CACTACEAE Juss.

(Cactus family; *Kaktusfamilie*)

by

P.J.D Winter, H.G. Zimmerman and B.K. Mashope

Perennial herbs, shrubs, trees or climbers with variously modified, mostly succulent stems, often spiny; spines, branches, flowers and often glochidia (in subfamily Opuntioideae) arise from raised or sunken cushions (areoles). **Leaves** rudimentary or absent, rarely well-developed, persistent (*Pereskia*), succulent, those of the brachyblasts (short shoots/areoles) mostly modified into bristles, spines or glochidia. **Flowers** bisexual, actinomorphic, or rarely zygomorphic, axillary, sessile or rarely pedunculate (*Pereskia*), one or rarely more per areole. **Tepals** numerous, in a graded series from scale-like, through foliaceous to petaloid, free. **Stamens** usually numerous, in several rows, arising in calyx throat, sometimes adnate to base of tepals; anthers 2-locular. **Ovary** mostly submerged in a pericarpel of peduncular origin that often extends above the ovary into a hypanthium, inferior (except in some *Pereskia* spp.), 1-locular; ovules many on 3–20 parietal placentas; style terminal, simple; stigmas as many as placentas. **Fruit** a berry, rarely dry, naked, scaly, hairy, bristly or spiny, indehiscent or variously dehiscent. **Seeds** many, sometimes strophiolate, in subfamily *Opuntioideae* entirely encased by an often pale bone-coloured aril (funicular envelope); testa smooth, shiny, or tuberculate, often black-brown (virtually black).

References: Barthlott & Hunt (1993), Anderson (2001), N.P. Taylor (*pers. comm*.).

Members of Cactaceae are primarily characterised by the presence of areoles, and all except the most primitive members have the ovary enveloped in a pericarpel. They typically have fleshy, leafless, often spiny, photosynthetic stems (long shoots), and showy, sessile flowers. *Pereskia* Mill. is an exception, with well-developed leaves along non-fleshy stems, and a branching inflorescence with 'pedicellate' flowers (Barthlott & Hunt, 1993; Anderson, 2001). The roots can be fibrous or tuberous, e.g. *Peniocereus* (A.Berger) Britton & Rose. Fleshy stems have diversified into a wide spectrum of forms, branched or unbranched. The branches are cylindric or columnar, often ribbed, sometimes winged or flattened, often segmented and variously adorned with hairs and/or (more usually) spines. Where leaves are present, e.g. in *Austrocylindropuntia subulata* (Muehlenpf.) Backeb., (Fig. 94), they are spirally arranged, simple, entire and without stipules. Leaves, scales, calyx and corolla often form a more or less continuous gradation of organs from ± foliar to petaloid. The flowers are zoophilous.

Fig. 94. Leaves of *Austrocylindropuntia subulata* (Muehlenpf.) Backeb.
(Picture by Helmuth G. Zimmermann)

In response to extreme habitats, the Cactaceae have also evolved special physiological traits which relate to nocturnal stomatal opening and a Crassulacean Acid Metabolism (CAM) photosynthetic pathway (as well as CAM-cycling), leading to efficient use of limited soil water. Special water storage cells are found in the inner cortex or in the pith of most species. They act as water reservoirs and release water when the plants are water stressed. In addition, the photosynthetic stems of many species contain large quantities of mucilage (a hydrophilic carbohydrate) found in the inner cortex and pith which also affects water relations. The thick layer of white spines found in several species e.g. *Cylindropuntia fulgida* (Engelm.) F.M.Knuth (Fig. 95) reflects incident sunlight and has a cooling effect. Many Cactaceae have a high tolerance for high temperatures. Of several species that have been assessed quantitatively, the tolerated high temperature averaged 68°C. Metabolic processes are severely curtailed in most plants at temperatures of 55 to 60°C. (Nobel, 1988). The roots of most cacti living in xerophytic conditions are shallow, no deeper than 15-30 cm below the soil surface but often extending laterally for considerable distances (Rundel & Nobel, 1991). This allows the plants to take full advantage of the limited precipitation typical for desert and desert-like climates. Combined with the morphological traits described above, these adaptations have allowed cacti to grow and survive in extreme hot and dry conditions (Nobel, 2002).

Fig. 95. Dense white spines of *Cylindropuntia fulgida* (Engelm.) F.M.Knuth.
(Picture by Helmuth G. Zimmermann)

The approximately 1 438 species in 124 genera (Hunt, 2006) occur in North and South America, with a single species of *Rhipsalis* Gaertn. which is widespread in tropical America, extending to Africa, Madagascar and Sri Lanka (Obermeyer, 1976; Barthlott, 1983; Smith & Steyn, 1997; Smith *et al*., 1999). Various species, in the *Opuntioideae* in particular, are widely naturalised in warmer regions of the Old World (Parfitt & Gibson, 2003).

