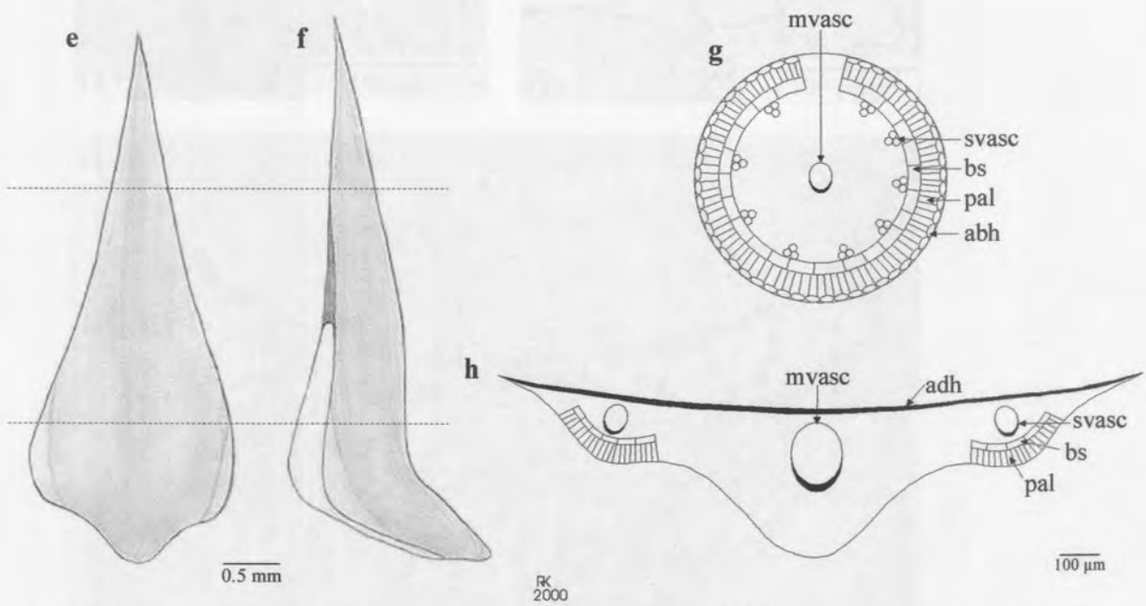


FIGURE 6.1: Diagrammatic representation of leaf types. **a – d** Section *Caroxylon*. **a** Abaxial view of leaf. **b** Lateral view of leaf. **c** Leaf Type H+. **d** Leaf Type H-. **e – h** Section *Salsola*. **e** Abaxial view of leaf. **f** Lateral view of leaf. **g** Section through tip of leaf showing Salsoloid-type Kranz-anatomy. **h** Section through base of leaf. ····· Indicates the position of the illustrated sections. abh - abaxial hypodermis; adh - adaxial hypodermis; bs - bundle sheath; mvasc - main vascular bundle; svasc - secondary vascular tissue; pal - palisade mesophyll.

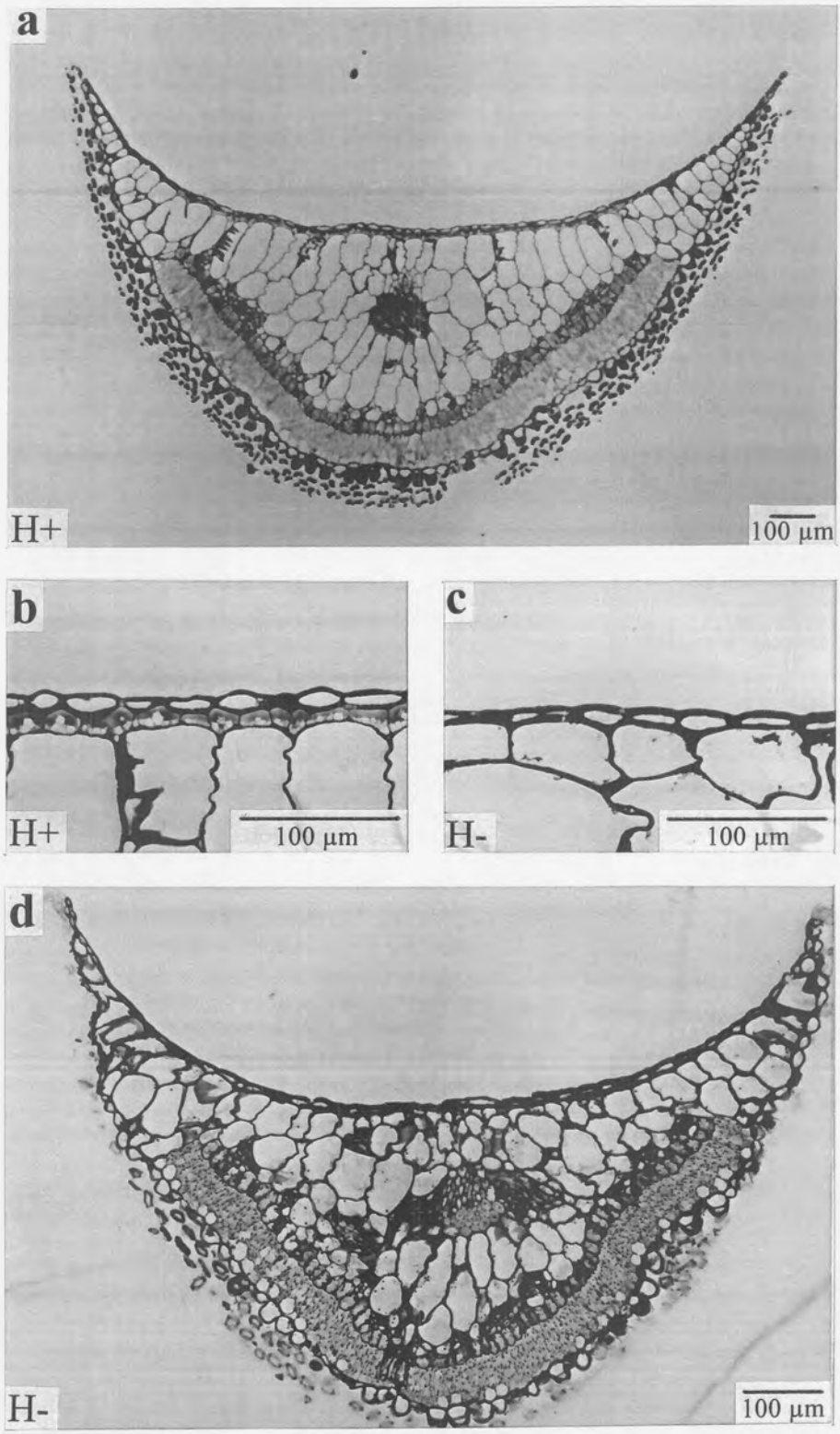


FIGURE 6.2: Leaf types. **a & b.** Leaf Type H+. **a** Internal structure of leaf. **b** Adaxial epidermis with underlying hypodermis. **c & d.** Leaf Type H-. **c** Internal structure of leaf. **d** Adaxial epidermis.

CHAPTER 7

TRICHOME CHARACTERS

7.1 INTRODUCTION

Trichomes can be of considerable systematic importance in comparative studies of angiosperms. This is mainly because trichomes are frequently present, of diverse structure and easy to observe. There are very few plants that do not have trichomes. A glabrous state can often be attributed to the early degeneration of trichomes, or to the fact that trichomes are lost shortly after maturing (Uphoff 1962; Metcalfe & Chalk 1979).

Presence or absence of trichomes has long been considered of taxonomic importance, but trichome type also holds considerable taxonomic value. Length, size and density of trichomes are more plastic and variable in response to varied environmental conditions. Therefore, the type of trichomes present on a plant is often a more reliable character to use in comparative studies and are of greater value; it can often be used to delimit species, genera and sometimes even families. Intraspecific variation in trichome type and density, found in many species, can generally be correlated to differing ecographic parameters. Simple, unbranched trichomes are extremely common amongst plants. They can be either unicellular or multicellular and can be divided into two subgroups, namely long and short trichomes. Each of these subgroups can be further subdivided into thin, basically uniseriate trichomes and thick, multiseriate trichomes (Metcalfe & Chalk 1979). Long, uniseriate trichomes are characteristic of plants growing in arid and semi-arid regions (Jordaan & Kruger 1992).

Xeromorphic plants often have hairy leaves, sometimes with distinct trichome types. It was once generally believed that the trichomes served as a physiological advantage to xerophytes, as it shields the stomata and thus reduces water loss during transpiration (Metcalfe & Chalk 1979). A dense indumentum causes a windless space around the epidermis in which the exchange of gas, including water vapour, is reduced. This reduces the amount of water that is lost during transpiration and is especially advantageous in habitats where dry winds prevail (Uphoff 1962; Fahn 1986). It has, however, been shown experimentally that this is not always the case (Metcalfe & Chalk 1983). The influence of

trichomes on the water diffusion boundary layer may be affected by the structural properties of the trichomes (Fahn 1986).

Abundant trichomes are also believed to insulate the mesophyll from excessive heat (Esau 1977). Thus trichomes can indirectly influence the water economy of plants through temperature regulation (Fahn 1986). In leaves with a dense covering of trichomes a larger part of the incident light is reflected than is the case in glabrous leaves (Uphoff 1962; Eller 1977). This prevents a sharp rise in temperature and therefor transpiration rate will not rise drastically. The indumentum decreases the damaging effect of insolation during the day by forming a light screen that protects the chlorophyll in the subtending tissue. Trichomes are clearly of special importance to plants in dry, hot environments. During the night, trichomes can even facilitate the condensation of dew, which might eventually be absorbed by the trichomes (Uphoff 1962; Fahn 1986). A prerequisite for water absorption by trichomes is the presence of living basal cells. Water absorption through trichomes during periods of drought may play a very important role in maintaining the water economy of the plant in combination with the transpiration reducing effect of a thick indumentum (Jordaan & Kruger 1992).

Young parts of plants are in the greatest need of protection and thus often have a denser indumentum than the mature parts of the same plant. This denser trichome covering on young parts can be attributed to the fact that trichomes developing on the young leaves are usually mature before the leaf is fully developed. As the leaf expands, the trichomes become less dense and may even be lost completely (Uphoff 1962).

The Chenopodiaceae family consists of a large number of xeromorphic plants, many of these having hairy leaves. Diversity of the hairy covering, formed by trichomes of various kinds, is an important family character. Trichomes of plants in this family often form a dense indumentum on the leaf surface (Metcalfe & Chalk 1983). Unicellular trichomes are not present in the Chenopodiaceae, but uniseriate ones are widely distributed (Solereder 1908; Uphoff 1962). Simple, uniseriate trichomes are commonly found in the Salsoleae. These trichomes are seated on one prominent epidermal cell or between such cells and are composed of a basal portion of one or a few thin-walled cells, and a long terminal portion consisting of one or a few thick-walled cells. Vesicular trichomes, that give rise to the so-called farinose surface, are found in many *Salsola* species. These bladder-like trichomes are of the capitate

type, but have no secretory function and consist of a unicellular or uniseriate stalk and a unicellular thin walled head that stores up water (Solereder 1908).

Hair distribution is regarded as one of the most important vegetative characters to be used when attempting a division of *Salsola* into natural groups (Botschantzev 1969a). Therefore, this and other characters of the indumentum were investigated to establish the different character states within the section *Caroxylon* of the genus in southern Africa.

In this chapter a key to the indumentum types is given, followed by a detailed description of each indumentum type. A list of species for each indumentum type is given, with an indication of the leaf type of each species. Hereafter the trichomes of each species are shortly described. For a detailed description of leaf types see Chapter 6.

7.2 RESULTS

Four main indumentum types can be identified on the basis of surface appearance. These indumentum types have been used as a secondary division (following leaf type) of the investigated species into four groups. One of the four indumentum types can be further subdivided according to the area of the leaf covered by the trichomes, and the number of elongated cells in the trichome (see Figure 7).

KEY TO INDUMENTUM TYPES

Trichomes long, round in transverse section, entangled.....*Indumentum Type 1*

Trichomes round to flattened in transverse section,
slightly adpressed to almost entangled.....*Indumentum Type 2*

Trichomes flattened in transverse section, adpressed.....*Indumentum Type 3*
Leaf margin[1] glabrate.....*Type 3a*
Trichome consisting of one elongated cell.....*Type 3a.i*
Trichome consisting of more than one elongated cell.....*Type 3a.ii*

Leaf margin not glabrate.....*Type 3b*
Trichome consisting of one elongated cell.....*Type 3b.i*
Trichome consisting of more than one elongated cell.....*Type 3b.ii*

Trichomes absent, at least on leaves.....*Indumentum Type 4*
Leaves glabrous; trichomes present on stems.....*Type 4a*

Leaves and stems glabrous.....*Type 4b*

[1] With leaf margin is meant the marginal zone consisting of an area ± 300 – 500 µm wide. This usually constitutes that part of the leaf margin zone where the palisade mesophyll and bundle sheath layers are absent.

DESCRIPTION OF INDUMENTUM TYPES

Indumentum Type 1

Trichomes non-glandular, simple, multicellular, uniseriate; long, round in transverse section, entangled, (195–) 290–595 (–765) µm long; basal cell short, elongated cells 1–3.

SPECIES POSSESSING INDUMENTUM TYPE 1 (Leaf Type in brackets)

S. araneosa (H+) *S. zeyheri* (H+)

TRICHOME DESCRIPTION OF SPECIES

S. araneosa

Trichomes (290–) 390–490 (–548) µm long; elongated cells two.

S. zeyheri

Trichomes (195–) 295–625 (–765) µm long; elongated cells 1–3.

Indumentum Type 2

Trichomes non-glandular, simple, multicellular, uniseriate; long to intermediate length, round to flattened in transverse section, slightly adpressed to almost entangled, (120–) 150–440 (–750) µm long; basal cell short, elongated cells 1–3; leaf margin sometimes glabrate, fringed; trichomes sometimes easily rubbed off.

SPECIES POSSESSING INDUMENTUM TYPE 2 (Leaf Type in brackets)

S. decussata (H-) *S. gemmata* (H-) *S. sericata* (H+)

S. dinteri (H-) *S. scopiformis* (H+)

TRICHOME DESCRIPTION OF SPECIES

S. decussata

Trichomes long to intermediate length, flattened in transverse section, (170–) 190–235 (–255) µm long; elongated cells two; leaf margin glabrate.

S. dinteri

Trichomes long, round in transverse section, 422–568 (–750) µm long; elongated cells three.

S. gemmata

Trichomes long, flattened in transverse section, (320–) 340–380 (–410) µm long; elongated cell one.

S. scopiformis

Trichomes of intermediate length to short, round to flattened in transverse section, (120–) 130–145 (–150) µm long; elongated cell one; easily rubbed off.

S. sericata

Trichomes long to intermediate length, flattened in transverse section, 200–270 (–330) µm long; elongated cell one; leaf margin glabrate, fringed.

Indumentum Type 3a.i

Trichomes non-glandular, simple, multicellular, uniseriate; long to short, flattened in transverse section, adpressed, (90–) 120–200 (–275) µm long; basal cell short, elongated cell one; leaf margin glabrate, fringed; indumentum sometimes not very dense; trichomes sometimes easily rubbed off.

SPECIES POSSESSING INDUMENTUM TYPE 3a.i (Leaf Type in brackets)

S. henriciae (H-)	*S. marginata* (H+)	*S. tuberculata* (H+)
S. kleinfonteini (H+)	*S. merxmuelleri* (H+)	*S. tuberculatiformis* (H+)

TRICHOME DESCRIPTION OF SPECIES

S. henriciae

Trichomes long to intermediate length, (170–) 215–250 (–275) µm long; indumentum not very dense.

S. kleinfonteini

Trichomes of intermediate length, (170–) 180–210 (–220) µm, long; easily rubbed off.

S. marginata

Trichomes short, (100–) 110–150 (–178) µm long.

S. merxmuelleri

Trichomes of intermediate length, (140–) 175–220 (–230) µm long; indumentum not very dense.