Cactaceae is closely related to families Anacampserotaceae and Portulacaceae *sensu stricto* (Nyffeler & Eggli, 2010). The fact that several taxa in the family appear to be of hybrid origin (Parfitt & Gibson, 2003) provides a challenge to attempts at improving its classification. Nomenclatural instability as a result of the general poor quality, or often total absence, of type material, is another obstacle that needs to be overcome by any student of this family. Cactaceae are generally poorly represented in herbarium collections, due to the extraordinary care required in preparing pressed and dried specimens. Spines and glochidia pose a hazard to those handling specimens. Ideally, stem parenchyma needs to be removed to speed up drying, since it contains a substance that releases water only with radical treatment e.g. microwave methods.

There are several species in the Cactaceae that are cultivated for fruit, fodder, 'nopalitos' (a green vegetable) and for cochineal production. The ornamental cactus trade has also developed into a formidable industry and is responsible for the inter-continental spread of many ornamental and useful cactus species. However, invasive or potentially invasive cactus species have been spread in this way (Fig. 96). In some countries spiny species are widely used as living fences (Fig. 97) which has also led to several species becoming invasive.

Economically, *Opuntia ficus-indica* (L.) Mill. is by far the most important species and it is widely cultivated as a drought tolerant crop for arid and semi-arid regions. Fruit production from many selected spineless cultivars is a fast growing industry. It is grown commercially for this purpose in at least 16 countries (Barbera *et al*., 1995). Their role in fodder production is regarded as even more important though. Globally, there are already c. 687 000 ha under cultivation exclusively for this purpose with Brazil the leading country (Mondragon-Jacobo & Perez-Gonzalez, 2001). Many thousands of hectares are also cultivated for cochineal (carmine) production based on the insect *Dactylopius coccus*. Peru, the Canary Islands, Chile, Bolivia and lately also Ethiopia are leading producers. Special cultivars have been developed in Mexico for the production of young leaf-pads, from which 'nopalitos' are produced. This product is consumed as a green vegetable in Mexico. For example, the consumption of 'nopalitos' is now also well established in Ethiopia and beyond. More than 10000 ha are cultivated for this purpose (Flores-Valdez, 1995).

New exotic, cactus-derived fruit crops are emerging which include the pitayas (pitahayas) from several columnar or vine cacti including the genera *Cereus* Mill., *Hylocereus* (A.Berger) Britton & Rose, *Selenicereus* (A.Berger) Britton & Rose and *Stenocereus* (A.Berger) Riccob. (Nerd *et al*., 2002). Some of these are now also seen on South African markets.

With global warming, land degradation and the need for food security in developing countries, cactus cultivation has been widely promoted by the FAO because of the ease of cultivation, drought tolerance and general resilience of the plants, making them some of the more promising new emerging crops.

A total of 29 species, with two infraspecific taxa, from 11 genera of the Cactaceae are known to be naturalised in South Africa. However, this list is expected to expand as soon as more people are able to identify cacti in the field and bring them to the attention of scientists. Obermeyer (1976) reported only 12 species for the same area 35 years ago. Glen (2002) has listed more than 200 species as being cultivated in southern Africa. In these works, some of the names are applied tentatively due to several sources of nomenclatural uncertainty. Though resolution of all these issues is beyond the scope of this treatise, we have attempted to highlight such problems, so that they can eventually be systematically dealt with. The listed taxa have been recorded in natural vegetation in southern Africa.

Fig. 96. Cacti are popular in the commercial horticultural trade.
(Picture by Helmuth G. Zimmermann)

Fig. 97. Plants of the spiny *Echinopsis schickendantzii* F.A.C.Weber established as a living fence. (Picture by PPRI)

Key to the genera:

Notes: (1) Where only one species has been recorded for the region, the species name is given in full. (2) The indigenous *Rhipsalis baccifera* (J.Mill.) Stearn subsp. *mauritiana* (DC.) Barthlott is included for comparison. (3) *Cleistocactus* Lem. has been recorded as persisting in abandoned gardens in Lekgalameetse Nature Reserve and Zebediela. As older stems of *C. samaipatanus* (Cárdenas) D.Hunt can appear similar to those of *Peniocereus serpentinus*, and as there was an unconfirmed report of invasion around Graaff-Reinet, it has been included in the key.

1. Woody climber; stems not modified to cylindrical or flattened cladodes; more vigorous shoots with paired recurved spines specially adapted for climbing; leaves conspicuous in growing season, flat, more than 1.5 cm broad; glochidia absent (Pereskioideae). . . . . ***Pereskia aculeata***

1'. Shrublets, shrubs or small trees, or climbers with cladodes; shoots never with paired, recurved spines; leaves usually inconspicuous and caducous (except in *Austrocylindropuntia*), subulate or terete, less than 8 mm broad (Opuntioideae) or absent (Cactoideae); glochidia present or absent **2**

2. Glochidia absent; flowers either large (> 6 cm in diameter), white and often nocturnal, or narrower than 4 cm, red or white, and diurnal (Cactoideae) . **3**

2'. Glochidia present in areoles; flowers 3–7(–10.5) cm in diameter, coloured (rarely white) and diurnal (Opuntioideae) **10**