S. tuberculata

Trichomes of intermediate length, (100–) 125–180 (–230) µm long.

S. tuberculatiformis

Trichomes short, (90–) 100–150 (–160) µm long.

Indumentum Type 3a.ii

Trichomes non-glandular, simple, multicellular, uniseriate; long to intermediate length, flattened in transverse section, adpressed, (95–) 120–275 (–380) µm long; basal cell short, elongated cells 1–2; leaf margin glabrate, sometimes fringed; trichomes sometimes easily rubbed off.

SPECIES POSSESSING INDUMENTUM TYPE 3a.ii (Leaf Type in brackets)

S. aphylla (H+) *S. cauliflora* (H-) *S. ceresica* (H+)

TRICHOME DESCRIPTION OF SPECIES

S. aphylla

Trichomes of intermediate length, (95–) 115–210 (–260) µm long ; elongated cells 1–2.

S. cauliflora

Trichomes long to intermediate length, (200–) 210–260 (–280) µm long; elongated cells two; leaf margin fringed; easily rubbed off.

S. ceresica

Trichomes long to intermediate length, (275–) 285–370 (–380) µm long; elongated cells two.

Indumentum Type 3b.i

Trichomes non-glandular, simple, multicellular, uniseriate; long to very short, flattened in transverse section, adpressed, (80–) 120–230 (–330) µm long; basal cell short, elongated cell one; leaf margin sometimes strongly fringed; trichomes sometimes easily rubbed off.

SPECIES POSSESSING INDUMENTUM TYPE 3b.i (Leaf Type in brackets)

S. albida (H+)	*S. huabica* (H+)	*S. microtricha* (H+)	*S. robinsonii* (H+)
S. etoshensis (H+)	*S. koichabica* (H+)	*S. okaukuejensis* (H+)	*S. warmbadica* (H+)
S. giessii (H+)	*S. melanantha* (H-)	*S. patentipilosa* (H+)	

TRICHOME DESCRIPTION OF SPECIES

S. albida

Trichomes long to intermediate length, (195–) 260–300 (–330) µm long.

S. etoshensis

Trichomes of intermediate length, (140–) 145–210 (–230) µm long.

S. giessii

Trichomes of intermediate length, (158–) 180–230 (–260) µm long; leaf margin strongly fringed.

S. huabica

Trichomes long to intermediate length, (195–) 200–230 (–245) µm long.

S. koichabica

Trichomes of intermediate length, (140–) 150–180 (–188) µm long; easily rubbed off.

S. melanantha

Trichomes very short to short, (80–) 95–120 (–128) µm long.

S. microtricha

Trichomes very short, 80–100 (–108) µm long.

S. okaukuejensis

Trichomes of intermediate length, 190–220 (–230) µm long.

S. patentipilosa

Trichomes short, 105–125 (–130) µm long; easily rubbed off.

S. robinsonii

Trichomes long to intermediate length, 200–260 (–300) µm long.

S. warmbadica

Trichomes of intermediate length, (125–) 150–170 µm long.

Indumentum Type 3b.ii

Trichomes non-glandular, simple, multicellular, uniseriate; intermediate length, flattened in transverse section, adpressed, (153–) 175–215 (–238) µm long; basal cell short, elongated cells two; trichomes easily rubbed off.

SPECIES POSSESSING INDUMENTUM TYPE 3b.ii (Leaf Type in brackets)

S. acocksii (H+)

Indumentum Type 4a

Mature leaves glabrous, sometimes fringed, sometimes with trichomes on young leaves and flowers, lost during maturing; trichomes on stem long, round to flattened in transverse section, sometimes entangled.

SPECIES POSSESSING INDUMENTUM TYPE 4a (Leaf Type in brackets)

S. aellenii (H-)	*S. exalata* (H+)	*S. humifusa* (H-)	*S. seminuda* (H-)
S. apterygea (H+)	*S. gemmifera* (H+)	*S. inaperta* (H-)	*S. smithii* (H-)
S. dealata (H+)	*S. glabra* (H-)	*S. minutifolia* (H-)	
S. denudata (H-)	*S. glabrescens* (H+)	*S. rabieana* (H+)	

TRICHOME DESCRIPTION OF SPECIES

S. aellenii

Trichomes on stem flattened in transverse section.

S. apterygea

Trichomes on stem long, flattened in transverse section, entangled.

S. dealata

Leaves fringed, trichomes on young leaves; trichomes on stem at leaf bases.

S. denudata

Trichomes on stem flattened in transverse section.

S. exalata

Leaves fringed, trichomes on young leaves and flowers; trichomes on stem long, round in transverse section, entangled.

S. gemmifera

Leaves fringed; trichomes on stem long, flattened in transverse section, entangled.

S. glabra

Trichomes on young leaves; trichomes on stem long, flattened in transverse section, entangled.

S. glabrescens

Trichomes on young leaves and flowers; trichomes on stem long, flattened in transverse section, entangled.

S. humifusa

Leaves fringed; trichomes on stem long, flattened in transverse section, entangled.

S. inaperta

Leaves fringed; trichomes on stem long, flattened in transverse section, entangled.

S. minutifolia

Leaves fringed, trichomes on young leaves.

S. rabieana

Trichomes on young leaves.

S. seminuda

Trichomes on stem long, flattened in transverse section, entangled.

S. smithii

Trichomes on stem round in transverse section.

Indumentum Type 4b

Leaves and stem glabrous.

SPECIES POSSESSING INDUMENTUM TYPE 4b (Leaf Type in brackets)

S. calluna (H-)

7.3 DISCUSSION

Of the 43 native species investigated, only 15 as well as the alien *S. kali*, have glabrous mature leaves. Most of these glabrous species do, however, have trichomes on their young developing leaves and/or flowers. This can be attributed to the fact that the young developing parts are in greater need of protection and that trichomes fulfil this protective role (Uphoff 1962). These trichomes are lost during or shortly after maturing of the leaves (Uphoff 1962; Metcalfe & Chalk 1979).

Trichomes are only present on the abaxial leaf surface and completely absent from the adaxial one. There are a number of other xeromorphic plants where trichomes occur only or are much more abundant on the abaxial leaf surface (Fahn 1986). This phenomenon may have

various explanations, as well as a number of benefits. In *Salsola* it can be easily explained by the fact that the adaxial leaf surface is adpressed against the stem and thus sufficiently protected.

In some species (those with Indumentum Type 3a), trichomes mostly occur where the palisade mesophyll and bundle sheath layers are present internally and not on the leaf margins subtended only by aqueous mesophyll. Stomata of all species also occur in this area only. The palisade mesophyll and bundle sheath are the most vital tissue of the leaf necessary for photosynthesis and thus need to be protected. Aqueous mesophyll does not contain chlorophyll and is perhaps not in such a great need of protection as the two chlorophyll containing layers. Trichomes provide protection to the subtending tissue against the damaging effect of insolation and to prevent extreme water loss (Uphoff 1962; Esau 1977; Metcalfe & Chalk 1979), but is costly to produce. Thus plants can conserve energy by not producing a dense trichome covering in areas where it is not needed, such as the leaf margins in this case. This can explain the glabrate nature of the leaf margins of these species.

All trichomes in the investigated species are non-glandular, simple multicellular, uniseriate trichomes. Trichomes are seated on a prominent basal epidermal cell and contain a terminal portion consisting of one to three elongated cells. This corresponds to the commonly found trichome types in the Chenopodiaceae and Salsoleae (Solereder 1908; Uphoff 1962; Metcalfe & Chalk 1979).

The majority of species (20), especially those with shorter trichomes, only have one elongated cell (see Table 7). Most species (21) possess flattened, adpressed trichomes forming a smooth surface. Only a small number of species have trichomes that are entangled (two species) or only slightly adpressed to almost entangled (five species).

Noteworthy is the weak association between leaf type and indumentum type (see Tables 6 & 7). Both species with Indumentum Type 1, that appears to be a very dense indumentum, possess Leaf Type H+. Species with Indumentum Type 2 are more or less evenly distributed between Leaf Type H+ (two species) and Leaf Type H- (three species). This indumentum type can be seen as an intermediate type between the long entangled trichomes of Indumentum Type 1 and the adpressed trichomes of Indumentum Type 3.