3. Branches cylindric, less than 7 mm wide, not ribbed; flowers usually 4 –10 mm across; fruit up to 8 mm wide, cream-coloured or somewhat translucent, smooth . . . . . .***Rhipsalis baccifera* subsp. *mauritiana***

3'. Branches winged, ribbed, or tubercled, more than 1 cm wide; flowers more than 2 cm across; fruit more than 8 mm wide, red, bearing scales (though these may be inconspicuous in *Myrtillocactus*) **4**

4. Branches scrambling or pendent (never erect or columnar), slender, often segmented, sometimes emitting aerial roots, 3–4(–7)-winged or angled, or 4–5-ribbed **5**

4'. Branches erect (sometimes columnar) or ascending, not scrambling, slender to very stout, not producing aerial roots, 3–4-winged or angled, or few- to many-ribbed, or tubercled **6**

5. Climbers; branches often emitting aerial roots; stem wings acute; spines absent or few, up to 7 mm long . . . . . ***Hylocereus***

5'. Shrubs, usually scandent or clambering; branches not rooting aerially (except occasionally at tip); ribs obtuse or rounded; spines present, more than 1 cm long . . . . . .***Harrisia***

6. Stems columnar or arching, only rarely branched above 0.5 m from base; ribs usually 9–15; troughs between ridges obscured by radial spines extending over them and interlacing; pericarpel with many hair-spines or hairs; scales conspicuous to obsolete **7**

6'. Stems erect, columnar when young, later usually with at least some branching above 0.5 m from base; ribs usually 5–8; troughs between ribs exposed, radial spines not extending over them, not interlacing; pericarpel (at anthesis) nearly naked, or with scales only **9**

7. Stems less than 6 cm in diameter; flowers appearing over a considerable length of the stem **8**

7'. Stems (6–)8–10(–13) cm in diameter; flowers restricted to the top 10 cm of the stem; pericarpel and hypanthium with long, blackish hairs . . . . . .***Echinopsis schickendantzii***

8. Stems up to 1.5 m tall; rib margins virtually entire; spines pale yellow on active growth; pericarpel with dark hairs; perianth red, narrow (< 40 mm) . . . . . ***Cleistocactus samaipatanus***

8'. Stems up to 3.0 m tall; rib margin ± tuberculate; spines white, purplish on active growth; pericarpel with white bristles; perianth white, broad (8–15 cm) . . . . . .***Peniocereus serpentinus***

9. Ribs 5–6, low; central spine 10–70 mm long, 3–6 mm broad at base; flowers diurnal, very small (c. 20 × 25 mm), up to 9 per areole; fruit 10–20 mm in diameter, dark purple . . . . . .***Myrtillocactus geometrizans***

9'. Ribs (3–)6–8(–12), prominent (irregularly broken and wavy in 'monstrous' forms); central spines 1–4, 1–5(–8) cm long, 1(–3) mm broad at base; flowers open from 20h00 to 10h00, large (15–29 cm long, 10–20 cm in diameter), solitary in each areole; fruit more than 4 cm in diameter, red, pink or orange . . . . . .***Cereus***

10. Spines with the epidermis separating either completely, or only at spine apex, as a deciduous papery sheath . . . . . ***Cylindropuntia***

10'. Spines without a papery sheath **11**

11. Branches, including terminal ones, cylindric or globose; > 1.5 cm in diameter; flowers scarlet, orange, or white to pale pink 12

11'. Branches compressed, i.e. modified to cladodes (at least the terminal ones), or, if all branches cylindric, then only up to 1 cm in diameter; flowers yellow to orange . . . . . .***Opuntia***

12. Arborescent; branches not segmented, growth indefinite, cylindric; areoles not sunken; flowers (5–)6–7 cm long, scarlet to orange; fruit more than 5 cm long . . . . . .***Austrocylindropuntia***

12'. Low shrub; branches segmented, moniliform, segments with determinate growth, globose or cylindric, up to 5 cm long; areoles sunken; flowers up to 4.5 cm long, white or pale pink; fruit less than 2 cm long . . . . . .***Tephrocactus articulatus***

Austrocylindropuntia Backeb.

Shrubs or small trees. Branches cylindric, growth indefinite, sometimes divided into segments; furrow delimiting each tubercle sharply defined; roots more or less tuberous. **Leaves** 4–40(–120) mm long, succulent, terete, rather persistent, finally deciduous. Areoles with hairs, spines and glochidia. Glochidia flattened at the base, spines smooth, not sheathed. **Flowers** 5–7 cm long; tepals orange-red (scarlet), typically ¼–⅓ flower length. **Fruit** thick-walled, ellipsoidal (without pulp between the seeds in South Africa, often without seeds). **Seed** globose to pyriform, (3.5–)7(–c.10) mm long, laterally compressed, or with lateral ridges in some species, with smooth to slightly rugose funicular envelopes covered with fine hairs; funicular girdle rudimentary.

References: Anderson (2001), Hunt *et al.* (2006).