In Indumentum Type 3 there are a small number of species with Leaf Type H- (only three out of a total of 21 species). These three species are *S. henriciae* (3a.i) and *S. cauliflora* (3a.ii), which are two of the nine species with Indumentum Type 3a, and *S. melanantha* (3b.i), which is one out of 12 species with Indumentum Type 3b. This difference in indumentum density between the two leaf types is clearly more pronounced in species with Indumentum Type 3b, where leaf margins are not glabrate and the overall trichome covering thus denser, than in Indumentum Type 3a.

Of the 15 indigenous glabrous species only six, namely *S. apterygea*, *S. dealata*, *S. exalata*, S. *gemmifera*, *S. glabrescens* and *S. rabieana* possess Leaf Type H+. Five of the nine glabrous species with Leaf Type H- belong to the subsection *Tetragonae*. Note that the only species in subsection *Tetragonae* with Leaf Type H+, *S. exalata*, also has glabrous leaves. This further complicates the question around the taxonomic position of this species. Other than the leaf type, the indumentum type supports the position of the species within the subsection.

In general those species possessing an adaxial hypodermis (Leaf Type H+) tend to have a denser indumentum than those species lacking an adaxial hypodermis (Leaf Type H-). This can be best seen in Indumentum Type 1 (long, entangled trichomes) where both species have an adaxial hypodermis, Indumentum Type 3 (flattened, adpressed trichomes) where the majority of species possess an adaxial hypodermis and Indumentum Type 4 (no trichomes) where the majority of species lack an adaxial hypodermis. This might be correlated to some environmental or other factors and certainly calls for further investigation.

TABLE 7: Comparison of trichome characters in southern African species of *Salsola* (Symbols are explained at the end of the table)

Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	Species	Leaf type	Indumentum type	Trichome length (µm)			Number of elongated cells			Leaf margin fringed	Trichomes easily rubbed off	Indumentum not very dense
				Min	Average	Max	1	2	3			
C	*S. araneosa*	H+	1	290	418	548		X				
C	*S. zeyheri*	H+	1	195	456	765	X	X	X			
C	*S. scopiformis*	H+	2	120	138	150	X				X	
C	*S. sericata*	H+	2	200	244	330	X			X		
C	*S. kleinfonteini*	H+	3a.i	170	193	220	X				X	
C	*S. marginata*	H+	3a.i	100	130	178	X					
C	*S. merxmuelleri*	H+	3a.i	140	191	230	X					X
C	*S. tuberculata*	H+	3a.i	100	152	230	X					
C	*S. tuberculatiformis*	H+	3a.i	90	131	160	X					
C	*S. aphylla*	H+	3a.ii	95	163	260	X	X				
C	*S. ceresica*	H+	3a.ii	275	335	380		X				
C	*S. albida*	H+	3b.i	195	272	330	X					
C	*S. etoshensis*	H+	3b.i	140	181	230	X					
C	*S. giessii*	H+	3b.i	158	205	260	X			XX		
C	*S. huabica*	H+	3b.i	195	218	245	X					
C	*S. koichabica*	H+	3b.i	140	166	188	X				X	
C	*S. microtricha*	H+	3b.i	80	93	108	X					
C	*S. okaukuejensis*	H+	3b.i	190	206	230	X					

Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	Species	Leaf type	Indumentum type	Trichome length (µm)			Number of elongated cells			Leaf margin fringed	Trichomes easily rubbed off	Indumentum not very dense
				Min	Average	Max	1	2	3			
C	*S. patentipilosa*	H+	3b.i	105	116	130	X				X	
C	*S. robinsonii*	H+	3b.i	200	234	300	X					
C	*S. warmbadica*	H+	3b.i	125	152	170	X					
C	*S. acocksii*	H+	3b.ii	153	190	238		X			X	
C	*S. apterygea*	H+	4a	-	-	-	-	-	-			
C	*S. dealata*	H+	4a	-	-	-	-	-	-	X		
C	*S. gemmifera*	H+	4a	-	-	-	-	-	-	X		
C	*S. glabrescens*	H+	4a	-	-	-	-	-	-			
C	*S. rabieana*	H+	4a	-	-	-	-	-	-	X		
C	*S. dinteri*	H-	2	422	526	750			X			
C	*S. gemmata*	H-	2	320	367	410	X					
C	*S. cauliflora*	H-	3a.ii	200	234	280		X		X	X	
C	*S. melanantha*	H-	3b.i	80	106	128	X					
C	*S. denudata*	H-	4a	-	-	-	-	-	-			
C	*S. glabra*	H-	4a	-	-	-	-	-	-			
C	*S. seminuda*	H-	4a	-	-	-	-	-	-			
C	*S. calluna*	H-	4b	-	-	-	-	-	-			
T	*S. exalata*	H+	4a	-	-	-	-	-	-	X		
T	*S. decussata*	H-	2	170	211	255		X				X

Subsection (following Botschantzev 1974c; 1978; 1981; 1983)	Species	Leaf type	Indumentum type	Trichome length (µm)			Number of elongated cells			Leaf margin fringed	Trichomes easily rubbed off	Indumentum not very dense
				Min	Average	Max	1	2	3			
T	*S. henriciae*	H-	3a.i	170	232	275	X					
T	*S. aellenii*	H-	4a	-	-	-	-	-	-			
T	*S. humifusa*	H-	4a	-	-	-	-	-	-	X		
T	*S. inaperta*	H-	4a	-	-	-	-	-	-	X		
T	*S. minutifolia*	H-	4a	-	-	-	-	-	-	X		
T	*S. smithii*	H-	4a	-	-	-	-	-	-			
S	*S. kali*	H+	4a	-	-	-	-	-	-			

Subsection: C = *Caroxylon*; T = *Tetragonae;* S = alien species from Section *Salsola*

Leaf type: H+ = with adaxial hypodermis; H- = without adaxial hypodermis

Trichome type: 1 = trichomes long, round in transverse section, entangled; 2 = trichomes round to flattened in transverse section, slightly adpressed to almost entangled; 3a.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin glabrate; 3a.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin glabrate; 3b.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin not glabrate; 3b.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin not glabrate; 4a = Leaves glabrous, trichomes on stems; 4b = leaves and stems glabrous

X = character state present

XX = character state very prominent

- = character state not applicable (trichomes absent)