The genus consists of eight species from the Andes mountain range in South America (Argentina, Bolivia, Ecuador and Peru). It is distinguished from *Cylindropuntia* by shoots with indefinite growth, unsheathed spines, rhomboid to ovate tubercles with sharply defined delimiting furrows, and the typically large, isodiametric seeds. Of all southern African naturalised Cactaceae, the two *Austrocylindropuntia* species are the most conventionally tree-like when fully grown. Tepals are typically scarlet and ¼–⅓ flower length.

Fruit encountered in South Africa for *Austrocylindropuntia subulata* lacks pulp and is often also devoid of seeds. Individuals in South Africa may represent sterile clones derived from a minimal number of introductions. Lack of pulp renders fruit unattractive to birds. This also explains why this species is not spreading as effectively as similar, but seeding species, or those with seeds embedded in pulp. Fruits in South Africa are thick-walled and act as vegetative propagules.

Key to the two species of *Austrocylindropuntia* naturalised in southern Africa:

1. Leaves up to 1.5 cm long and tepals up to 1.7 cm long . . . . . **1. *Austrocylindropuntia cylindrica***

1'. Leaves 4–8 cm long and tepals 2–3 cm long . . . . . **2. *Austrocylindropuntia subulata***

Incomplete specimens may be difficult to distinguish from species of *Cylindropuntia* if spine sheaths are not well-developed in the latter. In *Austrocylindropuntia* stem tubercles are sharply defined, whereas in *Cylindropuntia* they are undulating.

1. *Austrocylindropuntia cylindrica* (Lam.) Backeb.

In: *Jahrbuch der Deutsche Kakteengesellschaft* 2: 12 (1942).

=*Opuntia cylindrica* (Lam.) DC

Shrub or small tree up to c. 2 m tall; trunk woody; branch segments distinctly rhomboid-tuberculate, c. 25 cm long, arising laterally from previous segments, not fragile, dark or bluish green. **Leaves** up to 1.1(–1.5) cm long, rather persistent, finally deciduous. Spines 2–5(–8), 10(–30) mm long, sometimes with later accruals on older growth, porrect, straight, terete or slightly flattened, yellowish; a few long hairs sometimes present. **Flowers** up to 7 cm long; pericarpel elongate-urceolate; areoles numerous, glochidiate; spines occasional, bristly. **Tepals** hardly spreading, c. ¼ flower length, scarlet. **Fruit** ellipsoid to oblong-urceolate, up to 9 cm long. **Seed** subglobose, 4–6(– c. 10) mm across, girdle narrow, not prominent. **Distribution**: SA. (Fig. 98).

References: Backeberg (1958), Anderson (2001), Hunt *et al.* (2006).

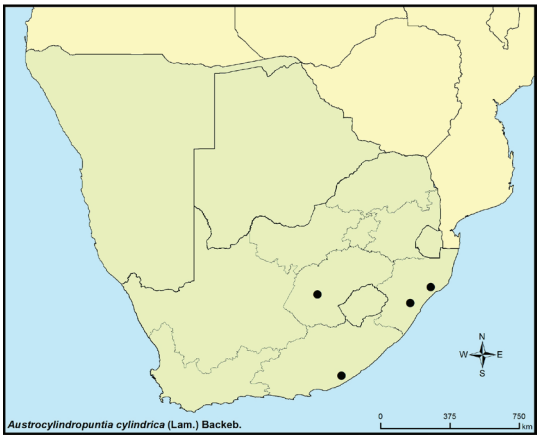

Fig. 98. Historical distribution of *Austrocylindropuntia cylindrica* (Lam.) Backeb.

The species with its snake-like, tuberculate stems (Fig. 99) is originally known from Ecuador (Pinchincha, Chimborazo and Cañar). In South Africa there are historical records from the Free State (Bloemfontein), KwaZulu-Natal (Black Umfolozi, Pietermaritzburg) and Eastern Cape (Katrivier catchment). Although most of these probably merely represent adventives, one herbarium specimen label records that it was becoming invasive in the Pietermaritzburg area in 1965. It is not a declared weed in South Africa.

Austrocylindropuntia cylindrica is also naturalised in Australia (Telford, 1984).

Fig. 99. Snake-like, tuberculate stems of *Austrocylindropuntia cylindrica* (Lam.) Backeb. (Picture by Helmuth G. Zimmermann)

2. *Austrocylindropuntia subulata* (Muehlenpf.) Backeb.

In: *Jahrbuch der Deutsche Kakteengesellschaft* 2: 12 (1942).

=*Austrocylindropuntia subulata* (Muehlenpf.) Backeb. subsp. *exaltata* (A.Berger) D.R.Hunt
=*Opuntia exaltata* A.Berger
=*Opuntia subulata* (Muehlenpf.) Engelm.

Common names: devil's rope, long-spine cactus (English); langdoringkaktus (Afrikaans).