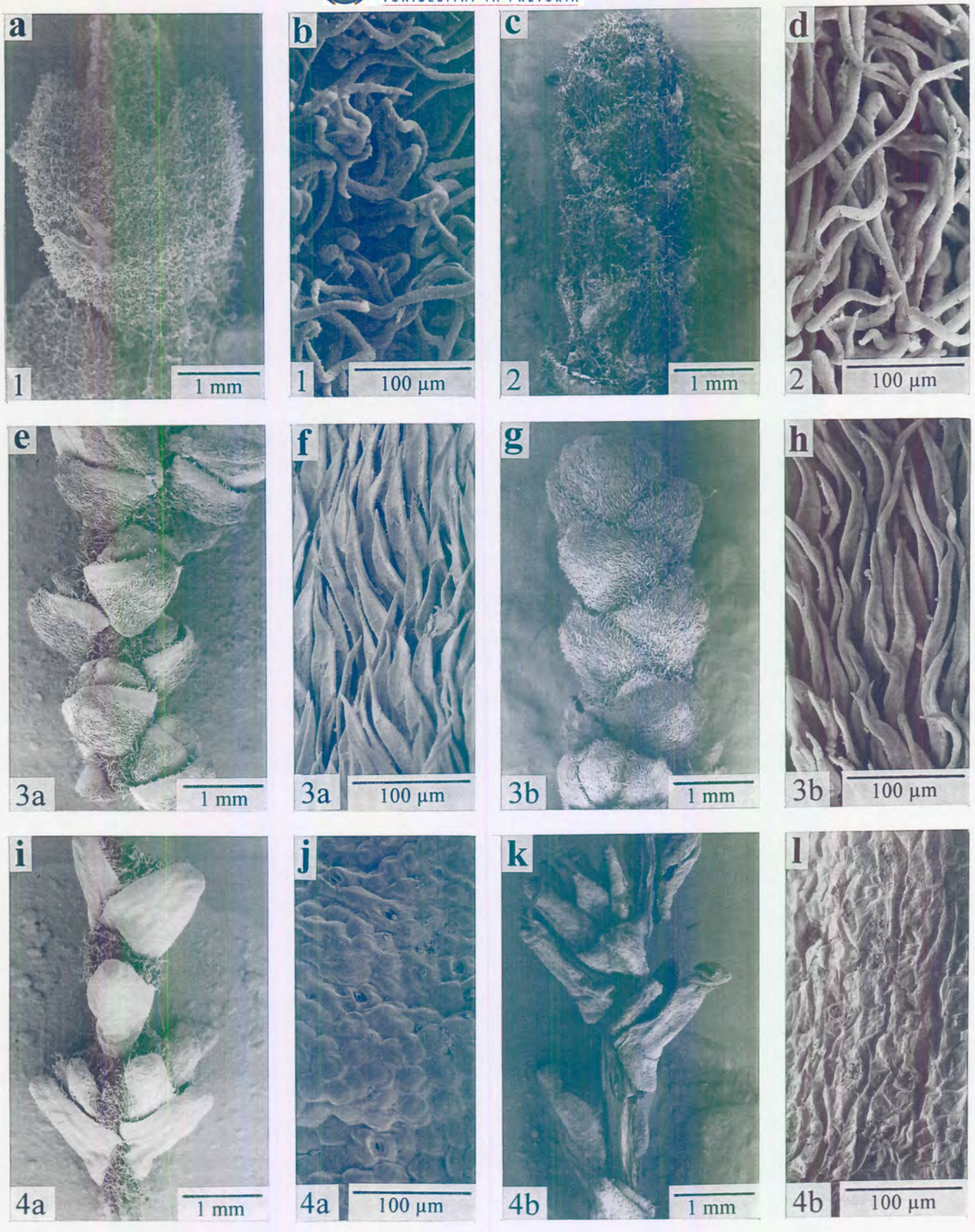


FIGURE 7: Indumentum types. **a & b.** Indumentum Type 1. **c & d.** Indumentum Type 2. **e & f.** Indumentum Type 3a. **g & h.** Indumentum Type 3b. **i & j.** Indumentum Type 4a. **k & l.** Indumentum Type 4b.

CHAPTER 8

GENERAL DISCUSSION AND KEY TO THE SPECIES

There are many taxonomic uncertainties within southern African members of *Salsola*, section *Caroxylon* (see Chapter 1). This is mainly due to the fact that the genus was initially not studied as an entity, but rather in the framework of the whole family, leading to the proposal of many artificial systems for the genus, that were almost all rejected (See Chapter 4). A further problem is the fact that the majority of the work done on southern African members of the genus was done outside of southern Africa with little or no fieldwork in the region. This is illustrated by the 69 species newly described from herbarium specimens by the Russian Victor Botschantzev in St Petersburg. Hitherto, very little taxonomic work has been done on the genus based on living plants and under natural conditions.

It is extremely difficult to distinguish between some of the proposed species of *Salsola* occurring in southern Africa, as they are morphologically very similar. The most recent key available for the southern African species is that of Botschantzev (1974c). This key relies heavily on fruit and flower characters. These characters are, however, not always visible on herbarium specimens as *Salsola* species only flower briefly during favourable climatic conditions. This renders the key of very little practical value for routine identification. A further drawback is the fact that no less than 21 new species was described (Botschantzev 1978, 1981, 1983) since the publication of this key (see Chapter 1 & 4).

Members of *Salsola* are of great agricultural, economic and ecological importance (see Chapter 3) and are a crucial component of Karoo vegetation. The great similarity between most southern African *Salsola* species and the uncertainty as to the exact identity of most species described by Botschantzev (see Chapter 1 & 4) is, with right, a major cause for concern, as it hampers research and management efforts where *Salsola* species are involved.

Botschantzev (1969a) states that the two most important characters to use when dividing the genus *Salsola* into natural groups are form and shape of the foliage leaves, and trichome distribution. The present investigation into leaf anatomy and indumentum composition of selected southern African *Salsola* species does indeed indicate that different groups exist within the section *Caroxylon*. Two leaf types and four main indumentum types

were identified. One indumentum type can be further subdivided on the basis of trichome distribution.

Species displaying Leaf Type H+ is by far the larger of the two groups, comprising 28 of the 43 investigated indigenous species. Of these 28 species all but one, *S. exalata*, belong to subsection *Caroxylon* (plants with alternate phylotaxis). The remaining 15 investigated native species possess Leaf Type H-. The latter leaf type is present in both subsections *Caroxylon* and *Tetragonae* (plants with opposite phylotaxis). Seven of the eight investigated species in subsection *Tetragonae*, however, possess Leaf Type H-. The only exception is *S. exalata* which possess Leaf Type H+. This association between leaf type and subsection may well be significant. However, work needs to be done on the remaining species not covered by this study to establish their leaf type, especially in subsection *Tetragonae*. The fact that *S. exalata* is the only species in this subsection with Leaf Type H+ raises questions about its position within the subsection. This certainly calls for a thorough investigation of this species, starting with the phylotaxis, as this is the main character used by Botschantzev to delimit the existing subsections.

The two largest indumentum types are Type 3b.i with 11 species and Type 4a with 14 species. The other indumentum types all consist of between one and six species. There is a weak association between indumentum type and subsection. Indumentum types are fairly evenly distributed in subsection *Caroxylon*, with all types occurring in this subsection. The investigated species of this subsection amounts to two species with Indumentum Type 1, four species with Indumentum Type 2, three species with Indumentum Type 3a.i, five species with Indumentum Type 3a.ii, 11 species with Indumentum Type 3b.i, one species with Indumentum Type 3b.ii, eight species with Indumentum Type 4a and one species with Indumentum Type 4b. In subsection *Tetragonae* Indumentum Types 1, 3a.ii, 3b.i, 3b.ii and 4b were not found. This smaller subsection contains one species with Indumentum Type 2, one species with Indumentum Type 3a.i and six species with Indumentum Type 4a. An association between indumentum type and subsection can therefore be most clearly seen in the two largest indumentum types. Indumentum Type 3b is entirely restricted to subsection *Caroxylon*, whereas six of the eight species investigated in subsection *Tetragonae* possess Indumentum Type 4a. The greatest majority of species in the latter subsection are thus

glabrous. However, the indumentum of the species in subsection *Caroxylon* varies from long entangled trichomes, through short adpressed trichomes to completely glabrous plants.

The association between leaf type and indumentum type is more pronounced. Only six of the 28 investigated species with trichomes possess Leaf Type H-, whereas nine of the 15 glabrous species possess Leaf Type H-. The six species with trichomes comprise three species with Indumentum Type 2, one species with Indumentum Type 3a.i, one species with Indumentum Type 3a.ii and one species with Indumentum Type 3b.i. These species mostly have glabrate leaf margins, an indumentum that is not very dense or trichomes that are rubbed off easily (see Table 7). There is therefore a general trend in species with an adaxial hypodermis to have a denser covering of trichomes than those without an adaxial hypodermis. This might be taxonomically very useful if an association can be found between leaf type and some other morphological or ecological character of the genus.

Leaf and indumentum types seem to be evenly distributed throughout the geographical range of the genus. No clear correlation could be found between these types and any other character. However, the limited amount of material used did not permit a thorough exploration of possible associations. Further investigations should focus on this aspect. Possible characters to be taken into account are geographical distribution of species in terms of climate, soil type, geology and topography and vegetation type; other anatomical characters of the leaves, flowers and fruit; and possibly even chemical constituents, palatability and the extend to which each species is utilised by livestock.

Although some species possess characters that clearly distinguish them from others, there exists no clear delimitation of most of the species within especially leaf and also indumentum types. All species can be easily grouped according to leaf and indumentum type. Some of these groups, however, contain a large number of species that is not always easily distinguished from each other, e.g. the group Leaf Type H+ with Indumentum Type 3bi consists of ten very similar species. Within each species, anatomy and macro-morphology seem homogenous, even in samples widely separated geographically. The species that showed the most variation during this study was *S. aphylla*. This species has a very wide and varied geographical range and the samples used were from vastly separated locations. For other species material was only available from very small areas and sometimes most probably

the same location. In future, more material throughout the range of each species should be studied. Only then may it be possible to demarcate groups within species, that might well be correlated with geographical distribution. Further investigation into this aspect is necessary, but it is important to remember that each species first needs to be clearly delimited, before infraspecific groups can be demarcated.

The second character used by Botschantzev (1974c), after phylotaxis, to divide the South African and Namibian species into major groups is the presence or absence of wings in the fruiting perianth. In subsection *Caroxylon* the only two investigated species without fruiting perianth wings are *S. apterygea* and *S. dealata*, both with Leaf Type H+. *S. cauliflora*, with Leaf Type H-, is the only species with dimorphic flowers and fruit and thus contains both fruit with wings and fruit without wings. In subsection *Tetragonae* only one of the investigated species, *S. humifusa* (Leaf Type H-), has fruit with wings according to Botschantzev (1972). Earlier references, however, state that the fruiting perianth of this species is without wings (Verdoorn 1963) and merely refers to indurated basal lobes of the fruiting perianth that were considered to be homologous to the fruiting perianth wings of other *Salsola* species (Bruce *et al.* 1951). This needs to be looked at in order to clarify the discrepancies that currently exist. The remaining seven investigated species of subsection *Tetragonae* do not have winged fruit. Winged fruit can thus be used as a possible indication of subsection, as the majority of species that lack a winged fruiting perianth is sorted into subsection *Tetragonae*. However, because subsection *Caroxylon* does contain a number of species with wingless fruit and subsection *Tetragonae* does contain a few species with winged fruit, this cannot be used as a generalisation. Further subtracting from the value of wings as a diagnostic character is the fact that wings only develop on the mature perianth and at some stages of development it cannot be determined whether a specimen will have wings or not (Verdoorn 1963). Unfortunately the presence or absence of a winged fruiting perianth does not show any clear association with the leaf types or indumentum types identified during this study. It is, nevertheless, noteworthy that both species in subsection *Caroxylon* with wingless fruit possess Indumentum Type 4a, as does five of the seven species with wingless fruit in subsection *Tetragonae* (see Figure 8).

No great discrepancies were found between indumentum type assessed during this study and those given by Botschantzev and other authors (Wright 1901; Bruce *et al.* 1951;

Verdoorn 1963; Botschantzev 1972, 1973, 1974a, 1974b, 1974d, 1978, 1981, 1983). For example, the indumentum of *S. zeyheri* and *S. araneosa* is described as 'densely pubescent with fairly long smooth curly tangled patent hairs' (Botschantzev 1974d). This clearly corresponds to Indumentum Type 1 (see Chapter 7). The indumentum of most species is generally described as 'sparsely or densely pubescent with short smooth thickened straight appressed hairs' (Botschantzev 1972, 1973, 1974a, 1974d, 1978, 1981, 1983). This corresponds to Indumentum Type 3 (see Chapter 7), that is, with 22 species, by far the largest of the four main indumentum types. The pubescent juvenile and glabrous mature leaves of species with Indumentum Type 4a also correspond with the descriptions of other authors (Bruce *et al.* 1951; Verdoorn 1963; Botschantzev 1972, 1973, 1974a, 1974b, 1974d). *S. calluna* is described as having glabrous leaves and stems, corresponding to Indumentum Type 4b (Wright 1901).

An important aspect that has been highlighted by this study is the exact anatomical structure of the leaves in southern African members of *Salsola*. Indigenous species of section *Caroxylon* show a variation on the typical Salsoloid-type Kranz-anatomy as described by Carolin *et al.* (1975) for northern hemisphere species, like *S. kali*. In southern African *Salsola* the palisade mesophyll and bundle sheath are not continuous around the leaf, but only present abaxially. This feature can be ascribed to the difference in the leaf shape between southern and northern hemisphere species (see Chapter 6).

The main aim of this study was to contribute towards the systematics of the genus *Salsola* in southern Africa and in particular to find additional characters which may facilitate the identification of the different species. During this study the leaf anatomy and macro-morphology proved to be very helpful for dividing the section *Caroxylon* into groups. In this respect the presence or absence of the adaxial hypodermis may be an important character to assist in the grouping and identification of species. It is unfortunately not very easily observed without the aid of at least hand sections or epidermal peels and simple colouring techniques. It could, nevertheless, be used as the basis of an identification system, especially if it can be correlated with some other more visible characters. The possible existence of such characters and their potential taxonomic significance calls for further investigation.

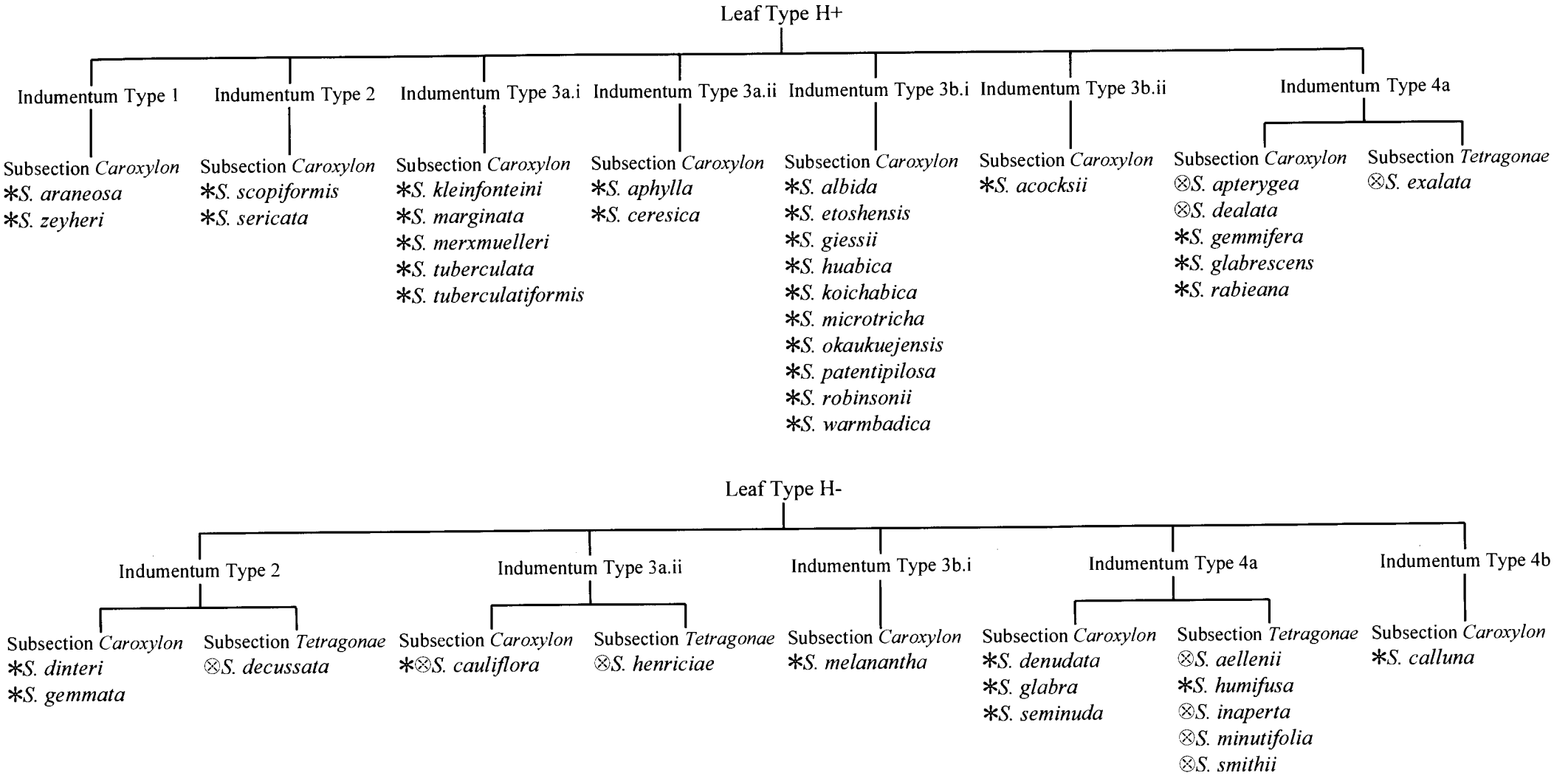


FIGURE 8: Diagrammatic representation of the grouping of investigated species of *Salsola* according to leaf and indumentum types, incorporating subsections and fruit types. (Subsections and fruit types according to Botschantzev 1972, 1973, 1974a, 1974b, 1974d, 1978, 1981, 1983)