Arborescent, 3–4(–5) m tall, abundantly branched, sometimes from below; branches elongate, tuberculate, up to 0.5 m long, green or somewhat glaucous. Tubercles in a few spirals, sharply defined, vertically rhomboid to decurrent-obovate. **Leaves** subulate, 4–8 cm long, persistent, with areoles at the upper extremities of tubercles. Spines (1–)2–4, strong, straight, up to 8 (–13) cm long, greyish-white (white or yellowish-brown when young). **Flowers** up to 6 cm long; pericarpel relatively long,

tuberculate, with porrect, subulate bract-scales resembling small leaves. **Perianth** not widely flaring, a third of the flower length; tepals 2–3 cm long, scarlet, orange or yellowish. **Fruit** elongate, obovoid-oblong to clavate or ± spherical, ± spiny, sometimes successively proliferous (mostly sterile in South Africa). **Seeds** (1–)19, globose or isodiametric, 8–10 mm across. **Distribution**: N, SA. (Fig. 100).

References: Backeberg (1958), Obermeyer (1976), Anderson (2001), Henderson (2001), Hunt *et al*. (2006).

In parts of its natural distribution range (La Paz, Bolivia, to Junín, Peru), and elsewhere, this shrub or small tree is widely cultivated as a hedge. In South Africa it is known from Limpopo (Phalaborwa), North-West (Potchefstroom), Gauteng (Pretoria), Free State (Ficksburg, Bloemfontein), KwaZulu-Natal (Pietermaritzburg), Eastern Cape (Umzimkulu) and Western Cape (near Stellenbosch). It also occurs around Windhoek, in Namibia. This species has been proposed for classification as a category 1b species under NEMBA (National Environmental Management: Biodiversity Act) and CARA (Conservation of Agricultural Resources Act) (Anonymous, 2009). It is often cultivated as a barrier plant (living fence) in Namibia (Fig. 101), and has been recorded as an invader in Kenya, forming dense stands, impenetrable hedges or thickets, often around abandoned homesteads. It is also expected to be cultivated in other African countries. In ancient Peru, its spines (Fig. 102) were once used as needles (Anderson, 2001).

Seeds are usually sterile (Backeberg, 1958), and reproduction is mostly vegetative by means of proliferating fruit. Each fruit is capable of rooting on contact with the soil, and forming several plantlets. This may explain why the species is not spreading as fast as similar species with fertile seeds. Infestations are mainly clumpy and localised (Fig. 103).

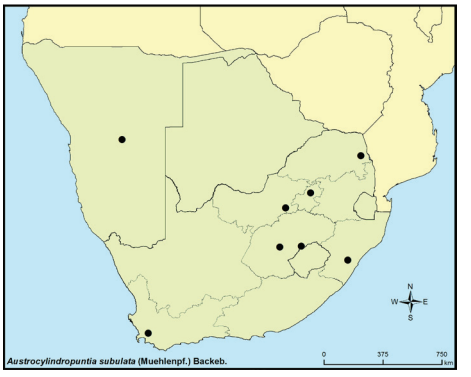

Fig. 100. Distribution map of *Austrocylindropuntia subulata* (Muehlenpf.) Backeb., mostly as casual aliens.

Fig. 101. Living fence of *Austrocylindropuntia subulata* (Muehlenpf.) Backeb. (Picture by Helmuth G. Zimmermann)

Fig. 102. Flowering branch of *Austrocylindropuntia subulata* (Muehlenpf.) Backeb., showing needle-like spines and furrows framing each tubercle (Picture by Helmuth G. Zimmermann)

Fig. 103. Localised infestation of *Austrocylindropuntia subulata* (Muehlenpf.) Backeb. (Picture by by Helmuth G. Zimmermann)

Cereus Mill.

Tree-like or shrubby, usually much branched; branches erect or ascending, strongly ribbed, often with annual constrictions, often glaucous; ribs 3–14, usually pronounced**.** Spines often numerous, acicular. **Flowers** medium to large, funnelform, nocturnal; pericarpel and hypanthium elongate, thick, naked or nearly so below, with scattered small scales above. Pericarpel areoles absent. **Perianth** broad, or moderately so, usually white. **Fruit** fleshy, globose, ovoid or oblong, usually red, sometimes orange, naked, splitting along one or more sides when mature to reveal white fruit pulp and small black-brown (virtually black) seeds, perianth remnant sometimes persistent (at least the style), blackening. **Seed** broadly ovoid, 1.8–4.0 × 1.1–3.0 mm, black-brown or brown, shiny or dull; smooth to tuberculate.

References: Taylor & Zappi (2004, 2006).

This genus consists of 25 species, from the Caribbean and South America (Taylor & Zappi, 2006). One or two members of subgenus *Cereus,* the largest subgenus with 13 species (Taylor & Zappi, 2006), are naturalised in southern Africa.

The extremely tall habit, mostly few-ribbed, cylindric or columnar stems with visible troughs between ribs, relatively large nocturnal flowers with virtually naked or merely scaly, spineless and glabrous pericarpel and hypanthium, and dehiscent fruit characterise locally naturalised representatives of this genus.