KEY TO THE INVESTIGATED SPECIES OF *SALSOLA* BASED ON LEAF AND INDUMENTUM TYPE

1. Leaves with a uniseriate hypodermis underlying adaxial epidermis (Leaf Type H+).....2

   Leaves without a hypodermis layer underlying adaxial epidermis (Leaf Type H-).....15

2. Leaves with trichomes.....3

   Leaves glabrous (Indumentum Type 4).....13

3. Trichomes long (290–595 µm), round in transverse section, entangled (Indumentum Type 1).....*S. araneosa*
   S. zeyheri

   Trichomes not long, round in transverse section, entangled.....4

4. Trichomes round to flattened in transverse section, slightly adpressed to almost entangled (Indumentum Type 2).....5

   Trichomes flattened in transverse section, adpressed (Indumentum Type 3).....6

5. Trichomes intermediate length to short (130–145 µm), round to flattened in transverse section, easily rubbed off.....*S. scopiformis*

   Trichomes long to intermediate length (200–270 µm), flattened in transverse section, leaf margin glabrate, fringed.....*S. sericata*

6. Leaf margin glabrate (Indumentum Type 3a).....7

   Leaf margin not glabrate (Indumentum Type 3b).....9

7. Trichomes consisting of one elongated cell (Indumentum Type 3a.i).....8

   Trichomes consisting of more than one elongated cell (Indumentum Type 3a.ii)...*S. aphylla*
   S. ceresica

8. Trichomes of intermediate length (135–200 µm).....*S. kleinfonteini*
   S. merxmuelleri
   S. tuberculata

   Trichomes short (110–150 µm).....*S. marginata*
   S. tuberculatiformis

9. Trichomes consisting of one elongated cell (Indumentum Type 3b.i).....10

   Trichomes consisting of more than one elongated cell (Indumentum Type 3b.ii).*S. acocksii*

10. Trichome long to intermediate length (145–230 µm).....11

    Trichomes short to very short (90–140 µm).....12

11. Leaf margin strongly fringed.....*S. giessii*

    Leaf margin not strongly fringed.....*S. albida*
    S. etoshensis
    S. huabica
    S. koichabica
    S. okaukuejensis
    S. robinsonii
    S. warmbadica

12. Trichomes very short (80–100 µm)..... *S. microtricha*

Trichomes short (105–125 µm)..... *S. patentipilosa*

13. Leaf margin fringed..... 14

Leaf margin not fringed..... *S. apterygea*
S. glabrescens
S. rabieana

14. Phylotaxis alternate (Subsection *Caroxylon*)..... *S. dealata*
S. gemmifera

Phylotaxis opposite (Subsection *Tetragonae*)..... *S. exalata*

15. Leaves with trichomes..... 16

Leaves glabrous (Indumentum Type 4)..... 21

16. Trichomes round to flattened in transverse section, slightly adpressed to almost entangled (Indumentum Type 2)..... 17

Trichomes flattened in transverse section, adpressed (Indumentum Type 3)..... 19

17. Leaf margin glabrate..... *S. decussata*

Leaf margin not glabrate..... 18

18. Trichomes round in transverse section..... *S. dinteri*

Trichomes flattened in transverse section..... *S. gemmata*

19. Leaf margin glabrate (Indumentum Type 3a)..... 20

Leaf margin not glabrate (Indumentum Type 3b)..... *S. melanantha*

20. Trichomes consisting of one elongated cell (Indumentum Type 3a.i)..... *S. henriciae*

Trichomes consisting of more than one elongated cell (Indumentum Type 3a.ii)..... *S. cauliflora*

21. Leaves and stems glabrous (Indumentum Type 4b)..... *S. calluna*

Leaves glabrous, trichomes on stems (Indumentum Type 4a)..... 22

22. Leaf margin fringed..... 23

Leaf margin not fringed..... 24

23. Palisade mesophyll and bundle sheath continuous over midrib of leaf..... *S. humifusa*
S. minutifolia

Palisade mesophyll and bundle sheath absent over midrib of leaf..... *S. inaperta*

24. Phylotaxis alternate (Subsection *Caroxylon*)..... *S. denudata*
S. glabra
S. seminuda

Phylotaxis opposite (Subsection *Tetragonae*)..... *S. aellenii*
S. smithii

CHAPTER 9

CONCLUSIONS

- Members of the genus *Salsola* are of considerable importance as pasture plants in the Karoo, especially during the winter months and during periods of prolonged drought.

- Some species also have medicinal and other valuable ecological and economic properties.

- Not all *Salsola* species are purely beneficial. Some species may cause diseases and deficiencies in livestock, leading to high mortalities and considerable financial loss.

- Most negative effects of *Salsola* species can be avoided to a great extend, providing that the harmful species are quickly and easily identified.

- Because of the occurrence of harmful and beneficial species within the same area, correct identification of the different species is of extreme importance. This is, however, rendered problematic by the frustrating morphological similarity of almost all southern African *Salsola* species.

- There is a great need for a system of easy identification that can be used in the herbarium as well as in the field. This is especially so since the existing key of V.P. Botschantzev (1910–1990) cannot be used to identify sterile specimens and because several new species were described since the publication of this key.

- There exists great uncertainty as to the exact identity of most of the 69 species newly described by Botschantzev. Many of the names have therefore hardly been taken up and used by South African botanists.

- Many species are only known from their type location. More material needs to be investigated in order to determine whether or not these are distinct species.

- A clear delimitation of the different character states within the genus would greatly facilitate and enhance the process of solving the systematic problems that exist within the genus.

- Leaf anatomy and indumentum composition proved to be very useful for delimiting groups within the section *Caroxylon* of the genus *Salsola* in southern Africa.

- Two main leaf types were identified, based on the presence or absence of a uniseriate adaxial hypodermis. Leaf Type H+ — leaves possess a uniseriate adaxial hypodermis; Leaf Type H- — leaves do not possess an adaxial hypodermis.

- There is a weak association between leaf type and subsection, with species from subsection *Tetragonae* mostly possessing Leaf Type H-. The only investigated species from this subsection with Leaf Type H+ is *S. exalata*.

- Four main indumentum types were identified, based on surface appearance. One of these can be further subdivided according to the area of the leaf covered by the trichomes and the number of elongated cells in the trichome.

- These indumentum types correspond to the characters of the indumentum given by Botschantzev and other authors in their description of each species.

- All indumentum types are present in subsection *Caroxylon*, while Indumentum Types 1, 3a.ii, 3b.i, 3b.ii and 4b are absent in subsection *Tetragonae*.

- The indumentum of the species in subsection *Caroxylon* varies from long entangled trichomes, through short adpressed trichomes to completely glabrous plants. The greatest majority of species in subsection *Tetragonae*, however, are glabrous.

- There is a weak association between leaf type and indumentum type. Species with Leaf Type H+ generally tend to have a denser indumentum than species with Leaf Type H-.

- There is no clear association between fruit type and leaf or indumentum type.

- Only one of the investigated species from subsection *Tetragonae* has winged fruit, while the other seven species have wingless fruit. This one species, *S. humifusa*, has, however, been previously described as having wingless fruit. Only two species from subsection *Caroxylon*

has wingless fruit, both of them possessing Indumentum Type 4a. *S. cauliflora* (subsection *Caroxylon*, Leaf Type H-) is the only species with dimorphic flowers and fruit.

- The leaf anatomy of southern African *Salsola* species shows a variation on the typical Salsoloid-type Kranz-anatomy, in that the palisade mesophyll and bundle sheath are not continuous around the leaf, but only present abaxially.