Species of *Cereus* have a history of cultivation spanning centuries, since they are popular garden plants with their attractive flowers, their popular fruit and their cylindric or columnar branches. This growth form sometimes leads to confusion with the indigenous and unrelated *Euphorbia ingens* E.Mey. ex Boiss. which can be found in many areas interspersed with *Cereus*. Cultivation almost inevitably leads to infestation of nearby savanna vegetation due to their attractive edible fruits, which are eagerly consumed by frugivorous birds. Seedlings are often found under fence lines and under trees and shrubs as a result of seed dispersal by birds.

In South Africa all naturalised populations belong to a group of five currently recognised species or subspecies (Taylor & Zappi, 2006), that appear closely related to, and include, *Cereus hexagonus* (L.) Mill., the type species of the genus. The other species in this group are: *C. jamacaru* DC. (two subspecies) and *C. hildmannianus* K.Schum. (two subspecies). Note that the image used to illustrate *C. hexagonus* in Anderson (2001) appears to be a species of *Stenocereus* (A.Berger) Riccob., judging by the densely areolate pericarpel, and rounded flowerbud apex.

Taylor & Zappi (1992) retained the name *Cereus jamacaru* so that it could be used in the usual sense, in case the entity was considered conspecific with *C. hexagonus*. Later they stated (Taylor & Zappi, 2006) that *C. jamacaru* appears to be closely related to *C. hexagonus*, which is said to usually have fewer branches and much shorter spines (the cultivated form being virtually spineless). The classification of Taylor & Zappi (2004, 2006) is followed in the present work.

As these taxa are difficult to distinguish from one another, particularly in the absence of dehiscing fruit, the group can be collectively referred to as the *Cereus hexagonus* species complex. Its known natural distribution range can be regarded as a geographical taxon replacement series, starting with *C. hexagonus* to the north of the Amazon River, from Venezuela, Trinidad and Tobago, to northern Brazil (Pará), in moist woodland (Taylor & Zappi, 2006). To the south and east of the Amazon, *C. hexagonus* is replaced by *C. jamacaru* (Taylor & Zappi, 2004). Continuing south- and westward, *C. hildmannianus* completes the series (Kiesling, 1982; Taylor & Zappi, 2004, 2006).

For many years the South African populations have been referred to the misapplied name *C. peruvianus* (Taylor & Walker, 1984), and more recently to *C. jamacaru* (Henderson, 1995). In the present work, two taxa (*Cereus hildmannianus* subsp. *uruguayanus* and *C. jamacaru* subsp. *jamacaru*) are considered naturalised or merely as casual aliens in South Africa.

A key to some taxa of the *Cereus hexagonus* complex is presented here as an aid to future interpretation of the variation in or among the populations that are naturalised in southern Africa [based on information in Anderson (2001) and Taylor & Zappi (2004, 2006)]:

Note: floral dimensions are as expected for fresh flowers.

Key to the *Cereus hexagonus* complex:

1. Flowers up to 18 cm long; fruit splitting along 3 lines . . . . . **1. *Cereus hildmannianus* subsp. *uruguayanus***

1'. Flowers 20–29 cm long; fruit splitting along 1–3 lines **2**

2 Flowers 10–15 cm wide **3**

2'. Flowers 15–20 cm wide **4**

3. Mostly spineless; fruit splitting along 3 lines from apex . . . . . **(*Cereus hildmannianus* subsp. *hildmannianus*)**

3'. Always spiny; fruit splitting from base along 1 line on the underside . . . . . **(*Cereus jamacaru* subsp. *calcirupicola* (F.Ritter) N.P.Taylor & Zappi)**

4. Areoles 1.5–4 cm apart; tree with dense branching; dry woodland habitat; fruit dehiscence along 1 line on the underside . . . . . **2. *Cereus jamacaru* subsp. *jamacaru***

4'. Areoles 1–2 cm apart; tree with few branches; moist woodland habitat; fruit dehiscence unknown . . . . . **(*Cereus hexagonus*)**

1. *Cereus hildmannianus* K.Schum. subsp. *uruguayanus* (R.Kiesling) N.P.Taylor

In: *Cactaceae Consensus Initiatives* 6: 15 (1998).

=*Cereus peruvianus* sensu auctt. non L. (Mill.) var. *monstrosus* DC.

Common names: pitaya, queen of the night (English); nagblom (Afrikaans).

Treelike or shrubby, c. 15 m tall, with or without a well-developed trunk; branches 8–12 cm in diameter, glaucous when young; branch tissue highly mucilaginous; ribs very variable in number, (5–)6–9(–12), (3–)3.5–5(–7) × 1–3 cm; juveniles only 3–5-ribbed; areoles 1–2 cm apart, c. 6 mm in diameter. Spines 5–10, (1–) 1.5–2 cm long, reddish-brown to black. **Flowers** 15–18 × 10–14 cm; outer tepals brownish or olive green, inner tepals white. **Style** 10–11 cm long**. Fruit** 5–12 × 7–12 cm, yellow, orange or reddish, splitting open from apex along c. 3 lines; pulp white. **Seed** c. 3 × 2.8 mm. **Distribution**: SA. (Fig. 104)

References: Anderson (2001), Taylor & Zappi (2004, 2006).

Cereus hildmannianus occurs from Rio de Janeiro and southwestern Minas Gerais to Paraguay, Uruguay and eastern Argentina (Entre Ríos and Buenos Aires) (Taylor & Zappi, 2004). The subspecies *uruguayanus* has a natural range from southern Brazil (Santa Catarina and Rio Grande do Sul), through Uruguay to the Rio de la Plata estuary in Argentina (Kiesling, 1982; Taylor & Zappi, 2006). It is cultivated in South Africa, and should be treated at least as potentially invasive.

This taxon differs from *Cereus hildmannianus* subsp. *hildmannianus* and also from the other two species in the complex by its shorter flowers (Anderson, 2001; Taylor & Zappi, 2004, 2006). The flowers (Fig. 105) are furthermore narrower (10–14 cm wide) than those of *C. hexagonus* or *C. jamacaru* subsp. *jamacaru* (15–20 cm wide), presumably due to shorter tepals. The collecting of additional material from South Africa is required to confirm the identification of the taxon present in the country.

The name *Cereus uruguayanus* was first applied as a replacement name for the occasional monstrose form (Fig. 106) with interrupted and/or contorted ribs (Kiesling, 1982). Such forms seem to occur in *C. jamacaru* as well.

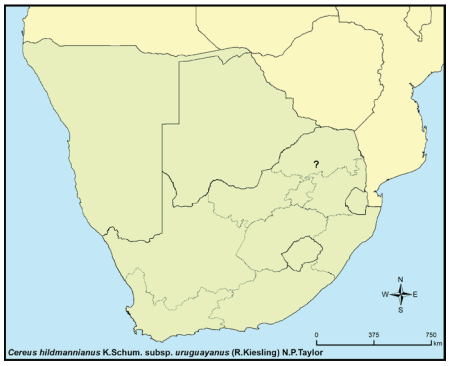

Fig. 104. Distribution map of *Cereus hildmannianus* K.Schum. subsp. *uruguayanus* (R.Kiesling) N.P.Taylor.

Anderson (2001) lists *Cactus peruvianus* as a synonym of *Cereus hildmannianus.* However, this is a misapplied name as *Cactus peruvianus* L. (which is the basionym of *Cereus peruvianus* (L.) Mill.) is a synonym of *Cereus repandus* (L.) Mill, a species in a different subgenus of *Cereus* (Hunt & Taylor, 1992; Taylor & Zappi, 2004, 2006).

Fig. 105. Flower of *Cereus hildmannianus* K.Schum. subsp. *uruguayanus* (R.Kiesling) N.P.Taylor. (Picture by Geoff R. Nichols)

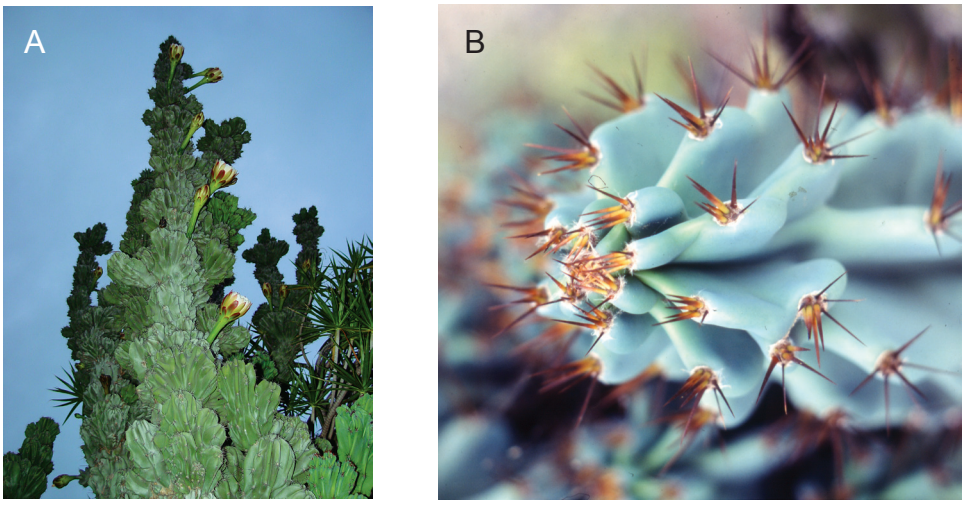

Fig. 106. *Cereus hildmannianus* K.Schum. subsp. *uruguayanus* (R.Kiesling) N.P.Taylor – A. Monstrose form; B. Spines. (Pictures by Geoff R. Nichols (A); Gideon F. Smith (B))

2. *Cereus jamacaru* DC.

In: *Prodromus Systematis Naturalis Regni Vegetabilis* 3: 467 (1828a), nom. cons., **subsp. jamacaru**.