- Further studies should concentrate on possible associations between leaf type and other anatomical or ecological characters. If leaf type can be correlated with other important and possibly more visible attributes, then this character can be used as the basis of an improved classification and identification system for the southern African *Salsola* species.

SUMMARY

Leaf structure in southern African species of *Salsola* L. (Chenopodiaceae)

by

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Magister Scientiae

Salsola L. is one of the largest genera within the Chenopodiaceae. It has been suggested that almost 90 species occur in southern Africa where the plants are most conspicuous in karroid areas. Members of *Salsola* are of considerable importance as pasture plants in the Karoo, especially during winter and periods of prolonged drought. Some species also have medicinal and other valuable properties. However, not all *Salsola* species are beneficial; some may cause diseases and deficiencies in livestock, leading to high mortalities and severe financial loss. Because of the occurrence of harmful and beneficial species within the same area, correct identification of the different species is of extreme importance. Correct identification is, however, rendered problematic by the great morphological similarity of almost all southern African *Salsola* species and uncertainties concerning the infrageneric classification of the group.

There is a great need for a system of easy identification that can be used in the herbarium as well as in the field. This is especially so since available keys to the group cannot be used to identify sterile specimens. There also exists great uncertainty as to the exact identity of most of the 69 new species described by V.P. Botschantzev (Komarov Botanical Institute, St Petersburg) between 1972 and 1983. For this reason many of the names have hardly been taken up and used by South African botanists. A clear delimitation of the different character states within the

genus would greatly facilitate and enhance the process of solving the systematic problems that exist within the genus.

A comparative anatomical study of the leaves of southern African *Salsola* species was conducted using LM and SEM techniques. Leaf anatomy proved to be very useful for delimiting groups within the genus. Of particular importance is the structure of the leaf in transverse section and the type of the indumentum.

The investigated species can be primarily divided into two main leaf types, according to the presence or absence of a uniseriate hypodermis underlying the adaxial epidermis. A secondary division can be made by indumentum types. Four main indumentum types have been identified based on the appearance of the abaxial leaf surface. One of these indumentum types can be further subdivided according to the area of the leaf covered by trichomes and the number of elongated cells in the trichomes.

There is a weak association between leaf type and subsection, as well as between leaf type and indumentum type. No obvious association could be found between leaf or indumentum type and fruit type or any other macromorphological character. Further investigation in this respect is required.

In general the species possessing an adaxial hypodermis tend to have a denser covering of trichomes than those species lacking one. This denser indumentum probably provides the plants with better insulation to help prevent excessive water loss and to protect subtending tissues from extreme heat in their arid environment. When studied in combination with other anatomical and ecological evidence these characteristics might prove to be very useful to help establish a classification system whereby *Salsola* species can be more easily identified.

Blaarstruktuur in Suider-Afrikaanse spesies van *Salsola* L. (Chenopodiaceae)

deur

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Salsola L. is een van die grootste genusse in die Chenopodiaceae. Daar word beweer dat bykans 90 spesies in suider-Afrika voorkom, hoofsaaklik in karoo-agtige gebiede. *Salsola*-spesies is van groot belang as weidingsplante in die Karoo, veral gedurende die winter en langdurige droogtes. Sommige spesies beskik ook oor medisinale en ander waardevolle eienskappe. Nie alle *Salsola*-spesies is egter voordelig nie. Sommige spesies kan lei tot siektes en tekorte in vee, wat hoë vrektesyfers en groot finansiële verliese tot gevolg kan hê. Aangesien skadelike en voordelige spesies in dieselfde gebiede voorkom, is korrekte identifikasie van die verskillende spesies van uiterste belang. Korrekte identifikasie word egter bemoeilik deur die groot morfologiese ooreenkomste tussen bykans alle Suider-Afrikaanse *Salsola*-spesies en die onsekerhede oor die infrageneriese klassifikasie van die groep.

Daar bestaan 'n groot behoefte vir 'n maklike identifikasie-metode wat in die herbarium sowel as in die veld gebruik kan word. Dit is veral die geval aangesien die bestaande sleutels nie gebruik kan word om steriele eksemplare te identifiseer nie. Daar bestaan ook groot onsekerheid oor die presiese identiteit van meeste van die 69 nuwe spesies wat tussen 1972 en 1983 deur V.P. Botschantzev (Komarov Botaniese Instituut, St Petersburg) beskryf is. Gevolglik is baie van die voorgestelde name kwalik deur Suid-Afrikaanse plantkundiges opgeneem en gebruik. 'n Duidelike beskrywing en omgrensing van die verskillende

kenmerkstate in die genus behoort grootliks te help om die taksonomiese probleme wat in die genus bestaan op te los.

'n Vergelykende anatomiese ondersoek van die blare van Suider-Afrikaanse *Salsola*-spesies is uitgevoer deur middel van LM en SEM tegnieke. Blaaranatomie blyk baie nuttig te wees vir die onderskeiding van groepe in die genus. Veral van groot belang is die struktuur van die blaar in dwars deursnee en die tipe indumentum.

Die ondersoekte spesies kan primêr verdeel word in twee hoof blaartipes, na aanleiding van die teenwoordigheid of afwesigheid van 'n uniseriale hipodermis direk onder die adaksiale epidermis. 'n Sekondêre verdeling kan gemaak word op grond van indumentumtipes. Vier hoof indumentumtipes is geidentifiseer op grond van die uitbeelding van die abaksiale blaaroppervlak. Een van hierdie indumentumtipes kan verder onderverdeel word na aanleiding van die deel van die blaar wat deur trigome bedek word en die aantal verlengde selle in die trigoom.

Daar is 'n swak assosiasie tussen blaartipe en subseksie, sowel as tussen blaartipe en indumentumtipe. Geen ooglopende verwantskap kon tussen blaar- of indumentumtipe en vrugtipe of enige ander makromorfologiese kenmerk gevind word nie. Verdere navorsing in hierdie opsig is nodig.

In die algemeen neig spesies wat wel 'n adaksiale hipodermis besit om 'n digter haarkleed te hê as spesies sonder een. Hierdie digter indumentum verskaf waarskynlik aan die plante beter isolasie en help om oortollige water verlies in hul ariede omgewings te beperk en om die onderliggende weefsel teen uiterste hitte te beskerm. Wanneer hierdie eienskappe in kombinasie met ander anatomiese en ekologiese kenmerke ondersoek word, sou dit waarskynlik bydra om 'n klassifikasiesisteem daar te stel waarmee *Salsola* spesies makliker geidentifiseer kan word.

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CURRICULUM VITAE

Ronell Renett Klopper (née Visser) was born on 26 January 1974 in Randfontein, Gauteng. She completed her primary education at Laerskool Impala (1980–1986) in Kempton Park, Gauteng and her secondary education at Hoërskool Kempton Park (1987–1991), obtaining distinctions in English and Geography in matric.

In 1992 she started her tertiary education at the University of Pretoria and obtained her BSc (Natural Sciences)-degree *cum laude* in 1994, with Botany and Zoology as majors and Archaeology as a third major. In her third year she received the Margaretha Mes Award for the best female third year student in Botany. She completed her BSc(Hons)-degree in Botany (Taxonomy) in 1995 and was awarded the degree *cum laude*. For her achievement in this degree she was awarded the HGWJ Schweickerdt-medal for the best honours student in the department of Botany with a project in a field other than plant physiology, as well as a Certificate for Outstanding Achievement as the best honours student for that year in the Faculty of Biological and Agricultural Sciences.

Ronell is interested in nature, palaeontology, geology, numismatics and philately, and collects semi-precious stones and minerals, stamps, old money and books. She is a member of the Fern Society of Southern Africa (FSSA) and is currently the editor of *Pteridoforum*, the journal of the FSSA. She is married to Arrie Klopper, currently an MSc student in Genetics at UP.

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APPENDIX

DISTRIBUTION MAPS

These distribution maps of all investigated species were compiled according to specimens housed at the National Herbarium in Pretoria (PRE), the HGWJ Schweickerdt Herbarium at the University of Pretoria (PRU) and the herbarium at the Grootfontein Agricultural College, Middelburg, Eastern Cape Province.