Common names: Peruvian apple cactus, pitaya, queen of the night (English); bobbejaanpaal, môrester, nagblom (Afrikaans).

Tree-like, 3–10(–18) m high, up to 10 m across, often with a short (0.5–2 × 0.3–1 m) trunk; densely branched; branches 7–20 cm in diameter, often strongly glaucous when young, later dark blue-green, tissue scarcely mucilaginous; ribs (3–)6–8(–10), up to 6 × 1.8–4.5 cm; margins weakly to strongly crenate; areoles 4–8 mm at first, enlarging greatly on trunk and older branches, grey-felted, 1.5–4 cm apart. Spines few to many, sometimes absent on upper branches, yellow or brown when young, eventually turning grey to blackish; central spines 1–4 or more, 1–2(–6) cm long, up to 3 mm broad at base; radial spines (4–)7–8(–12), up to 3.5 cm long. **Flowers** funnelform, 21–30 × 15–20 cm**. Pericarpel** and hypanthium up to 16 cm long; green, bearing small, red or reddish scales. **Tepals** 8–10 × 2–2.7 cm, outer tepals greenish, sometimes tinged crimson, inner tepals white. **Stigmas** 12–16(–20), 1.1–1.9 cm long, greenish. **Stamens** oblique in mature flower. **Fruit** ellipsoid, 6–10 × 4–8 cm, crimson to pinkish red, dehiscent by a longitudinal slit from the base on the underside; pulp white. **Seed** black-brown (virtually black). **Distribution**: N, SA. (Fig. 107)

References: Anderson (2001), Henderson (2001), Taylor & Zappi (2004, 2006).

Cereus jamacaru ranges from northern Brazil (Maranhão and perhaps Pará, where records could not be determined unambiguously) and throughout eastern Brazil to central Minas Gerais, mainly in drier thorn savanna ('caatinga') (Taylor & Zappi, 2004). The southern periphery of this range in Bahia and Minas Gerais is occupied by subsp. *calcirupicola* (F.Ritter) N.P.Taylor & Zappi, which has not been recorded in South Africa but should be watched for. It differs from subsp. *jamacaru* in the following characters (Taylor & Zappi, 2004, 2006): ribs 5–8 (in young plants 0.1–1.0 m tall); branch segments broadest immediately above the constrictions; spines uniformly short, dark red–brown; flowers 10–15 cm diameter, pericarpel and hypanthium up to 21 cm long, with green to brownish scales; tepals 5–7 cm long.

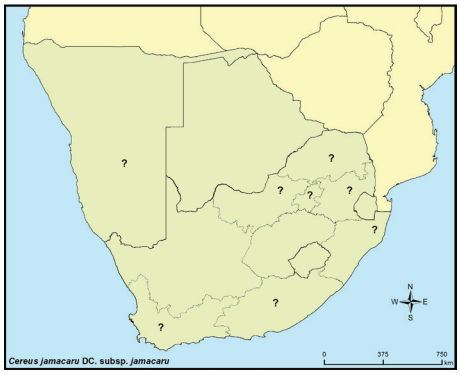

Fig. 107. Distribution map of *Cereus jamacaru* DC. subsp. *jamacaru.*

Cereus jamacaru subsp. *jamacaru* is naturalised across a large part of the savanna biome of South Africa (Henderson, 2007), and is a declared weed due to the transformation of woodland by rendering it impenetrable to livestock (Fig. 108). It has also been recorded in other biomes, e.g. some in the Western and Eastern Cape Provinces (Henderson, 2007) and has been proposed for classification as a category 1b invader under NEMBA and CARA (Anonymous, 2009). The species is often confused with the indigenous *Euphorbia ingens* (Fig. 109) but easily distinguished on account of the large fragrant flowers (Fig. 110, 111).

Control of isolated plants is best using registered stem-injected herbicides (Anonymous, 2004). Large infestations should be manually infested with the South American mealybug, *Hypogeococcus pungens* (also known as *H. festerianus*) which causes gall-like distortions, arresting growth and fruiting and eventually results in the death of the plants. This natural enemy is host-specific to several genera in the Cactoideae. The second biological control agent is a longhorn beetle, *Alcideon cereicola,* introduced from Argentina in 1990. It is very localised and a poor disperser, but effective in killing large and small plants once infected (Klein, 1999). *H. pungens* is most damaging, and the growth distortions are conspicuous, mainly at the growth tips. The insects may take a few years to suppress the infestations to acceptable levels (Klein, 1999).

This species is known for its delicious and attractive red fruit (Fig. 112), referred to variously as jamacaru, mandacaru or pitaya. It is now being developed as a new fruit for commercial cultivation in Israel, mainly for export to Europe (Nerd *et al*., 2002).

Fig. 108. Impenetrable woodland with *Cereus jamacaru* DC. subsp. *jamacaru.*
(Picture by PPRI)

Fig. 109. *Cereus jamacaru* DC. subsp. *jamacaru* (foreground) is often confused with *Euphorbia ingens* E.Mey. ex Boiss. (background). (Picture by Geoff R. Nichols)